# The breeding ecology of ground-nesting birds in Dartmoor National Park (UK)

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## Abstract

Upland breeding birds are under threat from a wide range of environmental and climatic changes, and many upland species are showing substantial population declines. A detailed understanding of the breeding ecology of these species is essential in order to monitor changes in breeding performance and to identify suitable conservation solutions. The primary aim to this thesis work was to build an increased understanding of the breeding ecology of ground-nesting passerines on upland moorlands.

My work used and further contributed to data collected over a 10 year period on ground-nesting birds on a  $4.3 \text{km}^2$  study site on the upland moorlands of Dartmoor National Park. An in-depth nest recording study was conducted for Meadow Pipit (*Anthus pratensis*), Stonechat (*Saxicola rubicola*) and Whinchat (*Saxicola rubetra*), and a broad nest recording effort captured the diversity of breeding species across the study site.

An assessment of the avian diversity of the study site identified a total of 34 breeding species, highlighting the need for community-focused conservation approaches which consider the breeding requirements across the avian community. For Meadow Pipit, Stonechat and Whinchat the breeding parameters of clutch size, brood size and nest success were established, and interannual variation was assessed. Clutch size showed no interannual variability, brood size showed minor variability in Stonechat and Meadow Pipit, and nest success was variable interannually across all three species.

The timing of breeding of the three species was assessed in the context of current upland vegetation management practices (vegetation burning and Bracken control). Considerable overlap was shown in the timing of breeding of all three species, and the current permitted timings of both vegetation management techniques. These results highlights a potential conflict between bird conservation and current upland management practices, and I identify recommended adjustments in those management timings to minimise these conflicts.

Nest site selection was investigated for two topographical components of mi-

croclimate; altitude and solar coefficient. Although Meadow Pipit, Stonechat and Whinchat showed interspecific differences in their nest microclimates, evidence for potential nest site selection was found only in Whinchat, and no links between nest success and nest site characteristics were found. Further work is needed to better understand the factors driving nest site selection in these three species.

The importance of foraging habitat for breeding performance was investigated in a study using Meadow Pipit as a focal species. No associations between breeding performance (nest success and nestling growth rate) were found for four main study site habitat characteristics and overall vegetation diversity. A wider range of spatial scales and habitat characteristics need to be investigated to improve understanding on how vegetation affects Meadow Pipit breeding.

Finally, the study looked into the wider usefulness of citizen science data, comparing two volunteer-driven survey approaches for Cuckoo (*Cuculus canorus*) occurrences in Devon. A citizen science initiative, collecting opportunistic Cuckoo sightings, was launched and compared with existing systematic breeding season surveys. The two survey methods are compared at two spatial scales. We find that whilst overall similarity between results from the two survey methods increases when results are aggregated to a scale more reflective of Cuckoo range sizes, findings remain significantly different. Further work is needed to establish the error associated with the different survey approaches.

Overall, this thesis contributed to an improved understanding of the breeding ecology of Meadow Pipit, Stonechat, Whinchat and Cuckoo. The breeding parameters established here provide a valuable baseline for monitoring change, and the details on bird diversity and timing of breeding can provide useful evidence to help minimise conflict between upland conservation management and bird conservation. Above all, I want to express my deepest thanks to the amazing field volunteers; Mark Lawrence, Mark Penney, Dave Scott, John Walters and numerous others who have contributed to the field work over the years. You have been welcoming, kind and inspiring, and I will fondly remember our days out on the moors together. Without Mark & Mark this project would never have existed. I deeply admire your knowledge of bird behaviour, your nest-recording skills, and your selfless dedication to this study for over a decade. Thank you especially to Mark Lawrence for mentoring me in the field across three field seasons, I thoroughly enjoyed learning from you and I cherish the skills I have acquired.

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Voor Jan, mijn "biologische" papa

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# List of Abbreviations

AES	Agri-Environment Scheme
AIC	Akaike Information Criterion
BB	Braun-Blanquet
ВТО	British Trust for Ornithology
DB	Devon Birds
DEFRA	Department for Environment, Food & Rural Affairs
DEM	Digital Elevation Model
dfr	daily failure rate
dgr	daily growth rate
DNPA	Dartmoor National Park Authority
glm	generalised linear model
IQR	Interquartile Range
NNR	National Nature Reserve
NRS	Nest Record Scheme
OS	Ordnance Survey
pers. obs	personal observation
SAC	Special Area of Conservation
$\mathbf{SC}$	Solar Coefficient
SD	Standard Deviation
SE	Standard Error
SSSI	Site of Special Scientific Interest
Stonechat	European Stonechat

# List of Species Names

## Birds

American Oystercatcher	Haematopus palliatus
Barn Swallow	Hirundo rustica
Bearded Vulture	Gypaetus barbatus
Blackbird	Turdus merula
Blackcap	Sylvia atricapilla
Black Skimmer	Rynchops niger
Blue Tit	Cyanistes caeruleus
Blue-winged Teal	Anas discors
Brewer's Sparrow	Spizella breweri
Bullfinch	Pyrrhula pyrrhula
California Least Tern	Sternula antillarum browni
Canary Island Stonechat	Saxicola dacotiae
Capercaillie	Tetrao urogallus
Carrion Crow	Corvus corone
Chaffinch	Fringilla coelebs
Chiffchaff	Phylloscopus collybita
Carrion Crow	Corvus corone
Clapper Rail	Rallus crepitans
Clay-coloured Sparrow	Spizella pallida
Coal Tit	Parus ater
Common Cuckoo	Cuculus canorus

Common Linnet	Linaria cannabina
Common Redshank	Tringa totanus
Common Redstart	Phoenicurus phoenicurus
Common Snipe	Gallinago gallinago
Corncrake	Crex crex
Corn Bunting	Emberiza calandra
Curlew	Numenius arquata
Dark-eyed Junco	Junco hyemalis
Dartford Warbler	Sylvia undata
Dotterel	Charadrius morinellus
Dunnock	Prunella modularis
Dusky Flycatcher	$Empidonax\ oberholseri$
Egyptian Vulture	Neophron percnopterus
European Goldfinch	Carduelis carduelis
European Greenfinch	Chloris chloris
European Nightjar	Caprimulgus europaeus
European Robin	Erithacus rubecula
European Stonechat	Saxicola rubicola
European Storm Petrel	Hydrobates pelagicus
Eurasian Jay	Garrulus glandarius
Eurasian Kestrel	Falco tinnunculus
Eurasian Magpie	Pica pica
Eurasian Skylark	Alauda arvensis
Eurasian Wren	$Troglodytes \ troglodytes$
Eastern Meadowlark	Sturnella magna
Golden Eagle	Aquila chrysaetos
Greater Prairie-Chicken	Tympanuchus cupido

Great Reed Warbler	Acrocephalus arundinaceus
Eastern Meadowlark	Sturnella magna
Fieldfare	Turdus pilaris
Golden Plover	Pluvialis apricaria
Grasshopper Sparrow	Ammodramus savannarum
Grasshopper Warbler	Locustella naevia
Great Crested Grebe	Podiceps cristatus
Greater Sage-Grouse	Centrocercus urophasianus
Great Tit	Parus major
Grey Heron	Ardea cinerea
Grey Wagtail	Motacilla cinerea
Great Tit	Parus major
Guillemot	Uria aalge
Hermit Thrush	Catharus guttatus
Horned Lark	Eremophila alpestris
Kittiwake	Rissa tridactyla
Lesser Prairie-Chicken	Tympanuchus pallidicinctus
Lesser Redpoll	Acanthis cabaret
lesser Spotted Eagle	Clanga pomarina
Long-tailed Tit	Aegithalos caudatus
Mallard	Anas platyrhynchos
Meadow Pipit	Anthus pratensis
Merlin	Falco columbarius
Mountain Chickadee	Poecile gambeli
Mourning Dove	Zenaida macroura
New Zealand Falcon	$Falco\ novae see landiae$
Northern Bobwhite	Colinus virginanus

Northern Lapwing	Vanellus vanellus
Northern Wheatear	Oenanthe oenanthe
Painted Honeyeater	Grantiella picta
Peregrine Falcon	Falco peregrinus
Pied Flycatcher	Ficedula hypoleuca
Pied Wagtail	Motacilla alba
Piping Plover	Charadrius melodus
Ptarmigan	Lagopus muta
Red-backed Shrike	Lanius colluria
Red Grouse	Lagopus lagopus scotica
Reed Bunting	Emberiza schoeniclus
Reed Warbler	Acrocephalus scirpaceus
Rusty Blackbird	Euphagus carolinus
Richard's Pipit	Anthus novaeseelandiae
Ring Ouzel	Turdus torquatus
Rock Ptarmigan	Lagopus muta
Sage Sparrow	Amphispiza belli
Savannah Sparrow	Passerculus sandwichensis
Scarlet Macaw	Ara macao macao
Song Thrush	Turdus philomelos
South Georgia Diving-petrel	Pelecanoides georgicus
South Island Saddleback	Philesturnus carunculatus carunculatus
Spoon-billed sandpiper	Eurynorhynchus pygmeus
Sprague's Pipit	Anthus spragueii
Superb Fairy-wren	Malurus cyaneus
Tawny Owl	Strix aluco
Tree Pipit	Anthus trivialis

Tree Swallow	Tachycineta bicolor
Turtle Dove	Streptopelia turtur
Upland Sandpiper	Bartramia longicauda
Whinchat	Saxicola rubetra
White-tailed Ptarmigan	Lagopus leucura
Willow Ptarmigan	Lagopus lagopus
Willow Warbler	Phylloscopus trochilus
Woodlark	Lullula arborea
Woodpigeon	Columba palumbus
Wood Warbler	Phylloscopus sibilatrix
Yellowhammer	Emberiza citrinella

## Other

Barbastelle Bat	Barbastellus barbastellus
Bilberry	Vaccinium myrtillus
Black-and-white Ruffed Lemur	Varecia variegata
Blue Ground Beetle	Carabus intricatus
Bracken	Pteridium aquilinum
Brown Trout	Salmo trutta
Common Lizard	Lacerta vivipara
Cotton-grass	Eriophorum angustifolium
Emperor Moth	Saturnia pavonia
European Adder	Vipera berus
European Badger	Meles meles
Gorse	Ulex spp.
Green Hairstreak	Callophrys rubi
Hazel Dormouse	Muscardinus avellanarius
Heather	Calluna vulgaris
High Brown Fritillary	Argynnis adippe
Japanse Knotweed	Fallopia japonica
Marsh Fritillary	Eurodryas aurinia
Narrow-bordered Bee Hawk Moth	Hemaris tityus
Otter	Lutra lutra
Pearl-bordered Fritillary	Boloria euphrosyne
Purple moor-grass	Molinia caerulea
Red Deer	Cervus elaphus
Red Fox	Vulpes vulpes
Salmon	Salmo salar
Small Pearl-bordered Fritillary	Boloria selene

StoatMustela ermineaTormentil Mining BeeAdrena tarsataThree-spined SticklebackGasterosteus aculeatusWildcatFelis silvestris

## **Declaration of Author Contributions**

I, Sara Zonneveld, made the following contributions to the data chapters presented in this thesis:

The majority of the nest data presented across all chapters were collected by Mark Lawrence, Mark Penney and Dave Scott. I contributed to the nest data collection during 2014, 2015 and 2016. For Chapter 2, I planned and conducted the statistical analyses and wrote the manuscript. I conceived and performed the study in Chapter 3, with support from Dr Malcolm Burgess. The solar coefficient dataset in Chapter 4 was developed by Ilya Maclean and Andrew Suggit, I planned the study, performed the data analysis and wrote the manuscript with support from Dr Robert Wilson. I designed the study in Chapter 5, and analysed all data and wrote the manuscript. I collected the majority of nestling biometric data, and the majority of nest habitat data were collected by Lowell Mills and several field assistants. I designed and co-ordinated the Cuckoo citizen science initiative described in Chapter 6, as well as planning the study, analysing the data and writing the manuscript.

All aspects of study design, fieldwork and manuscript preparation were supervised by Professor Charles R. Tyler.

# Chapter 1

# **General Introduction**



"It seems to me that the natural world is the greatest source of excitement; the greatest source of visual beauty; the greatest source of intellectual interest. It is the greatest source of so much in life that makes life worth living." Sir David Attenborough

### 1.1 Overview

This general introduction discusses upland landscapes, their conservation importance and the threats these habitats are currently facing. The landscape, wildlife and land use of Dartmoor are detailed, and the study site is described. The three main study species of this thesis are introduced, followed by information on their breeding ecology, focusing in particular on nest site selection, breeding parameters and the importance of understanding breeding ecology for conservation. Lastly, the aims and objectives of this thesis are described, and a thesis outline is provided.

## **1.2** Upland landscapes

Uplands around the world provide unique habitats including moorlands, peatlands and upland hay meadows (Jefferson, 2005; Holden et al., 2007; Ramchunder et al., 2009). There exists no single definition of an "upland", but in the UK uplands are often considered areas over at least 250m in altitude, or land above areas of enclosed farmland (Ratcliffe and Thompson, 1988; BRIG, 2008a). Approximately 40% of the UK is upland, mostly located in Wales, northern England, Northern Ireland and Scotland (Royal Society for the Protection of Birds, 2017).

The uplands are environmentally and economically important, providing numerous ecosystem services. Agriculture is the main land use type in the uplands; livestock is grazed on open moorland and grassland, mostly for the production of meat, wool and breeding stock (Chesterton, 2009). Upland livestock farming is generally considered of "High Nature Value" (through the maintenance of the upland's semi-natural habitats when employed at appropriate stocking densities), but of low economic value, and is highly dependent on subsidies (O'Rourke et al., 2016). The uplands provide an important source of genetic diversity in native sheep and cattle (Bunce et al., 2018a). Recreational activities are a key part of the upland economy in the UK, with an estimated 60 million day visits per year (Natural England, 2009). Furthermore, uplands are the most important surface water source for the supply of UK drinking water (Curtis et al., 2014), and provide carbon storage and protection against floods (Haines-Young and Potschin, 2009). They also provide a range of cultural services to local areas, for example through the production of Heather honey, and the aesthetic value of livestock such as Dartmoor and Exmoor Ponies (pers. comm.).

#### 1.2.1 Conservation importance

In Great Britain, the uplands cover 38% of the country, with 25% of this upland area covered by bogs and moorlands (Bunce et al., 2018a). These uplands support unique wildlife communities and a variety of rare species, as well as providing strongholds for species with broader national distributions. Upland wetlands support rare sedges, rushes and bryophytes, as well as breeding waders (e.g. Snipe (Gallinago gallinago) and Redshank (Tringa totanus)) and their invertebrate prey (BRIG, 2008b). Species of conservation importance in upland oak woodlands include red-listed birds such as Wood Warbler (*Phylloscopus sibilatrix*), Tree Pipit (Anthus trivialis) and Pied Flycatcher (Ficedula hypoleuca) (Mallord et al., 2016). Old conifer stands can provide important habitat for fungi, insects and declining birds such as Capercaillie (*Tetrao urogallus*) (Humphrey, 2005). The open moor, mostly dominated by gorse (*Ulex spp.*), heather (*Calluna vulgaris*) and grass, supports rare mosses and liverworts (Thompson and Macdonald, 1995; BRIG, 2008a). A wide range or rare and declining insects are found in these habitats, such as the Tormentil Mining Bee (Adrena tarsata), Small Pearl-bordered Fritillary (Boloria se*lene*) and High Brown Fritillary (Argynnis adippe) (JNCC; Fox et al., 2015), as well as an abundance of other insects such as beetles (Coleoptera) and craneflies (Tipulidae), which are known to be particularly important food sources for upland birds (Galbraith et al., 1993; Pearce-Higgins et al., 2010; Douglas and Pearce-Higgins, 2014).

Many breeding birds of conservation importance from across a range of bird families are found on the open moor. Iconic species, such as Golden Eagle (Aquila chrysaetos), Ptarmigan (Lagopus muta) and Golden Plover (Pluvialis apricaria) are found in the uplands, in addition to various well-known species of conservation concern, including the Cuckoo (Cuculus canorus), Nightjar (Caprimulgus europaeus) and Ring Ouzel (Turdus torquatus) (Hayhow et al., 2016). The uplands support a large community of ground-nesting passerines, with Meadow Pipit (Anthus pratensis), Skylark (Alauda arvensis), Whinchat (Saxicola rubetra), Stonechat (Saxicola rubicola) and Northern Wheatear (Oenanthe oenanthe) being some of the most abundant breeders in these areas. Many of these ground-nesting passerines have shown severe declines in recent decades (Hayhow et al., 2016).

This conservation importance of the uplands has been recognised through a wide range of protections and designations. The UK uplands are designated into a large number of protected areas such as Local and National Nature Reserves, Areas of Outstanding Natural Beauty (AONB), Sites of Special Scientific Interest (SSSI) and Special Areas of Conservation (SAC)(Askew et al., 2005; Bunce et al., 2018b).

It is clear that the uplands are a unique landscape, supporting important communities and a wide range of species of conservation concern. More generally, agricultural intensification in the lowlands has resulted in the upland habitats becoming important refuges for many species, such as Cuckoo and Snipe, which are declining in the lowlands (Bonn et al., 2009; Balmer et al., 2013). Furthermore, as climate change is resulting in numerous species shifting their distributions northwards and upwards, upland areas are likely to become increasingly important for biodiversity conservation (Berry et al., 2002).

#### 1.2.2 Threats to upland landscapes and wildlife

Upland landscapes and wildlife are under threat from a wide range of factors (Holden et al., 2007; Reed et al., 2009). Climatic change is likely to significantly change the upland landscape. As mentioned above, shifts in species distributions will change. thereby changing upland wildlife abundance and community composition. Climatic changes in the uplands can have wide-ranging effects. In a comprehensive review, (Orr et al., 2008) showed that changes in timing of bird breeding lead to reduced synchronicity with food availability, and that changes in weather patterns, such as severe storms, may affect vegetation and wildlife, through for example changes in flood risks, fire risks and pest outbreaks. Upland water ecosystems are directly affected by climate change through, for example, changes in pH, temperature and flow, which can in turn affect the movement and breeding of economically important fish species such as Salmon (Salmo salar) and Brown Trout (Salmo trutta) (Curtis et al., 2014). Upland waters are further affected by nutrient enrichment (which can affect for example plankton communities and food availability higher up in the food chain), as well as the historic effects of acidification, which has affected the species composition of upland aquatic environments (Curtis et al., 2014).

The upland peatlands are of great value for biodiversity and the storage of carbon and water, but historic drainage for agricultural practices has hugely degraded this ecosystem (Ramchunder et al., 2009). However, drainage ditches are increasingly being blocked with the aim of restoring peatlands, which has been shown to lead to improvements through both increased water storage and reduced Carbon losses (Grand-Clement et al., 2013). In some upland regions extensive vegetation burning for game management occurring on areas of deep peat has been shown to have negative effects on for example drinking water quality (Douglas et al., 2015). More generally, burning across upland landscapes for sheep grazing and grouse productivity has increased, and is changing the upland vegetation structure by encouraging new green shoots and reducing shrub cover and overall vegetation height (Yallop et al., 2006; Chesterton, 2009). Further agricultural intensification, including an increase in stocking levels, have resulted in overgrazing and severe declines in insect populations, which can in turn affect breeding birds (Orr et al., 2008; Dennis et al., 2008; Fox, 2013). The increasing use of the uplands for the generation of renewable energy has also raised concerns about wind farms due to displacement and collision impacts for birds (Pearce-Higgins et al., 2009; Madders and Whitfield, 2006).

An additional challenge for UK uplands is the potential impacts of increased human footfall. Human disturbance has already been shown to have negative impacts on a range of upland species. For example, (Langston et al., 2007) showed that unsuccessful Nightjar *Caprimulgus europaeus* nests were more likely to be found in areas with higher numbers of footpaths, and (Jayakody et al., 2011) showed that human presence may affect nutritional intake in Red Deer *Cervus elaphus*. With ever-growing populations, such anthropogenic pressures are likely to increase.

The potential impacts of future policy changes also need to be considered. For example, post-Brexit withdrawal or reductions in subsidies, such as payments for sheep farmers or EU Common Agricultural Policy (CAP) support for grouse moors, may lead to significant long-term habitat changes in the uplands (Bunce et al., 2018b). Grasslands may transition to shrub under lower grazing pressures, and afforestation may occur. Whether this is a positive or negative effect, will depend on the species communities of interest, and the extent of changes in management practice.

#### 1.2.3 Scientific importance

Given the conservation importance and anticipated future changes, scientific study of upland landscapes is essential for furthering conservation science. As a complex landscape, with large anthropogenic effects on habitat composition and individual species, a detailed understanding of these landscapes is needed in order to effectively protect them. Finding the right balance between conservation, recreation, agriculture and other ecosystem services relies on a detailed understanding of the interactions between management choices and habitat dynamics. This can lead on to understanding how changes in management and habitats will affect biodiversity and ecosystem service delivery. In addition to such landscape-scale studies, detailed studies on individual species, particularly those of conservation concern, can help elucidate the interactions between their populations and the wider ecological dynamics of the upland landscape. Mapping the exact breeding requirements of species will help inform appropriate habitat management, and recording the breeding performance of key species will help monitoring for negative or positive effects in response to management changes or reduced/increased public access. Evidence from scientific studies can be used to support wider policy development, and ensure future sustainable management of the UK's upland habitats.

In addition to traditional field studies conducted by research scientists, "citizen science" approaches are increasingly being employed to collect data. The value of citizen science to ecological research has been widely acknowledged (Dickinson et al., 2012), and although there are some concerns regarding errors and biases in the data (Dickinson et al., 2010), when studies are well-designed and/or conducted by experienced citizen scientists, this approach can help collect a volume of data that could never be realised in a traditional research study. An added benefit is the opportunity for outreach and education to members of the general public. Indeed, citizen science projects have been shown to increase ecological knowledge and environmental awareness (Branchini et al., 2015; Merenlender et al., 2016). In ornithology, the reporting of bird sightings and bird ringing data collected by volunteers has been fundamental in underpinning large amounts of research (see for example Robinson et al. (2011)). In the BTO Nest Record Scheme, skilled volunteer nest-finders with detailed knowledge of nesting behaviour and breeding ecology record the nest location and breeding progress of British breeding birds. First started in 1939, by 2003 the scheme had recorded more that 1.2 million nests, and resulted in over 250 scientific publications (Crick et al., 2003). In the case of the Nest Record Scheme, the extensive knowledge and skills of volunteer nest recorders are complementary to the research skills of professional ecologists, and collaboration between the two can ensure that nest-recording skills are passed on to future generations, whilst ensuring that nest record data is used to its maximum scientific potential. In this thesis, a collaboration between research scientists and local nest recorders was used to further understanding of Dartmoor's breeding birds. Furthermore, a citizen science initiative was set up to understand how opportunistic laymen surveying compares with standardised expert surveys in mapping the presence sites of Cuckoo, a strongly declining species found on the uplands of Dartmoor (Hayhow et al., 2016).

### 1.3 Dartmoor

#### 1.3.1 Landscape

Dartmoor (50° 31' 20"N, -3° 51' 30"W), which obtained national park status in 1951, is the most southern upland in the UK (Figure 1.1). It extends over an area of  $953 \text{km}^2$ , and ranges in elevation from 30 to 621 m above sea level (Mercer, 2009). The Dartmoor Special Area of Conservation covers  $232 \text{km}^2$  (JNCC, 2017). Three SSSIs (Sites of Special Scientific Interest); North Dartmoor SSSI (136km<sup>2</sup>), South Dartmoor SSSI (71km<sup>2</sup>) and East Dartmoor SSSI (21km<sup>2</sup>), cover a large part of the National Park, and there are a further  $34 \text{km}^2$  of smaller SSSIs, as well as four NNRs (National Nature Reserves) (Dartmoor National Park Authority, 2008; Natural England, 2017). The Dartmoor landscape contains habitats of national and international importance. Moor and heath (including blanket bog), cover 49% of the National Park, and other habitat types of national and international importance include ancient upland oak woodland and broadleaf woodland (English Nature and Dartmoor National Park Authority, 2001; Dartmoor National Park Authority, 2008). The main land use types of Dartmoor include livestock farming, tourism and the provision of drinking water (English Nature and Dartmoor National Park Authority, 2001). Furthermore, an area of  $130 \text{km}^2$  in the northwest of Dartmoor is in use as a military training zone by the Ministry of Defence (Ministry of Defence, 2017).

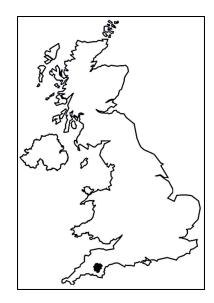


Figure 1.1: Location of Dartmoor in the UK.

#### 1.3.2 Wildlife

Dartmoor is home to a unique wildlife community with a wide range of species of conservation importance. Damp sites provide national strongholds for insects such as the Marsh Fritillary (*Eurodryas aurinia*) and Narrow-bordered Bee Hawk Moth (*Hemaris tityus*)(Mercer, 2009), and open water provides a habitat for Salmon (*Salmo salar*) and Otter (*Lutra lutra*) (English Nature and Dartmoor National Park Authority, 2001). Rare woodland species include the Blue Ground Beetle (*Carabus intricatus*) and Barbastelle Bat (*Barbastellus barbastellus*)(Dartmoor Biodiversity Steering Group, 2007; Mercer, 2009).

The open habitats support a large community of moorland breeding birds, including species of national conservation concern, such as the Cuckoo, Ring Ouzel, and Snipe (Dartmoor National Park Authority, 2011). The most common breeding birds on the open moor are the Meadow Pipit and Skylark (Dartmoor National Park Authority, 2011). The woodlands are home to the iconic upland oak woodland trio; the Pied Flycatcher, Redstart (*Phoenicurus phoenicurus*) and Wood Warbler (Mercer, 2009).

#### 1.3.3 Vegetation management

The habitats on the open moor are actively managed for both agricultural and conservation purposes. Controlled burning, or "swaling", is a traditional land management practice applied to prevent succession and increase fresh growth available for livestock grazing (DEFRA, 2007). Bracken (*Pteridium aquilinum*) control, both chemically and mechanically, is used to prevent this species from dominating areas and damaging archaeological features (Natural England, 2008).

### 1.3.4 Study site

The work presented in this thesis (with the exception of a broader-scale chapter focused on Cuckoo) was conducted on Holne Moor (50° 31' 20",  $-3^{\circ}$  51' 30"), an area of upland moorland on the southern side of Dartmoor. The study site spans  $4.3 \text{km}^2$ , and the habitat consists of largely open moor and grass. The central region of the study site consists of an open reservoir surrounded by a small area of conifer plantation (Figure 1.2). Nest recording took place only on the open moor and the border of trees and shrubs surrounding the reservoir. The study site is bordered by a woodland valley (White Wood) on the north side, and enclosed farmland on the east side. A tarmac road bisects the study site, with most of the study site located south of the road. The topography of the study site is varied; the altitude ranges from 211 to 457m, and there are many small ditches, leats and streams. Nest recording was already in place before the start of this thesis work and the data gathered by the nest recording volunteers was used to underpin this thesis work and other scientific work. Thus, the study site was fixed prior to the commencement of the scientific research for this thesis. The study area however is deemed to be typical of many areas on the lower reaches of Dartmoor that contain a mosaic of habitats.

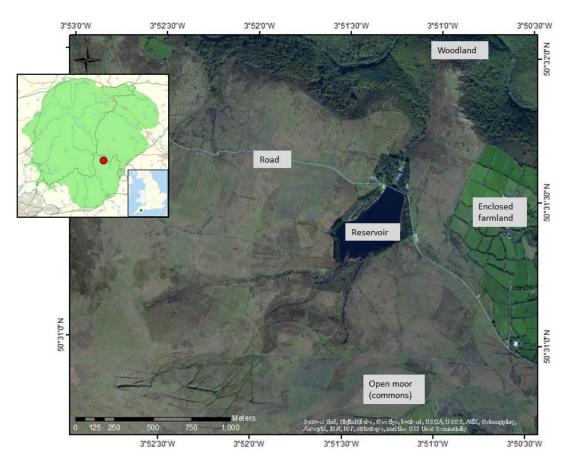


Figure 1.2: Map of the Holne Moor study site. Created in ArcMap (ArcGIS 10.4.1) using the Esri "world imagery" satellite basemap. The insert shows the location of the study site (red dot) within Dartmoor National Park, and the location of Dartmoor within England.

The study site sits within Dartmoor's common land, and is therefore grazed by ponies, cows and sheep. Vegetation burning, and to a lesser extent Bracken control, are usually carried out across selected areas of the site on an annual basis. The avian nest predators known to occur on the site include foxes (*Vulpes vulpes*), carrion crows (*Corvus corone*) and adders (*Vipera berus*). Other suspected nest predators include magpies (*Pica pica*), jays (*Garrulus glandarius*), badgers (*Meles meles*) and stoats (*Mustela erminea*).

### 1.4 Reproductive ecology

Reproductive biology is fundamental research for supporting conservation ecology (see for example Webb and Kelly (1993); Shine and Brown (2008); Hamby et al. (2016)). Studies into reproduction (e.g. the number of offspring and their survival) in wildlife species are needed to capture baseline information for understanding population dynamics and making assessments on factors that may affect breeding success, such as climatic conditions and food availability (Gill et al., 2002; Ancona et al., 2011). Phenological processes such as the seasonality and length of the reproductive cycle, and physiological factors relating to adult fecundity also need to be considered in order to build a full understanding of a species' needs for successful reproduction (see for example Tripp et al. (2009); Dillen et al. (2010); Fletcher et al. (2013)). Knowledge of reproductive characteristics can also help build an improved picture of the evolutionary history of related species (Friedman and Floyd, 2001). Furthermore, behaviour is an important consideration in understanding reproductive biology and success. For example, ovipositioning locations in insects can be influenced by the presence and posture of conspecifics (Byers and Eason, 2009), and the personality traits of birds can affect reproductive success (Both et al., 2005). Other important considerations in understanding the reproductive ecology of wildlife includes the locations where organisms choose to breed (e.g. the site characteristics and site fidelity of spawning fish (Skiftesvik et al., 2015; Binder et al., 2016) and the costs associated with reproductive interference between species (Cothran, 2015)).

Understanding of reproductive ecology can help uncover the mechanisms underlying population declines, and aid in designing and monitoring management interventions (Sæther et al., 1996; Hughes and Tanner, 2000). For example, a study on wildcats (*Felis silvestris*) in a Spanish Natural Park with public access areas showed that during the reproductive season, stress levels in wildcat were elevated, suggesting that visitor numbers needed to be limited particularly during this time (Pineiro et al., 2012). An understanding of the breeding ecology of species may also aid in the design of biotechnological approaches for species conservation. For example, understanding the basic reproductive characteristics of a species is necessary for the design of assisted reproductive techniques such as artificial insemination (Andrabi and Maxwell, 2007). Reproduction research can also help develop sustainable levels of hunting (Marboutin et al., 2003), and increase awareness of other anthropogenic effects on species. To illustrate this, a recent study highlighted the effects of the building of a dam on the reproduction of a threatened fish species, with colder water downstream from the dam leading to for example lower reproductive success compared to other sites (Nunes et al., 2015).

### 1.4.1 Timing of breeding

An understanding of timing of breeding and the different components of timing of breeding (such as the onset, peak and length of the breeding season) is valuable for addressing a range of research questions and conservation issues. For example, in a large review on the effects of climate change of bird breeding, Carey (2009) showed how monitoring timing of breeding has helped understand phenological responses to climate change in a wide range of species. Understanding the onset and length of the breeding season is also essential for understanding when land management practices may need to be avoided in order to prevent nest destruction. As an example of this, in a historic study Crick et al. (1994) showed that hedge cutting and other agricultural practices caused breeding failure for some of the UK's lowland Bunting species when carried out during the breeding season, with between 10%and 43% of all nest failures due to these management practices. Similarly, Pakanen et al. (2011) and Perlut and Strong (2011) showed that grazing by cattle in coastal meadows and grasslands during the bird breeding season resulted in significant numbers of ground-nesting bird nests being trampled. Thus, land managers need to consider timing of breeding when designing grazing practices. Furthermore, estimates of timing of breeding are essential for determining at which times of year human disturbance may be an issue, and to decide when breeding sites may need to be closed or have reduced visitor access in order to prevent nest failure. Watson et al. (2014) illustrated this through studies on the breeding success in European Storm Petrel (Hydrobates pelagicus), where breeding success was lower in areas with high disturbance. Supporting this, in a review of studies on the effects of human disturbance on colonial waterbirds, Carney and Sydeman (1999) outlined speciesspecific recommendations regarding limitations to numbers and frequency of visitors in order to minimise negative impacts from disturbance during the breeding season.

### 1.4.2 Reproductive parameters

A wide range of reproductive parameters are commonly studied in ornithology and conservation science. Clutch size (the number of eggs laid) and brood size (the number of nestlings) can be directly observed in nest studies, and subsequently hatching success and fledging success can be derived (Crick et al., 2003). Postfledging survival can also be estimated through methods such as mark-recapture methods (Thomson et al., 1999), and more recently using satellite tagging technology (Alderman et al., 2010). Two commonly studied biometric parameters are nestling mass and growth rate, which inform on nestling body condition. This can then be related to other variables to understand factors affecting nestling body condition. For example, Kalinski et al. (2009) showed that Great Tit (*Parus major*) mass varied with both nesting habitat and brood number. Ardia et al. (2010) showed that lower temperatures during incubation lead to lower nestling body mass after hatching in Tree Swallow (*Tachycineta bicolor*). Furthermore, egg size can be an informative proxy in understanding factors relating to breeding success (Nisbet, 1973; Williams, 1994); a recent review of 283 studies showed that egg size can be linked to hatching success, offspring survival, and nestling growth rate (Krist, 2011).

Knowledge of these reproductive parameters can be used in combination with information on other ecological factors to understand drivers of breeding performance. Information on causes of nest failure (such as nestling mortality and predation) can help understand potential causes for population declines (e.g. Parr (1992); Côté and Sutherland (1997); Schmidt (2003)). This information is essential for identifying conservation measures for improving breeding performance. For example, Zockler et al. (2010) showed that populations of the critically endangered Spoon-billed Sandpiper *Eurynorhynchus pygmeus* are in rapid decline due to poor post-fledging survival, and that extinction will occur unless conservation action is taken. Additionally, knowledge on the effects of breeding parameters on habitat condition and food availability can be used to determine how habitat management may help improve breeding performance (see for example Wilson et al. (2005); Johnson (2007)).

#### 1.4.3 Nest site selection

Another essential component of avian reproductive ecology is nest site selection. Understanding nest site selection is invaluable for developing targeted conservation efforts. As an illustrated example of this, a study on passerines nesting in Italian vineyards showed that nest density differed depending on the vineyards trellising system and age, resulting in recommendations for bird-friendly vineyard management (Assandri et al., 2017). Another example is a study in plantation woodlands, where it was shown that New Zealand Falcons (*Falco novaeseelandiae*) preferentially select nest sites in new forest stands near edges with older trees, in turn highlighting the need to create a mosaic of stand ages for optimising the conservation of this species (Seaton et al., 2010).

Depending on the species and research question, different aspects of nest site

selection are studied. As mentioned above, understanding the preferred nesting habitats and vegetation types is essential for informing successful vegetation management techniques. An understanding of breeding site topography (e.g. altitude, aspect) is necessary for monitoring potential responses to climatic change, in order to for example help predict future distributions for conservation management purposes (see for example López-López et al. (2006); Sekercioĝlu et al. (2012); Chamberlain et al. (2013)). Furthermore, when investigating predation effects, nests placement is an important consideration (Weidinger, 2002; Thompson, 2007). Illustrating this, in a study on Superb Fairy-wrens (*Malurus cyaneus*) it was shown that predation rate was related to both nest height and nest concealment (Colombelli-Negrel and Kleindorfer, 2009).

## 1.5 Study species and nest recording

Underpinning the work in this thesis is a multi-year nest recording study carried out by a group of highly experienced volunteers that have been collecting data on the ground-nesting birds on the Holne Moor study site since 2008, and providing these data to the BTO Nest Record Scheme (NRS). The NRS is a UK-wide nest observation scheme in which volunteers monitor nesting following standardised methodology (Crick et al., 2003). On this study site, total survey effort was not recorded between 2008 and 2012, but Table 1.1 below gives an indication of the yearly survey effort involved in this study based on information from 2013 to 2016. On average, there were 79 survey days between March and August each season. On each survey day, between 1 and 4 nest recorders were working for between 4 and 13 hours. On a typical day, 1-2 nest recorders would work for approximately 8 hours. The main species of interest for the nest recording volunteers on the Holne Moor study site, and focused on in this thesis, are the Meadow Pipit, European Stonechat and Whinchat.

Table 1.1: The number of days over which nest recording was carried out between 2013 and 2016 on the Holne Moor study site (Dartmoor National Park, UK), along with the first and last date of nest recording in each season.

	2013	2014	2015	2016	Total
Number of survey days	84	67	90	76	317
First recording date	$5 { m Mar}$	$17 { m Mar}$	$14 { m Mar}$	$11 \mathrm{Apr}$	-
Last recording date	$24 \mathrm{Aug}$	9 Aug	$20 { m Aug}$	$5 \mathrm{Aug}$	-

Out of 1550 nests of 34 species recorded over the 9-year study, 72% of those nests belonged to these three species (for more information on recorded nests and species see Chapter 2). These species represent a typical example of co-occuring upland ground-nesting bird species, and therefore provide a good case study to illustrate the breeding dynamics and breeding requirements of upland passerines. Due to the fact that the timing of breeding of these selected species show significant interspecific differences (see Chapter 3), they are also a well-suited choice for illustrating how a range of seasonal land management practices may impact on the nest success of upland avian communities, an issue for which little data are currently available. These three species are also of conservation importance, and concerns about their population trends mean a better understanding of their breeding ecology could help inform improved land management to support their breeding cycles. This is particularly pressing in the case of Whinchat and Meadow Pipit, which have shown UK-wide declines of 55% and 17% respectively over the last 30 years Hayhow et al. (2014)).

The population coverage on the study site covered in the nest monitoring work for the three main study species has not been formally investigated. For Whinchat, surveying for breeding pairs on the site is comprehensive, and it is thought that all of the breeding pairs are monitored. For Stonechat, surveying for breeding pairs at the start of the season is comprehensive, and again it is thought that is most years, all breeding pairs are captured for the first clutches. However, survey effort for Stonechat is reduced later in the season when volunteers focus more on surveying for Meadow Pipit, and therefore second broods and late pairs of breeding Stonechat are likely missed in this study. Meadow Pipit are numerous on the study site, making it difficult for any precise estimates to be made on the proportion of nests covered by nest monitoring efforts. It is believed however that the survey data represents minimally one third of the Meadow Pipit population in most years.

#### 1.5.1 Meadow Pipit

The Meadow Pipit is a passerine bird which breeds widely across Europe (BirdLife International, 2016). The species shows little sexual dimorphism, with both males and females having streaky-brown plumage with white outer tail feathers (Figure 1.3). Since the 1970s the UK population has declined by approximately 35%, causing the species to be amber-listed in the UK (Hayhow et al., 2016). Breeding Bird Survey (BBS) analyses estimate a UK breeding population size of between 4.0 and 5.1 million birds in 2006 (Newson et al., 2008). As a partial migrant, UK birds move from upland to lowland areas or to continental Europe during the non-breeding season (Cramp and Perrins, 1994; BirdLife International, 2016). Meadow Pipits breed across a wide variety of open habitats, such as grasslands, upland moorland and salt marshes, where they build nests low to the ground in clumps of grass or low shrub (Lack, 1933; Pearce-Higgins and Grant, 2006; Vandenberghe et al., 2009; van Klink et al., 2014). Eggs are cream-coloured with heavy brown spotting. UKwide data from the BTO Nest Record Scheme shows that Meadow Pipit typically produce two broods, and have a clutch size of four to five eggs, an incubation period of 13-15 days and a fledging period of 12-14 days (Robinson, 2017). Their median first egg-laying data in England, calculated based on 210 nests recorded after 1990, is 7 May (Joys and Crick, 2004).



**Figure 1.3:** Meadow Pipit (*Anthus pratensis*). Image by Charles R. Tyler.

#### 1.5.2 Stonechat

The European Stonechat, hereafter referred to as "Stonechat", is a small, partially migratory passerine found breeding across Europe and Asia. (Cramp and Perrins, 1994). The Stonechat genus is a complex phylogenetic group, with closely related Stonechat species and subspecies also found breeding in the Canary Islands and Africa (Wink et al., 2002). In winter, UK birds make local movements or overwinter in south-west Europe or northern Africa (Helm et al., 2006). In the UK, the species is found breeding in coastal habitats and both upland and lowland heath (Fuller and Glue, 1977). The UK breeding population is thought to be between 133,000 and 269,000 birds (Newson et al., 2008). Populations appear to be doing well, with a 29% UK population increase observed in the last 20 years (Hayhow et al., 2016). The species show strong sexual dimorphism. In breeding plumage, the male has a black head with a white collar, and a bright rust-coloured chest (Figure 1.4). The female's head and back are brown, and the chest is a drabber rust-colour. Eggs are coloured blue to green-blue with orange/brown spots. An analysis of 484 nest records, shows that 25 April is the median first egg-laying date for this species in England (Joys and Crick, 2004). Stonechat produce 2-3 broods per season, with each nest having a clutch size of 5-6 eggs, an incubation period of 15 days, and a fledging period of 14-15 days (Robinson, 2017).



**Figure 1.4:** Male Stonechat (*Saxicola rubicola*). Image by Charles R. Tyler.

#### 1.5.3 Whinchat

The Whinchat is a small, migratory passerine (Cramp and Perrins, 1994). The males have an apricot-coloured chest, and a dark-brown back and head with a striking white eye stripe (Figure 1.5). The female also has a white eye stripe, but is overall lighter and more drab in colour. Whinchat winter in sub-Saharan Africa, and breeding grounds extend from Europe to western Asia (BirdLife International, 2016). On their breeding grounds, they are found in heathlands and grasslands, where they are regularly found associated with Bracken (Fuller and Glue, 1977; Pearce-Higgins and Grant, 2006; Border et al., 2017). With a median first laying data of 25 April, Whinchat start breeding later than both Stonechat and Meadow Pipit (Joys and Crick, 2004). Females generally produce one clutch with five or six eggs, which are blue in colour. The incubation period is 13 days, with a subsequent fledging period of 14-15 days (Robinson, 2017). The species has been red-listed in the UK due to severe population declines of 53% over 20 years (Hayhow et al., 2016). Breeding population estimates for 2006 were between 49,000 and 198,000 birds (Newson et al., 2008).



**Figure 1.5:** Male Whinchat (*Saxicola rubetra*). Image by Charles R. Tyler.

#### 1.5.4 Cuckoo

The Common Cuckoo (Figure 1.6), hereafter referred to as "Cuckoo", winters in Africa and breeds in much of Europe and Asia, and is widely recognised by the male's well-known onomatopoeic call (Cramp and Perrins, 1994). The birds are approximately the size of a Collared Dove, and sexes are generally very similar in appearance; grey with underparts which are white with brown/black bars, although a distinctive rufous-coloured female morph also occurs (Davies, 2016). The Cuckoo's breeding season in the UK is short, with adults arriving around mid-April and generally departing during mid- to late June (Huin and Sparks, 2000; Hewson et al., 2016). Cuckoos are obligatory brood parasites. Through the famous historic observations by Edward Jenner and Edgar Chance we know that females remove an egg from a host nest, replacing it with one of her own, and that once the Cuckoo chick hatches, it evicts the remaining host eggs or chicks (Jenner, 1788; Chance, 1922). A single Cuckoo female is thought to lay around 10-20 eggs per season (Wyllie, 1981). Female Cuckoos belong to specific "gentes", genetically distinct groups which are specialised in parasitising a specific host species (Gibbs et al., 2000). The different gentes all produce distinct egg types which mimic a specific host species' eggs (de L. Brooke and Davies, 1988; Antonov et al., 2010). In the UK, the main host species are Meadow Pipit, Reed Warbler (Acrocephalus scirpaceus, Robin (Erithacus rubecula), Pied Wagtail (Motacilla alba) and Dunnock (Prunella modularis), with Cuckoos showing egg mimicry for all but the last species (Davies and de L. Brooke, 1989).

The habitats within which Cuckoo are found in a diverse and include marshlands, grasslands and moorlands, reflecting the ecological diversity in its host species (Glue and Morgan, 1972; Møller et al., 2011). The Cuckoo is red-listed in the UK, having declined by 43% between 1995 and 2014 (Hayhow et al., 2016). The 2006 population size was thought to be between 22,000 and 58,000 birds, with Breeding Bird Survey estimates suggesting substantial further declines since that study (Newson et al., 2008; Woodward et al., 2018). In Devon, the species is now mostly found in the uplands of Dartmoor and Exmoor, where it parasitises on Meadow Pipit (Beavan and Lock, 2016).



**Figure 1.6:** Juvenile Common Cuckoo (*Cuculus canorus*) and Meadow Pipit (*Anthus pratensis*) host (right). Image by Charles R. Tyler.

## **1.6** Thesis aims and objectives

With upland birds under increasing threat, a detailed knowledge of local breeding ecology is essential as a baseline for future monitoring and to aid conservation decision-making. The aim of this thesis is to build an increased understanding of the breeding ecology of ground-nesting birds in Dartmoor National Park. These aims are met through the following objectives:

- i) To assess avian biodiversity on a site of conservation interest.
- ii) To measure baseline breeding parameters and interannual variation therein.
- iii) To determine timing of breeding.
- iv) To assess potential conflicts between land management and bird breeding, and to suggest changes in current management to alleviate potential impacts.
- v) To understand nest site choice and potential associations with breeding success.
- vi) To test for associations between habitat characteristics and breeding performance.

Finally, this thesis moves beyond breeding ecology, to look in more detail at the use of citizen science for deriving distributional information for another threatened upland species, by aiming to:

vii) Compare opportunistic citizen science data and systematic volunteer surveys for understanding Cuckoo distributions in Devon.

# 1.7 Thesis outline

The objectives of this thesis are addressed in the following chapters, which are presented as manuscripts for publication:

• Chapter 2 aims to establish baseline knowledge of a) avian diversity on the study site, and b) reproductive parameters of the three focal species in this thesis; Meadow Pipit, Stonechat and Whinchat. Using nine years of nest monitoring data, the diversity of breeding birds on the Holne Moor study site is assessed. For Meadow Pipit, Stonechat and Whinchat, the breeding parameters of clutch size, brood size and nest success are determined. Breeding parameters are also tested for interannual variability.

- Chapter 3 sets out to test whether there is a conflict between current land management techniques and the breeding of upland birds. This chapter focuses on Meadow Pipit, Stonechat and Whinchat. Firstly, the length and peaks of the breeding seasons are quantified to determine the timing of breeding of the three species. Subsequently, the local timings of the land management practices of vegetation burning (swaling) and bracken control are identified, and the potential conflict between these management practices and the breeding of the three species is quantified.
- In Chapter 4 nest site choice is explored for the three study species. The aim of this chapter was to investigate whether the three species select for particular nest site characteristics, and whether nest site choice shows associations with breeding success. Furthermore, this chapter tests whether there are interspecific differences in nest site characteristics on the study site. The nest site characteristics investigated in this chapter are two topographic components of microclimate; altitude and solar coefficient.
- Chapter 5 tests the hypothesis that breeding performance varies with the vegetation that is found in the foraging area around the nest. This chapter uses the Meadow Pipit as a model species to test for associations between foraging habitat characteristics (vegetation diversity, grass cover and gorse cover) and two measures of breeding performance (nest success and nestling growth).
- Chapter 6 uses a citizen science initiative to record Cuckoo locations in Devon. The chapter discusses the development, promotion, public uptake and resulting data of the citizen science project. It compares the Cuckoo presence map obtained through this study to existing distribution maps from a previous mapping initiative.
- Chapter 7 presents a general discussion, where findings from the above chapters are brought together and discussed in the context of the thesis aims.

# References

Alderman, R., Gales, R., Hobday, A., & Candy, S. Post-fledging survival and dispersal of shy albatross from three breeding colonies in Tasmania. *Marine Ecology Progress Series*, 405:271–285, 2010.

- Ancona, S., Sanchez-Colon, S., Rodriguex, C., & Drummond, H. El Nino in the Warm Tropics: local sea temperature predicts breeding parameters and growth of blue-footed boobies. *Journal of Animal Ecology*, 80:799–808, 2011.
- Andrabi, S. & Maxwell, W. A review on reproductive biotechnologies for conservation of endangered mammalian species. *Animal Reproduction Science*, 99:223–243, 2007.
- Antonov, A., Stokke, B., Vikan, J., Fossøy, F., Ranke, P., Røskaft, E., Moksnes, A., Møller, A., & Shykoff, J. Egg phenotype differentiation in sympatric cuckoo *Cuculus canorus* gentes. *Journal of Evolutionary Biology*, 23:1170–1182, 2010.
- Ardia, D., Perez, J., & Clotfelter, E. Experimental cooling during incubation leads to reduced innate immunity and body condition in nestling tree swallows. *Proceedings* of the Royal Society B - Biological Sciences, 277:1881–1888, 2010.
- Askew, D., Evans, S., Matthews, R., & Swanton, P. MAGIC: a geoportal for the English countryside. *Computers, Environment and Urban Systems*, 29:71–85, 2005.
- Assandri, G., Giacomazzo, M., Brambilla, M., Griggio, M., & Pedrini, P. Nest density, nest-site selection, and breeding success of birds in vineyards: Management implications for conservation in a highly intensive farming system. *Biological Conservation*, 205:23–33, 2017.
- Balmer, D., Gillings, S., Caffrey, B., Swann, R., Downie, I., & Fuller, R. Bird Atlas 2007-2011: The breeding and wintering birds of Britain and Ireland. *BTO*, *Thetford*, 2013.
- Beavan, S. & Lock, M. Devon Birds Atlas 2007-2013. Devon Birds, 2016.
- Berry, P. M., Dawson, T. P., Harrison, P. A., & Pearson, R. G. Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography*, 11(6):453–462, 2002.
- Binder, R., Riley, S., Holbrook, C., Hansen, M., Bergstedt, R., Bronte, C., He, J., & Krueger, C. Spawning site fidelity of wild and hatchery lake trout (*Salvelinus namaycush*) in northern Lake Huron. *Canadian Journal of Fisheries and Aquatic Sciences*, 73:18–34, 2016.
- BirdLife International. Anthus pratensis. (amended version published in 2016). The IUCN Red List of Threatened Species, (Accessed July 2017 from http://www.birdlife.org), 2016.

- Bonn, A., Allott, T., Hubacek, K., & Stewart, J., editors. Drivers of environmental change in uplands. Routledge, 2009.
- Border, J. A., Henderson, I. G., Redhead, J. W., & Hartley, I. R. Habitat selection by breeding Whinchats *Saxicola rubetra* at territory and landscape scales. *Ibis*, 159(1):139–151, 2017.
- Both, C., Dingemanse, N., Drent, P., & Tinbergen, J. Pairs of extreme avian personalities have highest reproductive success. *Journal of Animal Ecology*, 74:667–674, 2005.
- Branchini, S., Meschini, M., Covi, C., Piccinetti, C., Zaccanti, F., & Goffredo, S. Participating in a citizen science monitoring program: Implications for environmental education. *PLOS ONE*, 10:e0131812, 2015.
- BRIG. UK Biodiversity Action Plan; priority habitat descriptions. Upland Heathland. 2008a.
- BRIG. UK Biodiversity Action Plan; priority habitat descriptions. Upland Flushes, Fens and Swamps. 2008b.
- Bunce, R., Wood, C., & Smart, S. The ecology of British up-land landscapes. I. Composition of landscapes, vegetation and species. *Journal of Landscape Ecology*, 11:120–139, 2018a.
- Bunce, R., Wood, C., & Smart, S. The ecology of British up-land landscapes. II. The influence of policy on the current character of the uplands and the potential for change. *Journal of Landscape Ecology*, 11:140–154, 2018b.
- Byers, C. & Eason, P. Conspecifics and their posture influence site choice and oviposition in the Damselfly *Argia moesta*. *Ethology*, 115:721–730, 2009.
- Carey, C. The impacts of climate change on the annual cycles of birds. *Philosophical transactions of the Royal Society B: Biological Sciences*, 364:3321–3330, 2009.
- Carney, K. M. & Sydeman, W. J. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds*, 22(1):68–79, 1999.
- Chamberlain, D. E., Negro, M., Caprio, E., & Rolando, A. Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. *Biological Conservation*, 167:127–135, 2013.

Chance, E. The Cuckoo's secret. Sidgwick and Jackson, London, 1922.

- Chesterton, C. Environmental impacts of land management. Natural England Research Report NERR030, 2009.
- Colombelli-Negrel, D. & Kleindorfer, S. Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). *Ecological Research*, 24:921–928, 2009.
- Côté, I. M. & Sutherland, W. J. The effectiveness of removing predators on bird populations. *Conservation Biology*, 11(2):395–405, 1997.
- Cothran, R. The importance of reproductive interference in ecology and evolution: from organisms to communities. *Population Ecology*, 57:339–341, 2015.
- Cramp, S. & Perrins, C. The birds of the Western Palearctic. Oxford University Press, 1994.
- Crick, H. Q., Baillie, S. R., & Leech, D. I. The UK Nest Record Scheme: Its value for science and conservation. *Bird Study*, 50(3):254–270, 2003.
- Crick, H. Q. P., Dudley, C., Evans, A. D., & Smith, K. W. Causes of nest failure among buntings in the UK. *Bird Study*, 41(2):88–94, 1994.
- Curtis, C. J., Battarbee, R. W., Monteith, D. T., & Shilland, E. M. The future of upland water ecosystems of the UK in the 21st century: A synthesis. *Ecological Indicators*, 37:412–430, 2014.
- Dartmoor Biodiversity Steering Group. Dartmoor Species Action Plan for Bats. 2007.
- Dartmoor National Park Authority. State of the Park Report, 2008.
- Dartmoor National Park Authority. Birds of the open moor, 2011.
- Davies, N. Cuckoos, cowbirds and other cheats. T & A D Poyser, 2016.
- Davies, N. B. & de L. Brooke, M. An experimental study of co-evolution between the Cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *Journal* of Animal Ecology, 58(1):207–224, 1989.
- de L. Brooke, M. & Davies, N. gg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature*, 335:630–632, 1988.

DEFRA. The Heather and Grass Burning Code (2007 version), 2007.

- Dennis, P., Skartveit, J., McCracken, D. I., Pakeman, R. J., Beaton, K., Kunaver, A., & Evans, D. M. The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology*, 45: 279–287, 2008.
- Dickinson, J., Zuckerberg, B., & Bonter, D. Citizen Science as an Ecological Research Tool: Challenges and Benefits. Annual Review of Ecology, Evolution and Systematics, 41:149–172, 2010.
- Dickinson, J., Shirk, J., Bonter, D., Bonney, R., Crain, R., Martin, J., Phillips, T., & Purcell, K. The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment*, 10:291–297, 2012.
- Dillen, L., Jordaens, K., De Bruyn, L., & Backeljau, T. Fecundity in the hermaphroditic land snail Succinea putris (Pulmonata: Succineidae): does body size matter? *Journal of Molluscan Studies*, 76:376–383, 2010.
- Douglas, D. J. T. & Pearce-Higgins, J. W. Relative importance of prey abundance and habitat structure as drivers of shorebird breeding success and abundance. *Animal Conservation*, 17(6):535–543, 2014.
- Douglas, D. J. T., Buchanan, G. M., Thompson, P., Amar, A., Fielding, D. A., Redpath, S. M., & Wilson, J. D. Vegetation burning for game management in the UK uplands is increasing and overlaps spatially with soil carbon and protected areas. *Biological Conservation*, 191:243–250, 2015.
- English Nature & Dartmoor National Park Authority. The nature of Dartmoor. A biodiversity profile. 2001.
- Fletcher, L., Forrest, B., Atalah, J., & Bell.J.J. Reproductive seasonallity of the invasive ascidian *Didemnum vexillum* in New Zealand and implications for shellfish aquaculture. *Aquaculture environment interactions*, 3:197–211, 2013.
- Fox, R. The decline of moths in Great Britain: A review of possible causes. Insect Conservation and Diversity, 6:5–19, 2013.
- Fox, R., Brereton, T., Asher, J., August, T., Botham, M. S., Bourn, N., Cruickshanks, K., Bulman, C., Ellis, S., Harrower, C., Middlebrook, I., Noble,

D., Powney, G., Randle, Z., Warren, M., & Roy, D. B. The State of the UK's Butterflies 2015. *Butterfly Conservation and the Centre for Ecology & Hydrology*, 2015.

- Friedman, W. & Floyd, S. Perspective: The origin of flowering plants and their reproductive biology - A tale of two phylogenies. *Evolution*, 55:217–231, 2001.
- Fuller, R. J. & Glue, D. E. The breeding biology of the Stonechat and Whinchat. Bird Study, 24(4):215–228, 1977.
- Galbraith, H., Murray, S., Duncan, K., Smith, R., Whitfield, D., & Thompson, D. Diet and habitat use of the Dotterel *Charadrius morinellus* in Scotland. *Ibis*, 135: 148–155, 1993.
- Gibbs, H. L., Sorenson, M. D., Marchetti, K., de L. Brooke, M., Davies, N. B., & Nakamura, H. Genetic evidence for female host-specific races of the Common Cuckoo. *Nature*, 407:183–186, 2000.
- Gill, V., Hatch, S., & Lanctot, R. Sensitivity of breeding parameters to food supply in Black-legged Kittiwakes *Rissa tridactyla*. *Ibis*, 144:268–283, 2002.
- Glue, D. & Morgan, R. Cuckoo Hosts in British Habitats. Bird Study, 19(4):187–192, 1972.
- Grand-Clement, E., Anderson, K., Smith, D., Luscombe, D., Gatis, N., Ross, M., & Brazier, R. Evaluating ecosystem goods and services after restoration of marginal upland peatlands in South-West England. *Journal of Applied Ecology*, 50:324–334, 2013.
- Haines-Young, R. & Potschin, M. Upland ecosystem services. Report to Natural England. Coordination contract. NE Project Code: PTY02/10/002.27. CEM Report No 10., 2009.
- Hamby, K., Bellamy, D., Chiu, J., Lee, J., Walton, V., Wiman, N., York, R., & Biondi, A. Biotic and abiotic factors impacting development, behavior, phenology, and reproductive biology of *Drosophila suzukii*. Journal of Pest Science, 89:605– 619, 2016.
- Hayhow, D., Conway, G., Eaton, M., Grice, P., Hall, C., Holt, C., Kuepfer, A., Noble, D., Oppel, S., Risely, K., Stringer, C., Stroud, D., Wilkinson, N., & Wotton, S. The state of the UK's birds 2014. *RSPB*, *BTO*, *WWT*, *JNCC*, *NE*, *NIEA*, *NRW* and SNH, Sandy, Bedfordshire., 2014.

- Hayhow, D., Bond, A., Douse, A., Eaton, M., Frost, T., Grice, P., Hall, C., Harrist,
  S., Havery, S., Hearn, R., Noble, D., Oppel, S., Williams, J., Win, I., & Wotton,
  S. The state of the UK's birds 2016. *RSPB*, *BTO*, *WWT*, *DAERA*, *JNCC*, *NE*, *NRW and SNH*, Sandy, Bedfordshire., 2016.
- Helm, B., Fiedler, W., & Callion, J. Movements of European stonechats Saxicola torquata according to ringing recoveries. Ardea, 94(1):33–44, 2006.
- Hewson, C. M., Thorup, K., Pearce-Higgins, J. W., & Atkinson, P. W. Population decline is linked to migration route in the Common Cuckoo. *Nature Communications*, 7:12296, 2016.
- Holden, J., Shotbolt, L., Bonn, A., Burt, T. P., Chapman, P. J., Dougill, A. J., Fraser, E. D., Hubacek, K., Irvine, B., Kirkby, M. J., Reed, M. S., Prell, C., Stagl, S., Stringer, L. C., Turner, A., & Worrall, F. Environmental change in moorland landscapes. *Earth-Science Reviews*, 82:75–100, 2007.
- Hughes, T. P. & Tanner, J. E. Recruitment failure, life histories, and long-term decline of caribbean corals. *Ecology*, 81(8):2250–2263, 2000.
- Huin, N. & Sparks, T. Spring arrival patterns of the Cuckoo Cuculus canorus, Nightingale Luscinia megarhynchos and Spotted Flycatcher Musciapa striata in Britain. *Bird Study*, 47:22–31, 2000.
- Humphrey, J. W. Benefits to biodiversity from developing old-growth conditions in British upland spruce plantations: A review and recommendations. *Forestry*, 78 (1):33–53, 2005.
- Jayakody, S., Sibbald, A., Mayes, R., Hooper, R., Gordon, I., & Lambin, X. Effects of human disturbance on the diet composition of wild red deer *Cervus elaphus*. *European Journal of Wildlife Research*, 57:939–948, 2011.
- Jefferson, R. G. The conservation management of upland hay meadows in Britain: a review. *Grass and Forage Science*, 60:322–331, 2005.
- Jenner, E. Observations on the natural history of the cuckoo. *Philosophical Trans*actions of the Royal Society B, 78:219–237, 1788.
- JNCC. UK priority species pages version 2. (http://jncc.defra.gov.uk/page-5169 Accessed August 2017).

- JNCC. Special Areas of Conservation (SAC). (http://jncc.defra.gov.uk/ Protected-Sites/SACselection/ - Accessed September 2017), 2017.
- Johnson, M. D. Measuring habitat quality: A review. The Condor, 109:489–504, 2007.
- Joys, A. C. & Crick, H. Q. P. Breeding periods for selected bird species in England. BTO Research Report No. 352, 2004.
- Kalinski, A., Wawrzyniak, J., Banbura, M., Skwarska, J., Zielinski, P., & Banbura, J. Haemoglobin concentration and body condition of nestling Great Tits *Parus major*: a comparison of first and second broods in two contrasting seasons. *Ibis*, 151:667–676, 2009.
- Krist, M. Egg size and offspring quality: a meta-analysis in birds. *Biological Reviews*, 86:692–716, 2011.
- Lack, D. Habitat selection in birds. With special reference of the effects of afforestation on the Breckland avifauna. *British Ecological Society*, 2(2):239–262, 1933.
- Langston, R., Liley, D., Murison, G., Woodfield, E., & Clarke, R. What effects do walkers and dogs have on the distribution and productivity of breeding European Nightjar *Caprimulgus europaeus*. *Ibis*, 149:27–36, 2007.
- López-López, P., García-Ripollés, C., Aguilar, J. M., García-López, F., & Verdejo, J. Modelling breeding habitat preferences of Bonelli's eagle (*Hieraaetus fasciatus*) in relation to topography, disturbance, climate and land use at different spatial scales. *Journal of Ornithology*, 147:97–106, 2006.
- Madders, M. & Whitfield, D. P. Upland raptors and the assessment of wind farm impacts. *Ibis*, 148:43–56, 2006.
- Mallord, J. W., Smith, K. W., Bellamy, P. E., Charman, E. C., & Gregory, R. D. Are changes in breeding habitat responsible for recent population changes of longdistance migrant birds? *Bird Study*, 63(2):250–261, 2016.
- Marboutin, E., Bray, Y., Peroux, R., Mauvy, B., & Lartiges, A. Population dynamics in European hare: breeding parameters and sustainable harvest rates. *Journal of Applied Ecology*, 40:580–591, 2003.
- Mercer, I. Dartmoor. 2009.

- Merenlender, A., Crall, A., Drill, S., Prysby, M., & Ballard, H. Evaluating environmental education, citizen science, and stewardship through naturalist programs. *Conservation Biology*, 30:1255–1265, 2016.
- Ministry of Defence. DTE South West public information leaflet. (www.gov.uk/guidance/defence-infrastructure-organisation-and-the-defencetraining-estate - Accessed September 2017), 2017.
- Møller, A., Antonov, A., Stokke, B., Føssoy, F., Moksnes, A., Røskaft, E., & Takasu,
  F. Isolation by time and habitat and coexistence of distinct host races of the common cuckoo. *Journal of Evolutionary Biology*, 24:676–684, 2011.
- Natural England. Bracken management and control (TIN048), 2008.
- Natural England. Agri-environment schemes in England 2009 (NE194), 2009.
- Natural England. Designated Sites View. http://jncc.defra.gov.uk/ Protected-Sites/SACselection/ - Accessed September2017. 2017.
- Newson, S. E., Evans, K. L., Noble, D. G., Greenwood, J. J. D., & Gaston, K. J. Use of distance sampling to improve estimates of national population sizes for common and widespread breeding birds in the UK. *Journal of Applied Ecology*, 45:1330–1338, 2008.
- Nisbet, I. C. T. Courtship feeding, egg size and breeding success in Common Terns. Nature, 241:141–142, 1973.
- Nunes, D., Magalhaes, A., Weber, A., Gomes, R., Normando, F., Santiago, K., Rizzo, E., & Bazzoli, N. Influence of a large dam and importance of an undammed tributary on the reproductive ecology of the threatened fish matrinxa Brycon orthotaenia Gunther, 1864 (Characiformes: Bryconidae) in southeastern Brazil. *Neotropical Ichthyology*, 13:317–324, 2015.
- O'Rourke, E., Charbonneau, M., & Poinsot, Y. High nature value mountain farming systems in Europe: Case studies from the Atlantic Pyrenees, France and the Kerry Uplands, Ireland. *Journal of Rural Studies*, 46:47–59, 2016.
- Orr, H., Wilby, R., McKenzie Hedger, M., & Brown, I. Climate change in the uplands: A UK perspective on safeguarding regulatory ecosystem services. *Climate Research*, 37:77–98, 2008.

- Pakanen, V., Luukkonen, A., & Koivula, K. Nest predation and trampling as management risks in grazed coastal meadows. *Biodiversity and Conservation*, 20: 2057–2073, 2011.
- Parr, R. The decline to extinction of a population of Golden Plover in north-east Scotland. Ornis Scandinavica, 23(2):152–158, 1992.
- Pearce-Higgins, J. W. & Grant, M. C. Relationships between bird abundance and the composition and structure of moorland vegetation. *Bird Study*, 53:112–125, 2006.
- Pearce-Higgins, J. W., Stephen, L., Langston, R. H. W., Bainbridge, I. P., & Bullman, R. The distribution of breeding birds around upland wind farms. *Journal* of Applied Ecology, 46(6):1323–1331, 2009.
- Pearce-Higgins, J. W., Dennis, P., Whittingham, M. J., & Yalden, D. W. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Global Change Biology*, 16(1):12–23, 2010.
- Perlut, N. & Strong, A. Grassland birds and rotational-grazing in the northeast: Breeding ecology, survival and management opportunities. *The Journal of Wildlife Management*, 75:715–720, 2011.
- Pineiro, A., Barja, I., Silvan, G., & Illera, J. Effect of tourist pressure and reproduction on physiological stress response in wildcats: management implications for species conservation. Wildlife Research, 39:532–539, 2012.
- Ramchunder, S., Brown, L., & Holden, J. Environmental effects of drainage, drainblocking and prescribed vegetation burning in UK upland peatlands. *Progress in Physical Geography*, 33(1):49–79, 2009.
- Ratcliffe, D. A. & Thompson, D. B. A. The British uplands: their ecological character and international significance. In: Ecological change in the uplands. Blackwell Scientific Publications, Oxford, 1988.
- Reed, M. S., Bonn, A., Slee, W., Beharry-Borg, N., Birch, J., Brown, I., Burt,
  T. P., Chapman, D., Chapman, P. J., Clay, G. D., Cornell, S. J., Fraser,
  E. D., Glass, J. H., Holden, J., Hodgson, J. A., Hubacek, K., Irvine, B., Jin,
  N., Kirkby, M. J., Kunin, W. E., Moore, O., Moseley, D., Prell, C., Price,
  M. F., Quinn, C. H., Redpath, S., Reid, C., Stagl, S., Stringer, L. C., Termansen,

M., Thorp, S., Towers, W., & Worrall, F. The future of the uplands. *Land Use Policy*, 26:S204–S216, 2009.

- Robinson, R., Julliard, R., & Saracco, J. Constant effort: Studying avian population processes using standardised ringing. *Ringing & Migration*, 24:199–204, 2011.
- Robinson, R. A. BirdFacts: Profiles of birds occurring in Britain & Ireland. BTO Research Report 407, 2017.
- Royal Society for the Protection of Birds. The uplands: Time to change. https://www.rspb.org.uk/Images/uplands\_tcm9-166286.pdf - Accessed September 2017. 2017.
- Sæther, B., Ringsby, T. H., & Røskaft, E. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos*, 77:217–226, 1996.
- Schmidt, K. A. Nest predation and population declines in Illinois songbirds: A case for mesopredator effects. *Conservation Biology*, 17(4):1141–1150, 2003.
- Seaton, R., Minot, E., & Holland, J. Nest-site selection of New Zealand Falcons (*Falco novaeseelandiae*) in plantation forests and the implications of this to forestry management. *Emu-Austral Ornithology*, 110:316–323, 2010.
- Sekercioĝlu, C. H., Primack, R. B., & Wormworth, J. The effects of climate change on tropical birds. *Biological Conservation*, 148:1–18, 2012.
- Shine, R. & Brown, G. Adapting to the unpredictable: reproductive biology of vertebrates in the Australian wet-dry tropics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363:363–373, 2008.
- Skiftesvik, A., Durif, C., Bjelland, R., & Browman, H. Distribution and habitat preferences of five species of wrasse (Family Labridae) in a Norwegian fjord. *ICES Journal of Marine Science*, 72:890–899, 2015.
- Thompson, D. B. A. & Macdonald, A. J. Upland heather moorland in Great Britain: A review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation*, 71:163–178, 1995.
- Thompson, F. R. Factors affecting nest predation on forest songbirds in North America. *Ibis*, 149(Suppl. 2):98–109, 2007.

- Thomson, D. L., Baillie, S. R., & Peach, W. J. A method for studying post-fledging survival rates using data from ringing recoveries. *Bird Study*, 46:S104–S111, 1999.
- Tripp, S., Phelps, Q., Colombo, Q., Garvey, J., Burr, B., Herzog, D., & Hrabik, R. Maturation and reproduction of Shovelnose Sturgeon in the middle Mississippi river. North American Journal of Fisheries Management, 29:730–738, 2009.
- van Klink, R., Mandema, F. S., Bakker, J. P., & Tinbergen, J. M. Foraging site choice and diet selection of Meadow Pipits Anthus pratensis breeding on grazed salt marshes. *Bird Study*, 61(1):101–110, 2014.
- Vandenberghe, C., Prior, G., Littlewood, N. A., Brooker, R., & Pakeman, R. Influence of livestock grazing on Meadow Pipit foraging behaviour in upland grassland. *Basic and Applied Ecology*, 10:662–670, 2009.
- Watson, H., Bolton, M., & Monaghan, P. Out of sight but not out of harm's way: Human disturbance reduces reproductive success of a cavity-nesting seabird. *Biological Conservation*, 174:127–133, 2014.
- Webb, C. & Kelly, D. The reproductive biology of New Zealand flora. Trends in Ecology & Evolution, 8:442–447, 1993.
- Weidinger, K. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *Journal of Animal Ecology*, 71:424–437, 2002.
- Williams, T. D. Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. *Biological Reviews*, 68:35–59, 1994.
- Wilson, J. D., Whittingham, M. J., & Bradbury, R. B. The management of crop structure: A general approach to reversing the impacts of agricultural intensification on birds? *Ibis*, 147:453–463, 2005.
- Wink, M., Sauer-Gürth, H., & Gwinner, E. Evolutionary relationships of stonechats and related species inferred from mitochondrial-DNA sequences and genomic fingerprinting. *British Birds*, 95:349–355, 2002.
- Woodward, I., Massimino, D., Hammond, M., Harris, S., Leech, D., Noble, D., Walker, R., Barimore, C., Dadam, D., Eglington, S., Marchant, J., Sullivan, M., Baillie, S., & Robinson, R. BirdTrends 2018: trends in numbers, breeding success and survival for UK breeding birds. *Research report 708. BTO, Thetford*, 2018.

Wyllie, I. The Cuckoo. Batsford, London, 1981.

- Yallop, A. R., Thacker, J. I., Thomas, G., Stephens, M., Clutterbuck, B., Brewer, T., & Sannier, C. A. D. The extent and intensity of management burning in the English uplands. *Journal of Applied Ecology*, 43:1138–1148, 2006.
- Zockler, C., Syroechkovskiy, E., & Atkinson, P. Rapid and continued population decline in the Spoon-billed Sandpiper *Eurynorhynchus pygmeus* indicates imminent extinction unless conservation action is taken. *Bird Conservation International*, 20:95–111, 2010.

# Chapter 2

# Breeding parameters of Meadow Pipit, European Stonechat and Whinchat on an upland moorland in the UK



Better than all measures Of delightful sound, Better than all treasures That in books are found, Thy skill to poet were, thou scorner of the ground! To a Skylark - Percy Bysshe Shelley

# Breeding parameters of Meadow Pipit, European Stonechat and Whinchat on an upland moorland in the UK

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Short title: Breeding parameters of three UK upland moorland passerines

**Keywords:** eggs - hatchling - Mayfield - success - Dartmoor - nest record scheme - survival

# 2.1 Abstract

Knowledge of site-specific avian biodiversity and breeding parameters is essential in informing effective bird conservation management. In this study, species diversity and the breeding parameters of clutch size, brood size and nest success were studied for breeding birds in an area of conservation importance: Dartmoor National Park (UK). A total of 1550 nests of 34 bird species were monitored on a 4.3km<sup>2</sup> upland moorland study site over a nine year period between 2008 and 2016. For Meadow Pipit (Anthus pratensis), European Stonechat (Saxicola rubicola) and Whinchat (Saxicola rubetra), three of the most abundant breeding bird species on the study site, average clutch size, brood size and Mayfield nest success across years were calculated. Clutch size did not show interannual variability in any of these species. Meadow Pipit and Stonechat showed interannual differences in brood size, although variation was relatively minor. In all three species, nest success showed significant differences between some, but not all, study years. Nest success was generally in line with findings from other studies in the UK and continental Europe. The estimates of diversity and breeding parameters presented in this study provide a baseline against which any future changes, for example in response to conservation management or other factors, can be quantified.

# 2.2 Introduction

The UK has seen severe biodiversity losses and wildlife population declines over recent decades. Species diversity has declined, including in economically important insects such as bees, and population sizes of protected species, including mammals such as the Hazel Dormouse (*Muscardinus avellanarius*), continue to fall (Biesmeijer et al., 2006; Goodwin et al., 2017). More generally, such changes in the UK's natural environment have been illustrated by changes in the "Biodiversity Intactness Index" (BII), which measures the proportion of biodiversity still present in an area, relative to an intact habitat (Newbold et al., 2016). Hayhow et al. (2016b) determined that the UK's BII is well below the global average in terms of the intactness of its biodiversity (29th lowest of 218 assessed countries).

In its 25 year environment plan, the UK government recognises the importance of environmental protection and improvement, not only for nature's intrinsic value, but also to ensure a continued supply of the ecosystem services upon which human populations rely. The plan sets out ambitions to recover nature, and for example aims to "improve the overall status of declining species groups", such as birds and wildflowers (HM Government, 2018). Some of the key locations for delivering such environmental improvements are the UK's National Parks. The UK's fifteen National Parks include a wide range of habitat types, ranging from lowland marshland to mountain landscapes. They are important areas for nature conservation, particularly so given they cover 10.8% of the land area in England and Wales, but are home to only 0.7% of the total human population (ONS, 2011). According to the Environment Act 1995, a statutory purpose for National Parks is to "conserve and enhance the natural beauty, wildlife and cultural heritage" (Environment Act 1995). Successful conservation action relies on well-informed, evidence-based management, and therefore National Park Authorities need to have access to detailed ecological and scientific data to underpin their decision-making.

In order to monitor whether National Parks are successful in delivering improvements in the status of declining species groups, baseline data on biodiversity is needed. Recording biodiversity is essential for monitoring local gains and losses, and helps build an understanding of the conservation value of specific sites. However, additional information is needed in order to effectively protect species. Recording diversity alone provides us with only limited information on whether individual species are thriving. It is necessary to have information also on population sizes, and factors which may affect population growth, such as adult survival and reproductive success.

Reproductive success can be affected by a wide range of ecological factors, including food availability, predation pressures and weather conditions (Lack, 1946; Klomp, 1970; Newton, 1994; Wood et al., 2016). This is further complicated by the fact that ecological factors can affect varying components of the breeding cycle in birds, such as clutch size, hatching success and post-fledging survival, and that these reproductive parameters can show substantial interannual variability (Lack, 1946; Chastel et al., 1993; Wood et al., 2016). Furthermore, management practices can directly or indirectly affect reproductive parameters. For example, fertiliser use, grazing regimes or other vegetation management techniques can strongly alter vegetation structure and vegetation diversity, which in turn can alter reproductive performance of wildlife (Sullivan and Sullivan, 2014; Combrink et al., 2017). As all the above factors can vary between geographical locations (see for example Rotenberry and Wiens (1989); Sanz (1998)), local conservation plans for National Parks and other sites should, wherever possible, be informed by local data on breeding biology and reproductive parameters. This will ensure that any changes in wildlife populations, for example in response to management interventions, can be more accurately measured. This is essential in order to successfully monitor whether conservation gains are being achieved.

Dartmoor National Park is one of the UK's southernmost upland moorland habitats. It provides a wide range of ecosystem services, including agriculture, drinking water and tourism (Dartmoor National Park Authority, 2014). It is home to several nationally declining bird species, for example Cuckoo (*Cuculus canorus*), Skylark (*Alauda arvensis*) and Snipe (*Gallinago gallinago*) (Dartmoor National Park Authority, 2011). As in many National Parks and protected areas, management for bird conservation can be in direct conflict with other interests, such as recreational use, agricultural productivity and archaeological protection. Land management practices such as swaling (land burning) can be beneficial for agriculture but can have detrimental effects on nesting birds (discussed in more detail in the next chapter of this thesis). Therefore, in order to be able to understand the current conservation status of birds on Dartmoor, and to be able to monitor any changes in response to future environmental or management change, there is a need for more detailed information on the diversity and reproductive parameters of Dartmoor's breeding birds.

In this study, we set out to obtain local baseline information on both avian biodiversity and breeding parameters on Dartmoor. In order to achieve this, a nine year study on bird breeding was conducted on a  $4.3 \text{km}^2$  area of upland habitat in Dartmoor National Park. Nests of breeding birds were recorded to assess avian diversity on the site. For three of the locally most abundant breeding bird species on the site; Meadow Pipit (Anthus pratensis), European Stonechat (Saxicola rubicola, hereafter referred to as "Stonechat") and Whinchat (Saxicola rubetra), a large number of nests was monitored in a detailed survey to determine baseline breeding parameters. These species were selected for in-depth study for two main reasons; their abundance on the study site, thereby allowing sufficient sample sizes for analyses, and the expertise and interest of the volunteer nest recorders upon which data collection relied. For these three species, we aimed to determine average clutch size, brood size and nest success. As mentioned above, these variables can show interannual variability, and we therefore use the multi-year data from this study to quantify interannual variability in these variables. This will allow for comparison of any future changes in breeding success against the natural variation seen in the current population. Population size, adult survival and other factors which may influence population size were not monitored in this study due to limitations in field time and resources, but some estimates of population sizes on (parts of) Dartmoor can be found in other studies (see for example Beavan and Lock (2016); Royal Society for the Protection of Birds (2017)).

## 2.3 Methods

#### 2.3.1 Study site and species

This study was carried out between 2008 and 2016 in Dartmoor National Park, southwest England (50° 31' 20"N, -3° 51' 30"W). The study site is a 4.3km<sup>2</sup> upland study site located at an altitude of between 211 to 457 meters above sea level. At the centre of the study site is an open reservoir surrounded by a narrow strip of planted conifers. The majority of the site is moorland vegetation, consisting of mainly low gorse, grass and bracken with scattered higher scrub and few isolated trees. Nests of all breeding bird species were recorded to provide an estimate of avian breeding diversity on the site, and additional information on UK conservation status and nesting habitat requirements were sourced from Eaton et al. (2015) and Ferguson-Lees et al. (2011) respectively. The UK conservation status established by Eaton et al. (2015) is widely used, for example in the national State of the UK birds reports (Hayhow et al., 2016a). It assigns species to either Red (most threatened), Amber or Green (least threatened) listing based on a range of criteria, including population trend, distribution change, global conservation status, and UK rarity.

The main survey effort during fieldwork focused on three of the locally most abundant species; Meadow Pipit, Stonechat and Whinchat in order to provide detailed information on the breeding parameters for these species. All three species are passerines which breed close to the ground in low vegetation, and are found to co-occur on the study site and across numerous areas on Dartmoor more widely.

#### 2.3.2 Nest data

Nest data were collected using the British Trust for Ornithology (BTO) Nest Record Scheme (NRS) protocol (Crick et al., 2003). Nests were found by observing adult birds displaying typical breeding behaviours such as the carrying of food or faecal material. These observations were conducted by observing breeding pairs from a distance (minimally 10m) using binoculars and camouflage clothing in order to minimise disturbance to the breeding pairs. If birds appeared disturbed (e.g. through alarm calling), the observation distance was increased until regular breeding behaviours resumed. The suspected nest location was derived from breeding behaviours. When females were incubating eggs this was determined by observing the vegetation patches she exited or entered as she came off to feed, or returned to the nest after feeding. Other signals facilitating locating nests with incubating females included watching males returning with food and calling the females off the nest to feed her. Nests were more easily located during nest building or when nests contained chicks. In the former cases, adult birds with nesting material in their bills were watched back to the nest vegetation patch. In the latter case the vegetation patch containing the nest was identified by observing birds entering the nest site with food or exiting the nest after feeding the chicks (then often carrying faecal sacs in their bills). Once the likely nest location had been established (with observation times ranging from 5 minutes to several hours across multiple days), the vegetation patch identified was searched carefully to locate the nest cup. After having located the nest, breeding progress was monitored by repeat visits between one and eight times across the breeding period to record the nest content (building stage, number of eggs, incubation or nestling age). The number of visits varied between one and eight due to variability in the observed breeding period (time between the nest being found and the brood fledging or the nest failing), and due to variability in available field time. Nest visits for Meadow Pipit, Stonechat and Whinchat were prioritised over other species on days when workload was higher than available hours. Breeding attempts were considered successful when at least one fledgling was re-sighted, adults were seen alarming or carrying food close to the nest location, or when nests were found empty and intact after the expected fledging date (often looking slightly flattened and dirty from containing large nestlings, a tell). Breeding was recorded to have failed when dead chicks, a destroyed nests or feather remains were found in or in close proximity to the nest, or when the nest was found to be empty before the earliest possible fledging date. When the outcome could not be determined with certainty, nests were recorded as "outcome unknown".

#### 2.3.3 Statistical analyses

For Meadow Pipit, Stonechat and Whinchat, nest data were analysed to derive of clutch size, number of hatchlings (hereafter referred to as "brood size") and nest success for each species. Nests which fail at early stages of the nesting cycle are less likely to be observed, which would lead to an overestimate of nest success if the proportion of failed vs. successful nests is used as a measure of nest success. To overcome this the Mayfield method (Mayfield, 1975) was used to calculate the probability of a nest successfully producing at least one fledgling, hereafter referred to as "nest success". This is done by firstly establishing the number of observation days of each nest. For nests with an unknown outcome, i.e. cases where it could not be determined whether nestlings fledged or were predated, observation days are counted from the first day the nest was observed to be active (i.e. containing eggs/nestlings), until the day at which the nest was last observed to be active. For nests with known outcomes (i.e. nests known to have fledged or known to have failed), the last observation day is considered to be the halfway point between the day at which the nest was last active, and the next nest check at which the nest was empty. From the number of observation days, daily nest survival across all nests is calculated as follows:

# Daily nest survival = $1 - \left(\frac{\text{total number of failed nests}}{\text{total number of observation days}}\right)$

This captures the total number of nests that survived per observation day. From this, nest success can be derived by calculating nest survival for the entire breeding period:

### Nest success = Daily nest survival p

with p representing the total nesting period for that particular species (in days). A p of 30.5, 33.95 and 32.29 was used for Meadow Pipit, Stonechat and Whinchat respectively. These nesting period values were obtained from the BTO Nest Record Scheme (Robinson, 2017) by summing the reported mean clutch size (as one egg is laid per day), mean number of incubation days and mean number of days from hatching to fledging. The nesting period values were derived from the national BTO data rather than the nesting data from this study as national estimates were deemed to be more reliable overall. This is due to the fact that the field methods used limit the possibility of accurately calculating breeding period length, as most nests are only monitored for part of the breeding cycle (e.g. being found after the start of incubation, and/or failing before fledging). Furthermore, nestling ages were generally estimated based on developmental stage rather than calculated from exact hatching dates. Therefore, we chose to use established national data rather than limited estimates from this study site to conduct the nest success calculations.

Although nest success is calculated for all nests combined, a confidence estimate for nest success can be obtained, using the following steps (following Johnson (1979)). The variance and Standard Error of daily nest survival can be calculated as:

 $Variance in \ daily \ nest \ survival = \frac{(total \ observation \ days - total \ failed \ nests) * total \ failed \ nests}{total \ observation \ days^3}$ 

Standard Error (SE) of daily nest survival =  $\sqrt{variance in daily nest survival}$ 

From this, 95% confidence limits for daily nest survival can be calculated as:

Lower confidence limit of daily nest survival = daily nest survival -2 \* SE

and

Upper confidence limit of daily nest survival = daily nest survival +2\*SE

This can then be converted into 95% confidence intervals for nest success by using:

Confidence limit of nest success = confidence limit of daily nest survival<sup>p</sup>

with p again representing the total nesting period for the species.

The calculation of daily nest survival and nest success outlined above is highly informative as it includes both nests with known and unknown outcomes in its estimate of nest success. However, a limitation of that method is that success is calculated as one value for all nests combined, thereby limiting options for statistical analysis of interannual variation. In order to be able to statistically test for differences in success between years, we adapt the above method slightly by calculating daily failure rate for each nest individually by dividing binomial nest outcome (1=fail, 0=success) by the number of observation days (see Hazler (2004)):

$$dfr = (\frac{binomial\ outcome}{number\ of\ observation\ days})$$

These data, which necessitates excluding any nests with unknown outcome, are used to test for interannual differences in daily failure rate.

Annual and average interannual clutch size ( $\pm$ SE), brood size (for successfully hatched nests only,  $\pm$ SE), nest success ( $\pm$ 95% confidence limits, see above) and daily failure rate ( $\pm$ SE) were calculated for each species. Statistical testing was conducted in R (R Core Team, 2015). Kruskal-Wallis tests were used to test for interannual and interspecific differences in clutch size, brood size and daily failure rate. Dunn Tests with Bonferroni correction were used for post-hoc testing. The Dunn test was selected due to the fact that it accounts for ties in the data when conducting pairwise comparisons after a significant Kruskal-Wallis test (R Core Team, 2015). As data on numbers of eggs, numbers of hatchlings and nest outcome were not available for all nests, sample sizes differ between analyses.

# 2.4 Results

#### 2.4.1 Avian diversity

A total of 1550 nests were monitored across the nine years of the study. The total recorded breeding bird diversity was 34 species across a range of avian groups. This likely represents the full breadth of the avian breeding diversity at this site as no other breeding evidence, such as the presence of pairs or fledglings, was recorded for other species. A full overview of all recorded species by year is shown in Table 2.1. Their UK conservation status and nesting habitats are detailed in Table 2.2. Of the 34 species found on the site, nine are of Red conservation status, eight are Amber species, and 17 are Green in their status (see section 2.3.1 and Eaton et al. (2015) for more information on the methods for categorisation of species into Red, Amber and Green status). The species show a wide range of nesting ecologies. It includes a variety of open-nesting species typically found on moorland, such as those requiring very low, grassy vegetation (e.g. Skylark), and those breeding in higher patches of shrub (e.g. Yellowhammer and Linnet). Species found across a wide range of UK habitats, such as Willow Warbler and Lesser Redpoll, were also found nesting in suitable moorland shrub. In wetter areas, species such as Reed Bunting and Snipe were found. Species such as Song Thrush, Woodpigeon and Great Tit were found breeding on the study site edge, where moorland transitions into woodland. For further information on the diversity of nesting habitats used by the 34 species found on the study site, see Table 2.2.

Common name	Scientific name	2008	2009	2010	2011	2012	2013	2014	2015	2016	Total
Blackbird	Turdus merula	0	0	4	చ	చ	0	2	UT	1	18
Blue Tit	Cyanistes caeruleus	0	0	0	0	0	0	1	0	0	Ц
Bullfinch	Pyrrhula pyrrhula	0	0	2	⊢	0	0	0	0	0	ట
Chaffinch	Fringilla coelebs	0	0	ట	0	4	4	1	0	1	13
Chiffchaff	$Phylloscopus\ collybita$	0	0	1	0	0	1	0	0	0	2
Carrion Crow	Corvus corone	0	2	1	2	1	4	ယ	<u> </u>	1	15
Cuckoo*	Cuculus canorus	4	6	4	6	2	1	0	2	7	32
Dartford Warbler	Sylvia undata	0	0	2	1	1	0	0	0	0	4
Dunnock	Prunella modularis	0	1	0	ట	6	2	2	1	0	15
Goldfinch	Carduelis carduelis	0	0	1	0	0	0	0	0	0	1
Grasshopper Warbler	Locustella naevia	0	0	2	Ц	0	0	0	0	0	ట
Great Crested Grebe	Podiceps cristatus	0	0	0	0	0	0	0	0	1	1
Greenfinch	Chloris chloris	0	0	9	ట	1	1	0	0	1	15
Grey Heron	Ardea cinerea	0	0	0	0	1	ట	0	2	0	6
Great Tit	Parus major	0	0	1	1	0	1	0	0	0	లు
Lesser Redpoll	Acanthis cabaret	0	0	1	0	6	σ	ယ	1	ట	19
Linnet	Linaria cannabina	0	0	ω	2	10	10	10	14	7	56
Long-tailed Tit	$A egithalos\ caudatus$	0	0	1	0	2	0	0	0	0	ట
Meadow Pipit	Anthus pratensis	22	45	55	58 58	70	80	53	143	100	626
Pied Wagtail	$Motacilla\ alba$	0	0	0	1	0	0	0	0	0	1
Redstart	Phoenicurus phoenicurus	0	0	0	0	0	0	1	0	0	1
Reed Bunting	Emberiza schoeniclus	ట	1	თ	4	σ	4	2	თ	2	31
Robin	Erithacus rubecula	0	0	0	0	0	0	0	0	1	1
Skylark	$A lauda \ arvens is$	ట	4	ట	9	9	17	9	20	6	74
Snipe	$Gallinago\ gallinago$	0	0	1	0	0	0	0	0	0	1
Song Thrush	$Turdus \ philomelos$	0	0	2	ట	2	2	1	2	1	13
Stonechat	Saxicola rubicola	4	9	19	36	38	<b>48</b>	36	60	65	315
Tree Pipit	Anthus trivialis	ట	1	2	7	2	12	7	0	0	34
Wheatear	Oenanthe oenanthe	0	0	0	0	1	0	0	0	0	1
Whinchat	$Saxicola\ rubetra$	11	13	17	<b>23</b>	<b>21</b>	<b>24</b>	11	31	<b>18</b>	169
Willow Warbler	Phylloscopus trochilus	4	υ	8	10	ట	υ	υ	2	7	49
Woodpigeon	$Columba\ palumbus$	0	0	0	0	1	0	0	0	0	1
Wren	$Troglodytes\ troglodytes$	0	0	0	0	1	0	0	0	0	1
Yellowhammer	Emberiza citrinella	0	4	ట	1	сл	ట	2	2	2	22
Total		54	91	150	172	192	227	149	291	<b>224</b>	1550

<b>Table 2.2:</b> Conservation status and nesting habitat of species monitored between 2008 and 2016 on a study site in
Dartmoor National Park, UK. Nest habitat information is adapted from Ferguson-Lees et al. (2011). Conservation
statuses were sourced from Eaton et al. (2015). Focal species of the study (Meadow Pipit, Stonechat and Whinchat)
are shown in bold.

	Status	Nesting habitat
Blackbird	Green	Found across most habitats which provide higher shrub layer, including farmland hedgerows, urban parks,
		moors and upland valleys. Nests at $<4m$ height mostly in fork of tree or bush.
Blue Tit	Green	Widespread cavity-nester, nesting off the ground at up to 5m. On study site, found in woodland edge.
Bullfinch	Amber	Nests at 1-2m height in dense undergrowth in range of habitat types, e.g. thick bramble or gorse.
Chaffinch	Green	Found in any wooded and/or scrubby area, nesting in forks of trees or bushes mostly at 1-4m high.
Chiffchaff	Green	Builds domed nests slightly off ground (10-30cm) in thick herb/shrub cover, mostly under mature trees.
Carrion Crow	Green	Nests in high forks of taller trees in wide range of habitats, often areas of lower vegetation with scattered
		trees. On study site found in larger isolated trees on open moor.
Cuckoo	$\operatorname{Red}$	Cuckoos are brood parasites of various species, see Meadow Pipit for host nest habitat on the study site.
Dartford Warbler	Amber	On the study site, Dartford Warbler are seen in patches of higher, relatively mature gorse. Dartford
		Warbler is protected under Schedule 1 in the Wildlife and Countryside Act 1981, therefore detailed
		information on nest habits is not provided here or in (Ferguson-Lees et al., 2011). Nests were monitored
		by a licensed volunteer.
Dunnock	Amber	Open-cup nester (15-150cm height) in a wide variety of bushes, trees and climbers in both built-up and
		rural habitats.
Goldfinch	Green	Nests at height (1.5-15m) in trees and large bushes in habitats with scattered trees (e.g. gardens,
		hedgerows, woodland edges).
Grasshopper Warbler	$\operatorname{Red}$	Found in open habitats which provide thick tussocky vegetation with higher bushes for perching. Nests
		in tussocks or low bushes on or just off ground (<30cm). On study site found in patches of higher, more
		mature gorse-rich shrub.

Common name	Status	Nesting habitat
Great Crested Grebe	Green	Nests on open water, often amidst reed or branches in e.g. lakes slow-flowing rivers. On study site found on reservoir at center of study area
Greenfinch	Green	Nests in scrub or canopy (2-4m) in both urban and rural habitats, e.g. woodland edge, parks, scrubland.
Grey Heron	Green	Mostly nests in the tops of tall trees (up to 25m) near water, on the study site nests in conifers surrounding
		the reservoir located at the center of the site.
Great Tit	$\operatorname{Green}$	Cavity-nester (0-5m) across wide range of habitats, usually preferring nest boxes. On study site found in
		natural tree cavities within mixed woodland edge adjacent to open moor.
Lesser Redpoll	Red	Nests in fork of bushes and small trees (usually at 1-5m) in a wide variety of habitats. On study site
		found in gorse on open moor.
Linnet	$\operatorname{Red}$	Breeds in shrub (often gorse) in for example heathland, hedgerows and thorny grasslands. Nest in shrub
		can opy at height of mostly $<2m$ .
Long-tailed Tit	Green	Buids ball-shaped nests from cobwebs and moss, attached to outside of mostly thorny bushes at 1-3m
		height. Found across wide range of habitats, on study site in woodland edge.
Meadow Pipit	$\mathbf{A}$ mber	Ground-nesting in areas of low-height vegetation. Nests typically located in grassy or rushy
		tussocks, and in mix of grass and low gorse/heather.
Pied Wagtail	Green	Nests on ledges and in holes (usually <2m high) across open habitats in both very urban and rural areas,
		including banks of upland roads.
$\operatorname{Redstart}$	Amber	Breeds in holes in trees, walls and banks $(<3m)$ in woodland, parks and open heath with scattered trees.
Reed Bunting	Amber	In open vegetation, often in waterlogged soil, nest placed in vegetation tussock slightly raised off the
		ground (up to 1m). On study site found in wet sites on open moor.
$\operatorname{Robin}$	Green	Wide variety of nest sites and habitats. Often nests <2m height in holes in walls, tree trunks or stumps
		sheltered by vegetation. On study site found in bank on open moor with low, grassy vegetation.
$\mathbf{Skylark}$	$\operatorname{Red}$	Nests in scrapes mostly in short grass, often in areas with a mixture of low vegetation and bare ground.

Common name	Status	Nesting habitat
Snipe	Amber	Typically breeds in damp areas such as bogs, wet moorland and wet grassland, nests in shallow scrape
		in grasses or marsh plants. On study site found in wetter, boggy parts of open moor.
Song Thrush	$\operatorname{Red}$	Nests in areas which have good scrub/bush cover, e.g. woodland edge and wasteland. Nests in bush or
		tree, often in ivy (1-4m high). On study site found in high bushes on woodland edge.
Stonechat	$\mathbf{Green}$	Open areas with some higher perches, nest placed on the ground in low gorse, grass, bracken
		or other low shrub.
Tree Pipit	$\operatorname{Red}$	Nests on open, tussocky ground with scattered perches. Nest placed on ground in bank or in/under low
		vegetation (on study site e.g. grass and bracken).
Wheatear	Green	Nests at up to 1m in height in rock cavities in open, rocky habitats. On study site found in rocky area
		of open moor.
Whinchat	$\mathbf{Red}$	Ground-nesting in open areas with perches, often on slopes and in ditches. Nests typically
		found in grass tufts, under bracken or small shrub.
Willow Warbler	Amber	Nests in areas of mixed-height vegetation, such as woodland edge and open vegetation with some
		trees/bushes. Nests in depression on ground near low perch. On study site found in shrub on open
		moor, as well as on woodland edge.
Woodpigeon	Green	Widespread in many habitats, including built-up areas. Nests in trees and higher bushes mostly at 3-5m
		nest height. On study site found in woodland edge of study area.
Wren	Green	Found across most UK habitats, nesting at 0-5m height in crevices in e.g. trees, banks and walls, but
		also in more open locations such as bramble or heather.
Yellowhammer	$\operatorname{Red}$	Breeds in a range of habitats, including farmland hedgerows, heathland and open woodland. Nests on
		ground, or slightly raised off ground, under bush, young tree, bracken or bramble. On study site typically
		found in patches of higher gorse.

#### 2.4.2 Breeding parameters

For the three focal species, 1110 nests (626 Meadow Pipit, 315 Stonechat and 169 Whinchat) were monitored across the nine years of the study. Numbers monitored varied between years, with numbers of recorded Meadow Pipit nests ranging from 22 to 143, Stonechat from 4 to 65, and Whinchat from 11 to 31. A full breakdown of nest numbers can be found in Table 2.1. Figure 2.1 shows average clutch size, brood size and nest success across all years by species. Average clutch size across all years was  $3.85\pm0.04$  (n=246) for Meadow Pipit,  $4.93\pm0.05$  (n=176) for Stonechat and  $5.34\pm0.09$  (n=108) for Whinchat. Average brood size across all years was  $3.64\pm0.04$ (n=518) for Meadow Pipit,  $4.58\pm0.06$  (n=274) for Stonechat and  $4.89\pm0.12$  (n=123)for Whinchat. Across all years nest success was 0.22 (95% CI [0.18, 0.27], n=573) for Meadow Pipit, 0.38 (95% CI [0.32, 0.46], n=308) for Stonechat and 0.25 (95% CI [0.18, 0.35], n=164) for Whinchat. The three species showed interspecific differences in all breeding parameters (See Figure 2.1). Clutch size was significantly different between all three species (Kruskal-Wallis chi-squared=271.71, p<0.001), brood size differed only between Meadow Pipit and the two other species (Kruskal-Wallis chisquared=144.67, p<0.001), and nest success differed only between Stonechat and Whinchat (Kruskal-Wallis chi-squared = 6.9611, p=0.003).

#### 2.4.3 Interannual differences

Figure 2.2 shows the annual clutch sizes, brood sizes and nesting success for all three species. Clutch size did not differ significantly between years for any of the species (Kruskal-Wallis Rank Sum test, Meadow Pipit: Kruskal-Wallis chi-squared=10.58, p=0.227; Stonechat: Kruskal-Wallis chi-squared=4.05, p=0.852; Whinchat: Kruskal-Wallis chi-squared=9.51, p=0.301). Brood size did not differ significantly between years in Whinchat (Kruskal-Wallis Rank Sum test, Kruskal-Wallis chi-squared=3.318, p=0.913). Figure 2.2 shows that it did differ significantly interannually for both Meadow Pipit (Kruskal-Wallis chi-squared=20.53, p=0.008) and Stonechat (Kruskal-Wallis chi-squared=21.66, p=0.006). Evaluation of the interannual differences shows that in both species variation was relatively minor, with no continuous increase or decrease in brood size apparent over time. Nest success was variable between years in all three species. For Meadow Pipit this ranged from 0.06 to 0.62 across the nine years of the study, for Stonechat from 0.22 to 1.00, and for Whinchats from 0.04 to 0.65.

As outlined in the methodology, daily failure rates for each nest were calcu-

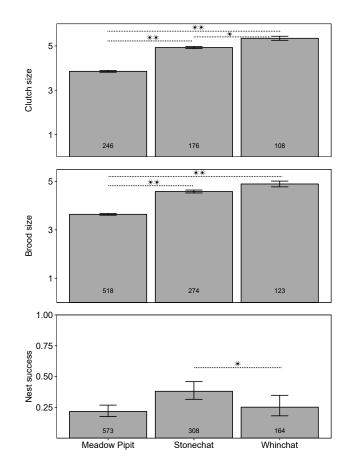
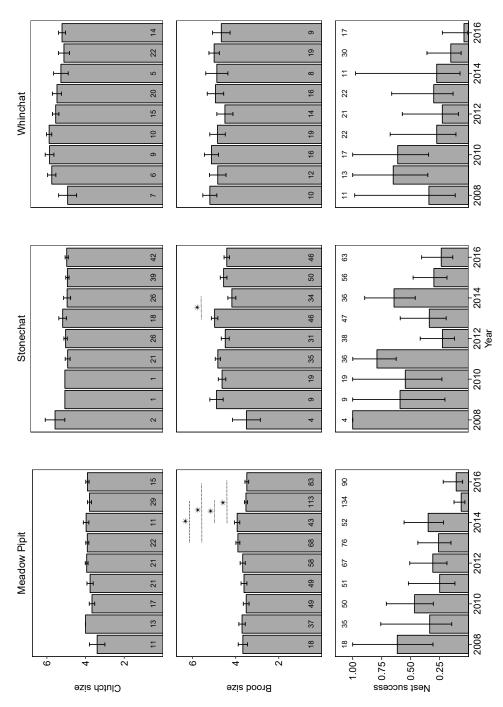


Figure 2.1: Average clutch size, brood size and nest success across nine study years for Meadow Pipit, Stonechat and Whinchat nests on a study site in Dartmoor National Park, UK. Grey bars indicate means. Vertical lines show SE for clutch size and brood size. Nest success is calculated as one value across all nests using the Mayfield method. Therefore, standard error estimates are not available and 95% confidence intervals are shown instead (see methodology). Sample sizes (number of nests) are shown on the bars. Significant differences between species (Dunn test) are indicated with horizontal lines; \* indicates p<0.05, \*\* indicates p<0.001.

lated in order to test for interannual differences in nest success rates. Figure 2.3 shows the mean daily failure rate ( $\pm$ SE) by year for all three species. In Meadow Pipit the year with the highest daily failure rate (2015), was significantly different (Kruskal-Wallis chi-squared=30.95, p<0.001) from years with very low daily failure rates. Stonechat also showed significant differences in daily failure rate between years (Kruskal-Wallis chi-squared=32.33, p<0.001). The years with the lowest daily failure rates, 2010 and 2011, showed significant differences with some, but not all, years of higher nest success. Interannual variation in daily failure rate also occurred for Whinchat (Kruskal-Wallis chi-squared=29.88, p<0.001). The years 2015 and 2016, which showed the highest daily failure rates, were significantly different from three years with low daily failure rates (see Figure 2.3).



Whinchat nests monitored on a study site in Dartmoor National Park, UK. Grey bars indicate means, vertical lines success is derived based on the Mayfield method of calculating one value for nest survival across all nests, for which reason standard error estimates are not available (see methodology). Sample sizes (number of nests by year) are Figure 2.2: Clutch size, brood size and nest success across nine study years for Meadow Pipit, Stonechat and show standard error for clutch size and brood size. For nest success, 95% confidence intervals are shown as nest shown on or above the bars. Significant differences between years (Dunn test) are indicated with horizontal lines; \* indicates p<0.05, \*\* indicates p<0.001

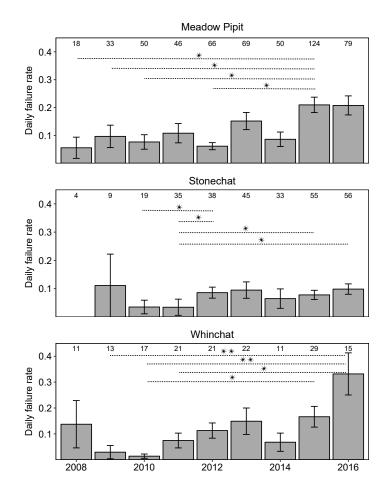


Figure 2.3: Daily failure rate (calculated using Mayfield method) across nine study years for Meadow Pipit, Stonechat and Whinchat nests monitored on a study site in Dartmoor National Park, UK. Only nests with known outcomes are included in this analysis. Grey bars show means and vertical lines indicate standard error for clutch size and brood size. Sample sizes (number of nests by year) are shown above the bars. Significant differences between years (Dunn test) are indicated with horizontal lines; \* indicates p<0.05, \*\* indicates p<0.001.

## 2.5 Discussion

The aim of this study was to assess the diversity and breeding parameters of birds on a study site in Dartmoor National Park. A total of 34 breeding bird species were found to co-occur on the  $4.3 \text{km}^2$  study site. As the potential avian diversity of a site depends on many factors, including the survey methodology, size of the study area and land cover characteristics, it is challenging to compare the diversity recorded in this study against that found on other sites. However, some recent studies have investigated avian diversity in similar habitats. For example, Newey et al. (2016) surveyed the avian biodiversity on 26 Scottish upland estates. Here, they recorded on average thirteen species per estate, with the number of species ranging from 7 to 27 on different estates. In a study on moorlands in the Peak District, between 8 and 24 species were recorded during 1km transect surveys, with 56 species being encountered on the total of 32 surveyed squares (Dallimer et al., 2010). In a similar survey on Irish peatlands, a total of 21 species were recorded during 1km transects on twelve study sites (Bracken et al., 2008). Our recorded diversity of 34 species in an area of  $4.3 \text{km}^2$  is high compared with those reported in these studies in comparable habitats in the UK. However, these studies described above both used a different methodology, the Breeding Bird Survey (BBS) (see for example Newson et al. (2008)), compared with the study on Holne Moor presented in this thesis. This may explain the lower diversity estimates in those studies compared with those found in this study. This is because during BBS surveys less time is spent on a site compared to the nest-finding approach adopted for this thesis work, and therefore the chances of recording less abundant birds is reduced. Nonetheless, these results and the comparison with the studies outlined above suggest the Holne Moor site supports a relatively high diversity of bird species, highlighting the importance of this area, and Dartmoor more generally, for avian wildlife.

More than half of the species recorded breeding on the study site are of conservation concern (Amber or Red-listed), further highlighting the conservation importance of this upland moorland site. A wide diversity of niches is supported by these upland habitats, with species breeding on the open moorland of the study site ranging from Linnet and Chiffchaff, which are known to nest in higher shrubs, to Reed Bunting, nesting in tussock in wet areas, and Skylark, nesting on open ground. Numbers of nests varied between years, but as survey effort differed across years, information on population size or population changes cannot and should not be inferred from these numbers. However, previous studies have shown severe declines in many upland moorland bird species (Henderson et al., 2004; Sim et al., 2005), illustrating the pressing need to maintain and enhance the habitats of this avian community.

The average Meadow Pipit clutch size of 3.85 recorded in this study is slightly lower than the average reported in other studies across the UK and Europe, where clutch size appears to range from approximately 4.04 to 5.38 (Pedroli, 1978; Seel and Walton, 1979; Halupka, 1998; Pavel et al., 2000; Evans et al., 2005). Geographical variation in clutch size might explain part of this difference, as Meadow Pipit clutch size has been shown to decrease with altitude (Coulson, 1956; Rose, 1982). However, some of this difference remains unexplained, as previous studies conducted at similar altitudes showed larger mean clutch sizes than those reported in this study. For example, Coulson (1956) found an average clutch size of 4.07 at altitudes of over 305 meters (1000 feet). Similarly, Rose (1982) recorded a mean clutch size of 4.31 at 200-300m, and 4.07 at 400-600m.

No significant interannual variation in clutch size was recorded in this study, which is consistent with previous findings (for example Halupka (1998)). Average brood size, which showed only minor differences between years in this study, was consistent with previous studies (see for example Rose (1982)). Nest success in Meadow Pipit ranged from 6% to 62% (22% across years) across the nine years of study, and statistical tests on nest daily failure rate confirmed this significant interannual variability in breeding success. A previous study on Meadow Pipits in Switzerland reported a higher overall nest success of 56% (Pedroli, 1978), although this study did not employ the Mayfield method, meaning the success rates are not directly comparable. Two other studies on Meadow Pipits in the UK did calculate nest success using the Mayfield method, allowing direct comparison to the nest success rates calculated in this study. Evans et al. (2005) reported nest success rates of 62% and 45% in the early and late breeding season respectively; higher than the average nest success rate found in our current study, but within the range of values found in individual years. Fletcher et al. (2010) reported nest success rates of 52% (under predator control) and 28% (no predator control). Our study site does not receive any predator control, and our nest success rate of 22% appears on the low side, but is nevertheless relatively consistent with the 28% found in this Evans et al. (2005) study.

For Stonechat, the mean clutch size found in this study (4.93) falls within the range of average clutch sizes reported in other European studies (ranging from 4.88 to 5.50 in Fuller and Glue (1977); Revaz et al. (2008) and van Oosten (2016)).

No significant interannual variability in clutch size was found, which is consistent with Revaz et al. (2008), who reported no difference in mean clutch size between years in Stonechats in Switzerland. The average brood size for the current study (4.58), that showed minor interannual differences between two years only, is also in line with previous findings for Stonechats in the UK. For example, Fuller and Glue (1977) showed an average brood size of 4.34 in a study of 489 nests, and Greig-Smith (1985) an average of 4.30 in a study of 69 nests. Stonechat showed a higher average breeding success (38%) compared to both Meadow Pipit and Whinchat, although substantial interannual variability was seen (from 22% to 100%), with statistical tests showing significant differences in daily failure rates between many of the study years. Although in some study years average nest success was as high as recorded in other studies, on average Stonechat nest success appears on the lower end of success values reported in other European populations, where reported mean success rates ranged from 38% to 59% (Flinks et al., 2008; Revaz et al., 2008). This discrepancy, however, might be caused by methodological differences between the studies, as these two studies did not use the Mayfield method to derive nest success, and true next success in these populations is therefore likely to be lower.

Clutch sizes in Whinchats are known to vary strongly across Europe, and average clutch sizes as high as 6.75 have been reported in northern Russia (Shitikov et al., 2015). The clutch sizes, and correspondingly the brood sizes, reported in the current study are in line with values recorded previously in the UK (Fuller and Glue, 1977). Average nest success and interannual variability in Whinchat was similar to Meadow Pipit, showing an average success of 25% and ranging from 4% to 65% across years. The very low 4% nest success in this study, which occurred in 2016, was due to high predation rates, likely due to the fact that in this year, all Whinchat nests were located in relatively close proximity to one another in one area within the study site, and therefore suspectedly being predated by one or few predators roaming this area. The range of nest success rates we record is similar to values reported in previous studies, where nest success rate of 66% through territory observations, whereas Grüebler et al. (2012) show nest survival rates ranging from less than 10% to over 70% depending on land management regimes.

In the above comparisons, some limitations to the findings need to be acknowledged. In the first instance, in the first three years of this study sample sizes were low, especially for estimates of clutch size. Therefore, inaccuracies in the annual breeding parameters are more likely for these years. However, the mean reproductive parameters across all years are based on a large number of nests, and therefore represent an accurate representation of the study population. Another limitation in this study is that Stonechat and Meadow Pipit often produce second broods, resulting in the potential of pseudo-replication in the analysis of breeding parameters; as birds were not individually marked in this study, double-brooding could not be monitored and therefore could not be considered. Future work should focus on quantifying double-brooding, and explore its effect on the estimates of breeding parameters. It is also important to note that methodological differences (such as the use of the Mayfield method) and differences in land management (for example predator control) between the studies we compare above can affect the estimated nest success, and studies are therefore not always directly comparable. As studies are often conducted over the course of a few years only, random events such as extreme weather conditions can also affect the estimates of average breeding success (see for example Indykiewicz (2015) and Fisher et al. (2015)).

Anecdotal evidence from the site in this study suggests that the most important cause of nest failure in Meadow Pipit, Stonechat and Whinchat is predation. Although some other causes of nest failure were recorded, most notably a high number of Stonechat nestlings found dead in 2012 following unusually high levels of rainfall, by far the majority of unsuccessful nests were due to predation (i.e. nests found empty before the predicted fledging date, regularly with traces of feathers found in/near the nest site). Confirmed predators on the site include Carrion Crows (*Corvus corone*) and Adder (*Vipera berus*), which were both seen to predate nests during a trial of the use of nest cameras. Other known predators include mammals such as foxes (*Vulpes vulpes*) and badgers (*Meles meles*), which are regularly seen on site and can be distinguished at the nest site from other predators as foxes and badgers do not simply take eggs or chicks from the nest, but show obvious nest destruction, with a habit of ripping out the nest cup from the surrounding vegetation (pers.obs., Part and Wretenberg (2002)).

In all three monitored bird species, our annual reported nest survival rates fall within the range of values reported in the literature, indicating that nest survival rates on Dartmoor appear to be are relatively consistent with those found previously in these species in other locations, although causes of failure could vary between sites. Future work should focus on building a better understanding of other breeding bird species on Dartmoor. The choice of focal species in this study was constrained by the interests and expertise of the field volunteers, and therefore an assessment of the breeding parameters of other key moorland species could not be included in this study. More work is needed to understand the breeding habits of other species of conservation interests, in particular declining species such as Cuckoo, Skylark and Snipe. Most importantly, as this research focused on breeding parameters only, more research is needed to explore the relationship between breeding success and the population trends of Meadow Pipit, Stonechat and Whinchat, in order to better understand the importance of breeding success and other factors in driving population sizes of these species. Exploring the avian diversity and breeding parameters on other Dartmoor upland moorland sites, as well as trials on the effects of land management on breeding parameters, would also be highly informative for informing future conservation efforts.

In summary, this study assessed the avian diversity of a Dartmoor upland moorland study site, and provided baseline estimates of the breeding parameters of three of the most common species; Meadow Pipit, Stonechat and Whinchat. A total of 34 species were recorded, suggesting a relatively high diversity of bird species compared to other studies of similar spatial size in comparable habitats. Breeding parameters recorded here, with some exceptions, are broadly in line with previous studies in other locations. We reported no interannual variation in clutch size, and while some significant interannual differences were present in brood size, variation was relatively minor. Breeding success (measured as daily failure rate) showed significant differences between some, but not all, study years in all three species. The diversity of bird species found in this study highlights the fact that conservation management decisions should consider the entire breeding bird community wherever possible. In particular, the diversity of nest habitats and niches emphasises the need for maintaining sufficient vegetation diversity on moorland sites to allow bird diversity to be maintained in the future. This will be of fundamental importance in order for National Parks and other protected areas to deliver on the UK government's ambition of improving the status of UK wildlife. We recommend that land owners and managers on Dartmoor and other upland sites use the information on species and nest habitats presented here and in other scientific studies to ensure that the diversity of habitats for nesting sites is safeguarded when management changes are made. Most importantly, land burning (which is a common management practice on Dartmoor), if and where needed, should be carried out in a rotation pattern which ensures that habitat patches of various ages (and therefore different vegetation heights and species composition) are maintained. We recommend that any changes in management are accompanied by the monitoring of breeding parameters of key species wherever possible, to ensure that no adverse effects of these land management practices occur on avian wildlife. More broadly, we hope that the information presented in this study can be used as a helpful baseline against which to compare, measure and evaluate changes in avian diversity and reproductive output, in response to local conservation management decisions or other factors, both in Dartmoor and the UK more widely.

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# References

Beavan, S. & Lock, M. Devon Birds Atlas 2007-2013. Devon Birds, 2016.

- Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J., & Kunin, W. E. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313(5785):351–354, 2006.
- Bracken, F., McMahon, B., & Whelan, J. Breeding bird populations of Irish peatlands. *Bird Study*, 55:169–178, 2008.
- Broyer, J., Curtet, L., & Boissenin, M. Does breeding success lead meadow passerines to select late mown fields? *Journal of Ornithology*, 153:817–823, 2012.
- Chastel, O., Weimerskirch, H., & Jouventin, P. High annual variability in reproductive success and survival of an Antarctic seabird, the Snow Petrel Pagodroma nivea - A 27-year study. Oecologia, 94(2):278–285, 1993.
- Combrink, L., Combrink, H., Botha, A., & Downs, C. Habitat structure and diversity influence the nesting success of an endangered large cavity-nesting bird, the Southern Ground-hornbill. *Koedoe*, 59:1–8, 2017.
- Coulson, J. C. Mortality and egg production of the Meadow Pipit with special reference to altitude. *Bird Study*, 3(2):119–132, 1956.
- Crick, H. Q., Baillie, S. R., & Leech, D. I. The UK Nest Record Scheme: Its value for science and conservation. *Bird Study*, 50(3):254–270, 2003.

- Dallimer, M., Marini, L., Skinner, A., Hanley, N., Armsworth, P., & Gaston, K. Agricultural land-use in the surrounding landscape affects moorland bird diversity. Agriculture, Ecosystems and Environment, 139:578–583, 2010.
- Dartmoor National Park Authority. Birds of the open moor, 2011.
- Dartmoor National Park Authority. Dartmoor National Park Management Plan 2014-2019., 2014.
- Eaton, M., Aebischer, N., Brown, A., Hearn, R., Lock, L., Musgrove, A., Noble, D., Stroud, D., & Gregory, R. Birds of conservation concern 4: The population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds*, 108:708–746, 2015.
- Environment Act 1995. https://www.legislation.gov.uk/ukpga/1995/25/section/1/enacted - Accessed November 2018.
- Evans, D. M., Redpath, S. M., & Evans, S. A. Seasonal patterns in the productivity of Meadow Pipits in the uplands of Scotland. *Journal of Field Ornithology*, 76(3): 245–251, 2005.
- Ferguson-Lees, J., Castell, R., & Leech, D. A field guide to monitoring nests. BTO, Thetford, 2011.
- Fisher, R., Wellicome, T., Bayne, E., Poulin, R., Todd, L., & Ford, A. Extreme precipitation reduces reproductive output of an endangered raptor. *Journal of Applied Ecology*, 52:1500–1508, 2015.
- Fletcher, K., Aebischer, N. J., Baines, D., Foster, R., & Hoodless, A. N. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecology*, 47:263–272, 2010.
- Flinks, H., Helm, B., & Rothery, P. Plasticity of moult and breeding schedules in migratory European Stonechats Saxicola rubicola. Ibis, 150:687–697, 2008.
- Fuller, R. J. & Glue, D. E. The breeding biology of the Stonechat and Whinchat. Bird Study, 24(4):215–228, 1977.
- Goodwin, C. E. D., Hodgson, D. J., Al-Fulaij, N., Bailey, S., Langton, S., & Mcdonald, R. A. Voluntary recording scheme reveals ongoing decline in the United

Kingdom Hazel Dormouse *Muscardinus avellanarius* population. *Mammal Review*, 47(3):183–197, 2017.

- Greig-Smith, P. Weight differences, brood reduction, and sibling competition among nestling Stonechats Saxicola torquata (Aves: Turdidae). Journal of Zoology, 205 (3):453–465, 1985.
- Grüebler, M. U., Schuler, H., Horch, P., & Spaar, R. The effectiveness of conservation measures to enhance nest survival in a meadow bird suffering from anthropogenic nest loss. *Biological Conservation*, 146:197–203, 2012.
- Halupka, K. Nest-site selection and nest predation in Meadow Pipits. Folia Zoologica, 47(1):29–37, 1998.
- Hayhow, D., Bond, A., Douse, A., Eaton, M., Frost, T., Grice, P., Hall, C., Harrist,
  S., Havery, S., Hearn, R., Noble, D., Oppel, S., Williams, J., Win, I., & Wotton,
  S. The state of the UK's birds 2016. *RSPB*, *BTO*, *WWT*, *DAERA*, *JNCC*, *NE*, *NRW and SNH*, *Sandy*, *Bedfordshire*., 2016a.
- Hayhow, D. B., Burns, F., Eaton, M. A., Al Fulaij, N., August, T. A., Babey, L., Bacon, L., Bingham, C., Boswell, J., Boughey, K. L., Brereton, T., Brookman, E., Brooks, D. R., Bullock, D. J., Burke, O., Collis, M., Corbet, L., Cornish, N., De Massimi, S., Densham, J., Dunn, E., Elliott, S., Gent, T., Godber, J., Hamilton, S., Havery, S., Hawkins, S., Henney, J., Holmes, K., Hutchinson, N., Isaac, N. J. B., Johns, D., Macadam, C. R., Mathews, F., Nicolet, P., Noble, D. G., Outhwaite, C. L., Powney, G. D., Richardson, P., Roy, D. B., Sims, D., Smart, S., Stevenson, K., Stroud, R. A., Walker, K. J., Webb, J. R., Webb, T. J., Wynde, R., & Gregory, R. D. The state of Nature 2016. The State of Nature partnership, 2016b.
- Hazler, K. R. Mayfield Logistic Regression: A practical approach for analysis of nest survival. *The Auk*, 121(3):707–716, 2004.
- Henderson, I. G., Fuller, R. J., Conway, G. J., & Gough, S. J. Evidence for declines in populations of grassland-associated birds in marginal upland areas of Britain. *Bird Study*, 51:12–19, 2004.
- HM Government. A Green Future: Our 25 year plan to improve the environment., 2018.

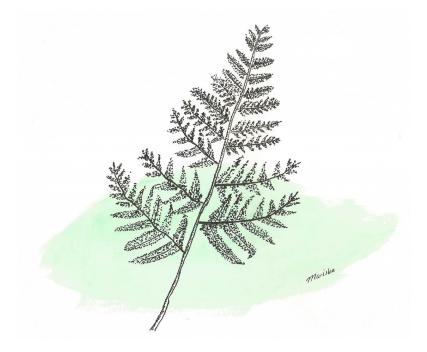
- Indykiewicz, P. Egg losses caused by cold snap in the Black-Headed Gull Chroicocephalus ridibundus L. Polish Journal of Ecology, 63:460–466, 2015.
- Johnson, D. Estimating nest success: The Mayfield method and an alternative. *The Auk*, 96:651–661, 1979.
- Klomp, H. The determination of clutch size in birds: A review. Ardea, 58(1-2): 1–121, 1970.
- Lack, D. The significance of clutch-size. *Ibis*, 89(2):302–352, 1946.
- Mayfield, H. F. Suggestions for calculating nest success. The Wilson Bulletin, 87 (4):456–466, 1975.
- Newbold, T., Hudson, L. N., Arnell, A. P., Contu, S., De Palma, A., Ferrier, S., Hill,
  S. L. L., Hoskins, A. J., Lysenko, I., Phillips, H. R. P., Burton, V. J., Chng, C.
  W. T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz,
  K., Simmons, B. I., Whitmee, S., Zhang, H., Scharlemann, J. P. W., & Purvis,
  A. Has land use pushed terrestrial biodiversity beyond the planetary boundary?
  a global assessment. *Science*, 353(6296):288–291, 2016.
- Newey, S., Mustin, K., Bryce, R., Fielding, D., Redpath, S., Bunnefeld, N., Bronwen, D., & Irvine, R. Impact of management on avian communities in the Scottish highlands. *PLoS ONE*, 115:e0155473, 2016.
- Newson, S. E., Evans, K. L., Noble, D. G., Greenwood, J. J. D., & Gaston, K. J. Use of distance sampling to improve estimates of national population sizes for common and widespread breeding birds in the UK. *Journal of Applied Ecology*, 45:1330–1338, 2008.
- Newton, I. Experiments on the limitations of bird breeding densities: a review. *Ibis*, 136:397–411, 1994.
- ONS. 2011 Census: Characteristics of National Parks., 2011.
- Part, T. & Wretenberg, J. Do artificial nests reveal relative nest predation risk for real nests? *Journal of Avian Biology*, 33:39–46, 2002.
- Pavel, Â., Buresï, S., Weidinger, K., & Kovarï, P. Distraction displays in Meadow Pipit (Anthus pratensis) females in central and Northern Europe. Ethology, 106: 1007–1019, 2000.

- Pedroli, J.-C. Breeding success of the Meadow Pipit Anthus pratensis in the Swiss Jura. Ornis Scandinavica, 9(2):168–171, 1978.
- R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2015.
- Revaz, E., Schaub, M., & Arlettaz, R. Foraging ecology and reproductive biology of the Stonechat *Saxicola torquata*: Comparison between a revitalized, intensively cultivated and a historical, traditionally cultivated agro-ecosystem. *Journal of Ornithology*, 149:301–312, 2008.
- Robinson, R. A. BirdFacts: Profiles of birds occurring in Britain & Ireland. BTO Research Report 407, 2017.
- Rose, L. N. Breeding ecology of British pipits and their Cuckoo parasite. *Bird Study*, 29(1):27–40, 1982.
- Rotenberry, J. T. & Wiens, J. A. Reproductive biology of shrubsteppe passerine birds: Geographical and temporal variation. *The Condor*, 91(1):1–14, 1989.
- Royal Society for the Protection of Birds. East Dartmoor Moorland Breeding Bird Survey 2016. 2017.
- Sanz, J. J. Effects of geographic location and habitat on breeding parameters of Great Tits. *The Auk*, 115(4):1034–1051, 1998.
- Seel, D. C. & Walton, K. C. Numbers of Meadow Pipits Anthus pratensis on mountain farm grassland in North Wales in the breeding season. *Ibis*, 121:147– 164, 1979.
- Shitikov, D. A., Vaytina, T. M., Gagieva, V. A., & Fedchuk, D. V. Breeding success affects site fidelity in a Whinchat *Saxicola rubetra* population in abandoned fields. *Bird Study*, 62:96–105, 2015.
- Sim, I. M. W., Gregory, R. D., Hancock, M. H., & Brown, A. F. Recent changes in the abundance of British upland breeding birds. *Bird Study*, 52:261–275, 2005.
- Sullivan, T. & Sullivan, D. Fertilisation, cattle grazing and voles: collapse of meadow vole populations in young forests? Wildlife Research, 41:367–378, 2014.
- van Oosten, H. H. Comparative breeding biology of three insectivorous songbirds in Dutch dune grasslands. Ardea, 104(3):199–2012, 2016.

Wood, K. A., Newth, J. L., Hilton, G. M., Nolet, B. A., & Rees, E. C. Inter-annual variability and long-term trends in breeding success in a declining population of migratory swans. *Journal of Avian Biology*, 47:597–609, 2016.

# Chapter 3

# Timing of Meadow Pipit, European Stonechat and Whinchat breeding activity and potential conflicts with upland vegetation management



"Five eggs, pen-scribbled o'er with ink their shells Resembling writing scrawls which fancy reads As nature's poesy and pastoral spells" The Yellowhammer's nest - John Clare

# Timing of Meadow Pipit, European Stonechat and Whinchat breeding activity and potential conflicts with upland vegetation management

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Short title: Overlap between timing of breeding and vegetation management

**Keywords:** breeding success - burning - Agri-Environment Scheme - moorland - Bracken control - ground-nesting birds

# 3.1 Abstract

Current permitted timings of upland burning and Bracken control in land management practices are likely to result in nest failures in populations of some upland breeding bird species. The aim of this study was to quantify the timing of breeding activity of Meadow Pipit (Anthus pratensis), European Stonechat (Saxicola rubicola) and Whinchat (Saxicola rubetra) and assess overlap with the timing of two potentially damaging upland land management practices; burning and Bracken control. 498 nests were monitored across a  $4.3 \mathrm{km}^2$  area of upland Dartmoor (southwest England) between 2008 and 2014, and the onset and timing of breeding activity, and variation between species and years were quantified. Overlap between breeding activity and burning and Bracken control was then quantified for several realistic scenarios of the timing of these upland moorland management practices. We show considerable overlap between potentially damaging upland management practises and breeding activity of European Stonechat, Meadow Pipit and Whinchat. In all three permitted burning cessation scenarios (weeks 11, 13 and 15) there was overlap with breeding activity of European Stonechat and Meadow Pipit. The commencement of Bracken control in July also overlapped substantially with breeding activity, with half of Whinchat nests and more than a quarter of European Stonechat and Meadow Pipit nests potentially affected. Overlap would be much reduced if Bracken control instead commenced in August. We illustrate the potential for frequent and substantial overlap between breeding activity and specific current upland land management practices. These practices may be causing nest failure for significant numbers of upland breeding birds each year. We suggest a change in the permitted burning and Bracken control timing, where the effectiveness of the management techniques is not unduly compromised.

## 3.2 Introduction

Vegetation management is an important technique for conservationists, land managers and farmers. It is generally applied in order to manage changes in habitat structure (Ausden, 2007), and can provide a wide range of benefits for biodiversity and human ecosystem services, for example by boosting the population of species of conservation concern (Butchart et al., 2006), increasing numbers of game for hunting (Bergman et al., 2014; Ferreira et al., 2014), and reducing pest populations (Lambert et al., 2008; Gurr et al., 2017). Methods of vegetation management include for example mowing, scrub removal, grazing, manipulation of water levels, and the sowing of additional seed or planting of new seedlings (Ausden, 2007).

In the UK uplands, active management of habitats has been carried out for thousands of years, primarily to provide grazing for livestock, maintain high densities of game birds, or for biodiversity conservation through preventing widespread vegetation succession on moorlands (Webb, 1998). The landscapes found in uplands today are therefore strongly shaped by this management (Yallop et al., 2006; Chapman et al., 2009). Such habitat management for biodiversity and ecosystem services is not only carried out by conservationists, but also encouraged by government through incentive schemes for farmers and landowners. In UK uplands, this is realised in particular through Agri-Environment Schemes (AES); a 2009 report by Natural England showed that over 80% of upland heath and blanket bog in England is under AES agreements (Natural England, 2009).

Two widely applied vegetation management techniques on UK moorlands and uplands are vegetation burning and the control of Bracken (*Pteridium aquilinum*) (Natural England, 2009). Burning provides new spring growth preferred by grazing livestock, and where applied in a well-controlled manner and on a long rotation can create mosaics of dwarf shrubs of different ages, which can be desirable for biodiversity conservation (Natural England, 2009, 2013; Allred et al., 2011). It can provide or maintain habitats for early successional and upland specialist species, such as fritillary butterflies, other insects and certain moorland birds (Natural England, 2009; Bargmann et al., 2015; Bubova et al., 2015). For example, Douglas et al. (2017) showed that Golden Plover (*Pluvialis apricaria*) increases in abundance when larger areas are burned across years. However, potential negative side-effects of burning on species and wider ecosystem services also needs to be acknowledged. The negative effects on carbon storage and flood protection need to be considered alongside the positive effects on the densities of species such as Red Grouse (*Lagopus lagopus*  *scotica*) (Robertson et al., 2017). Additionally, whilst some species benefit from the open vegetation structure created soon after burning, other species rely on later successional stages of vegetation growth, and are therefore negatively affected by land burning. For example, a study of burning on grasslands in Kansas showed that whilst Upland Sandpiper (*Bartramia longicauda*) were more abundant in recently burnt areas, three other grassland species including Eastern Meadowlark (*Sturnella magna*) showed lower abundances (Powell and Busby, 2013).

From a conservation perspective, Bracken can be desirable through providing habitat for various species of conservation concern, such as Pearl-bordered Fritillary (*Boloria euphrosyne*), Nightjar (*Caprimulgus europaeus*) and Whinchat (*Saxicola rubetra*) (Burge and Kirkwood, 1992; Natural England, 2008a). On the other hand, stands of Bracken are regularly controlled as they can be considered detrimental for various reasons. Bracken can be invasive on heathlands and in ericaceous and acidic grassland habitats, consequently dominating large areas and thereby excluding most specialist species of conservation concern (Natural England, 2008a; Alday et al., 2012). From an agricultural perspective, Bracken reduces the extent of grass and dwarf-shrubs available for livestock grazing (Pakeman et al., 2001; Natural England, 2008b). Furthermore, AES can fund the removal of Bracken and other scrub from Scheduled Ancient Monuments as it is thought Bracken rhizomes can damage archaeological features (Crow and Moffat, 2005; Natural England, 2013).

In recent decades, Bracken control has been achieved mainly by aerial chemical spraying, but this practise is now in decline since the EU withdrew the approval for the use of the main active chemical, asulam (Regulation (EU) No 1045/2011, 2011). Spraying nevertheless is still widespread through both Emergency Authorisations for asulam use (Regulation (EC) No 1107/2009, 2009), and the use of other chemical agents such as glyphosate, for which there is also an emerging environmental concern (Annett et al., 2014; Bai and Ogbourne, 2016; Myers et al., 2016). An alternative widespread Bracken control method is the cutting and crushing of vegetation, achieved through both manual (e.g. cutting with scythes or bashing with sticks) and mechanical means (e.g. using motorised tools, quad bikes or rollers) (Crow and Moffat, 2005; Maren et al., 2008; Natural England, 2008b).

Over recent decades many upland breeding birds found partly or exclusively in upland habitats in the UK have shown substantial declines (Henderson et al., 2004; Sim et al., 2005). For example, since 1988 Ring Ouzel (*Turdus torquatus*) have suffered a 72% decline, and since 1995, Whinchat, Cuckoo (*Cuculus canorus*) and Meadow Pipit (*Anthus pratensis*) have declined by 55%, 49% and 17% respectively

(Hayhow et al., 2014). Several ecological factors, such as predation, in part explain these population declines, and it is known that both phenology and breeding success can affect population size in upland birds (Fletcher et al., 2010; Pearce-Higgins et al., 2010; Sim et al., 2013). Both vegetation burning and Bracken control practices have been important management techniques in upland areas for many years, however, changes in the extent, frequency and technique of upland management potentially impact greatly on several upland breeding bird species (see for example Tharme et al. (2001)). Within most English upland national parks there has been an increase in the frequency with which areas of moorland are burned, and the extent of new burns increased significantly between the 1970s and 2000 (Yallop et al., 2006), with further increases since 2000 (Douglas et al., 2015). In addition to indirect impacts, such as reductions in the availability of suitable breeding habitats, direct impacts of vegetation management (e.g. the destruction of nests) needs to be considered. Given that, as mentioned above, phenology and breeding success can affect population size, understanding on the potential impact of overlap between land management practices and timing of breeding is needed, in order to help prevent further species declines.

Nests are inevitably destroyed when practices such as land burning and Bracken control are implemented during the breeding season. Compared to spraying, the most practised alternative Bracken control method of cutting and crushing is likely to have much more severe direct consequences for nesting birds. This is due to the fact that in order to be effective, this practice needs to be timed earlier in the summer compared to spraying, and evidence shows that at most sites, it has to be repeated twice per year and across multiple years in order to achieve optimal control (Stewart et al., 2008; Natural England, 2008b; Milligan et al., 2016). As chemicals used for Bracken control are being increasingly banned due to environmental concern (Regulation (EU) No 1045/2011, 2011), the use of mechanical control could be expected to become more widespread, thereby potentially increasing the conflict between mechanical Bracken control and bird breeding.

The timing of vegetation management practices is regulated through AES prescriptions and the Heather and Grass Burning Code, and can be constrained by setting commencement and cessation dates (DEFRA, 2007b; Natural England, 2015). Although these are designed to avoid overlap with the bird breeding season whilst still achieving the desired management aims, they do often not consider interannual variation in timing of breeding naturally shown by birds as a plastic response to interannual variations in environmental conditions (Davies and Deviche, 2014). Furthermore, a trend to earlier breeding in a range of bird species in response to climatic change, see for example Both and te Marvelde (2007); Charmantier et al. (2008), could result in increased overlap between bird breeding activity and vegetation management in the future.

Studies of the direct impact of vegetation burning and cutting on nest outcomes are scarce (as experimental field studies with an inevitable outcome of next failure would be unethical), but the fact that these management practices result in breeding failure has been evidenced through historical and observational studies, particularly in ground-nesting farmland birds negatively affected by mowing. For example, extensive observational studies in Switzerland have highlighted the direct impact of early mowing on Whinchat breeding success (e.g. Müller et al. (2005); Grüebler et al. (2012); Strebel et al. (2015)). Similar effects have been described for other ground-nesting birds such as Corncrake (*Crex crex*) and breeding waders (Vickery et al., 2001). The direct impact of burning has been illustrated by several studies on grass prairies in the United States, which showed high failure rates due to controlled land burning across a range of bird species (Erwin and Stasiak, 1979; Kruse and Piehl, 1984).

To better understand how risk to breeding birds varies with timing of vegetation management, it is possible to combine known breeding data and information on land management timings, and use these data as a tool to quantify the potential negative impact of land management on nesting birds. Whilst the general UK-wide timing of breeding of most UK species is well-established and available through long term nest recording studies, site-specific analysis of the overlap between nesting and land management is not generally readily available. Such information is essential for political leverage in order for conservationists to successfully influence local land-management decision-making regarding for example, the timing of burning and bracken control on upland moorlands. In this case study in Dartmoor National Park (UK), we use 7 years of field data collected on ground-nesting birds, and quantify onset and timing of bird breeding activity for three co-occurring widespread UK upland birds, Meadow Pipit, European Stonechat (Saxicola rubicola, hereafter referred to as "Stonechat") and Whinchat. We combine this with information on land management practices to assess overlap between breeding activity and currently permitted timings of burning and Bracken control.

# 3.3 Methods

Overlap between timing of vegetation management and bird breeding activity was calculated using timing of breeding data across all years combined. The rationale behind this is that a retrospective view, quantifying overlap in past individual years with variable breeding onset, is not informative for advising future vegetation management guidelines, as the onset of breeding in future years cannot be reliably predicted. Instead, it is necessary to quantify the extent of conflict between bird breeding and land management that could be expected in any hypothetical future years. Therefore, by analysing overlap in timing across all years, interannual variability is incorporated, and we obtain an indication of the full potential timing conflict that could be expected in future years, regardless of breeding onset.

#### 3.3.1 Study site

The study was conducted between 2008 and 2014 on a 4.3km<sup>2</sup> area within Dartmoor National Park, southwest England (50° 31' 20"N, -3° 51' 30"W) located at 211-457 meters above sea level. The habitat is predominantly open, mostly comprising of acid grassland and dwarf shrubs with isolated low trees, interspersed by extensive areas of Bracken. On this study site and in Dartmoor National Park more widely, land owners and commoners carry out vegetation burning yearly on a rotational basis, following the regulations for timing and burning extents from the Heather and Grass Burning Code (DEFRA, 2007b). Bracken is controlled by land owners, commoners and conservation organisations as and where need arises.

#### 3.3.2 Bird breeding

Nests of Stonechat, Meadow Pipit and Whinchat were found by intensive searching guided by observing breeding behaviours such as birds carrying nest material or food. Each nest was visited between 1 and 8 times whilst active, and after fledging where relevant, in order to monitor breeding and determine nest outcome. At each nest visit the breeding stage and contents were recorded following the protocol and coding system of the British Trust for Ornithology (BTO) Nest Record Scheme (NRS). Nest recorders with experience in ageing passerine nestlings determined developmental stage according to the NRS status codes, which records the growth of nestlings based on feather development (Crick et al., 2003). Figure 3.1 shows photographic examples of nestling development recorded at this study site. For further photographic examples and description of day-by-day nestling feather development

<4 dph	4 dph	5 dph	6 dph
No photographic record from this study		No photographic record from this study	
Eyes closed, mostly naked with little down, no pin feathers emerging	Eyes mostly still closed. Body downy, first sign of emergence of pins from skin	Eyes beginning to partially open, pin feathers emerging further from skin	Eyes noticeably open, pin feathers noticeably emerged.
NRS code: "naked", "blind"/"downy")	NRS code: "blind", "downy"/"in pin"	NRS code: "in pin"	NRS code: "eyes open", "in pin")
7 dph	8 dph	>	•8 dph
		No photographic record from this study	
Tips of feathers beginning to unsheathe from pins NRS code: "Feathers small"	Tips of feathers continuing to unsheathe from pins NRS code: "Feathers small"	Between 9 days post-hatching and fledging, body growth and feather emergence continues During these days, NRS codes progress from "Feathers small" to "Feathers medium" (1/3 to 2/3 of each feather emerged), "Feathers large" (more than 2/3 emerged from sheath), and finally "Ready to fledge".	

**Figure 3.1:** Photographic examples of nestling development (recorded as days post-hatching, dph) for a selection of Meadow Pipit nestlings for which hatching was observed, and exact age therefore known. Descriptions of the relevant BTO Nest Record Scheme (NRS) codes used by nest recorders to record developmental progress are included.

Timing of hatching and fledging for each nest was determined from the field observations and allocated a sequential week number, with week one representing

1-7 January and week 52 representing 25-31 December. Hatch week was determined either from finding eggs hatching during a nest visit (which only happened in few instances), or was back-calculated based on nestling developmental stage when nestlings were first encountered at a visit. Deriving hatch week from nestling developmental stage was deemed appropriate as feather development follows a predictable day by day pattern, and was shown to be a reliable indicator for ageing passerine nestlings in for example Barn Swallow (*Hirundo rustica*) and Sprague's Pipit (Anthus spraqueii) (Jongsomjit et al., 2007; Morales Fernaz et al., 2012). Some developmental delay of feather tracts is possible (e.g. by 1 to 4 days in Barn Swallow) under bad weather conditions (Morales Fernaz et al., 2012), which may lead to some nests with an inaccurate estimate of derived hatch week, but this was deemed unlikely to have caused any substantial error in the data as little exceptionally bad weather was observed during the years of the study. Fledging week was determined by comparing the last visit date in which nestlings were recorded alive in the nest, and the visit date at which the nest was found empty. For nests in which hatch week could not be accurately determined, but fledge week could be, hatch week was assigned by subtracting two weeks from the fledge week as for all three study species young fledge at approximately two weeks old.

We determined the full period of breeding activity from nest building through to fledging for each nest using the assigned hatch and fledge weeks, with onset of breeding being 4 weeks before the hatch week (allowing for 1 week of nest building, 1 week of egg laying and 2 weeks of incubation). The length of the full breeding season for each species was defined as the period between the week of onset of the first nest and the week of fledging of the last nest. As many birds are able to wait for cues or optimal conditions before initiating egg laying or incubation (Visser et al., 2010), we used hatching date as our metric for examining differences between species in breeding activity. To identify the peak of the breeding season and to compare timing of breeding between species we calculated the median hatch week for each species separately, across all years combined. The interquartile range was quantified in order to extract the core breeding period for each species; defined here as the weeks around the median hatch week during which 50% of all nests hatch.

#### 3.3.3 Vegetation management

#### Burning

In England, the Heather and Grass Burning Code prescribes that upland vegetation burning is only permitted between 1 October and 15 April (i.e. the last week burning can take place is week 15). In our study area, which is situated within a National Park, the Dartmoor National Park Authority recommends that no burning takes place after 31 March (week 13) specifically to reduce overlap with the ground-nesting bird breeding season (DEFRA, 2007a; Dartmoor National Park Authority, 2011). No exact data on burning dates on Dartmoor were available for the purposes of this study, but anecdotal evidence suggests that the voluntary burning code is mostly adhered to, although burning generally takes place at the end of the burning period. This is because at this time the vegetation, weather and soil are deemed to be in optimal condition for burning. For each species, we calculated the number of weeks of overlap between the bird breeding period and weeks in which burning was permitted. As detailed above, the nest data for all years were combined for these analyses. In addition, we calculated the percentage of nests that were active during weeks when burning was permitted, using three scenarios of cessation of burning; week 11 (the week of 15 March), 13 (31 March) and 15 (15 April). We also quantified the overlap with burning by breeding stage (building, laying, incubation and nestling).

#### Bracken control

Chemical Bracken control is undertaken from mid-July when fronds are fully unfurled, until fronds senesce in late September (Natural England, 2008b). Cutting and crushing is most effective when carried out twice within the first year of control (once in May or June and again in July or August), and annually thereafter (Scotland's Environmental and Rural Services, 2008). Both mechanical and chemical control of Bracken are regularly supported through Agri-Environment Schemes (Natural England, 2016), and on Sites of Special Scientific Interest (SSSIs) consent to carry out Bracken control can be required (Natural England, 2008b). Consent dates vary between agreements, but on Dartmoor consent is known to have been granted for as early as 1 July (pers. comm. with local landowner). Using data for all years combined, we calculated the overlap between the Bracken control consent period and bird breeding activity under two scenarios, an early but permissible week 26 (starting 1 July) and a later scenario; week 31 (1 August).

## 3.3.4 Statistical analyses

To test for differences in the median hatch weeks of the three species, Kruskal-Wallis rank sum tests were used with pairwise Mann-Whitney U tests with Bonferroni correction used as post-hoc tests. All data were analysed using R version 3.0.2 (R Core Team, 2015).

# 3.4 Results

#### 3.4.1 Timing of breeding activity

Between 2008 and 2014, timing of breeding was recorded for a total of 498 nests; 268 Meadow Pipit nests, 145 Stonechat nests and 85 Whinchat nests. The order of breeding onset between species was consistent throughout all years of the study, with Stonechat commencing breeding first in all years followed by Meadow Pipit then Whinchat. Figure 3.2 shows the numbers of nests hatched in each week for all years combined, with the earliest hatch weeks for each year shown in Figure 3.3. All species showed interannual variation in onset of breeding, with onset between years varying by up to 4 weeks for Stonechat, 2 weeks for Meadow Pipit and 3 weeks for Whinchat. Over years combined the median earliest week of onset of breeding, was week 12 for Stonechat, week 14 for Meadow Pipit and week 18 for Whinchat.

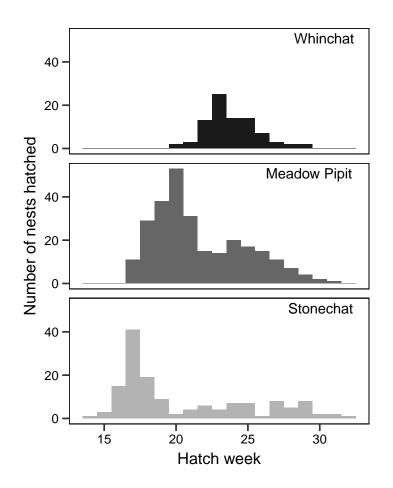


Figure 3.2: The number of nests hatched by week for Whinchat, Meadow Pipit and Stonechat nests between 2008 and 2014. Weeks were numbered according to week one representing 1 January to 7 January.

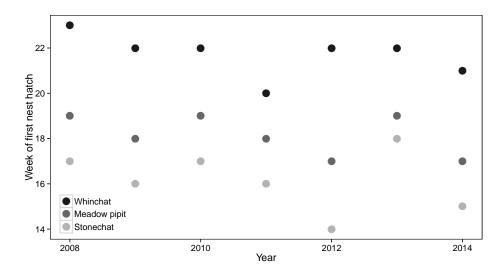


Figure 3.3: Earliest week of hatching for Whinchat, Meadow Pipit and Stonechat nests between 2008 and 2014. Each data point represents the week in which the first nest hatched for that year and species. Weeks were numbered according to week one representing 1 January to 7 January.

Between years, the length of the breeding season, from the onset of the first nest to the fledging of the final nest, ranged from 15 to 23 weeks in Stonechat, with the average breeding season length being 19 weeks. For Meadow Pipit, the length of the breeding season was between 12 and 20 weeks, with an average of 17 weeks. Whinchat, the only long-distance migrant of these three study species, had the shortest breeding season with an average of 12 weeks, ranging from 9 to 13 weeks between years.

The full duration of the breeding season across all years combined is shown in Figure 3.4. The earliest Stonechat breeding activity was in week 10 when one nest (0.7% of all Stonechat nests) was found to be at the building stage. Meadow Pipit breeding activity started in week 13, when 4% of nests were at the nest building stage. Whinchat breeding activity started in week 16, at which point 2% of nests were at the building stage.

Median hatch weeks and interquartile ranges across years are shown in Figure 3.5. The median hatch week was week 18 for Stonechat, week 21 for Meadow Pipit and week 23 for Whinchat. Although there was considerable overlap between species in breeding activity, median hatch weeks differed significantly between all species (Kruskal Wallis test,  $\chi^2$ =64.979, p<0.001). The median hatch week of Stonechat was significantly earlier than both Meadow Pipit (Mann-Whitney U test with Bonferroni correction, p<0.001) and Whinchat (p<0.001). Whinchat median hatch week was latest and differed significantly from that of Meadow Pipit (p<0.001). The hatch

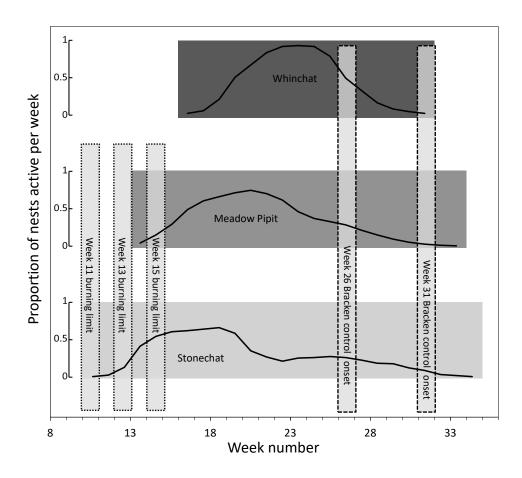


Figure 3.4: Length of breeding season (horizontal bars) and the proportion of all nests active per week (line graphs) for Whinchat, Meadow Pipit and Stonechat between 2008 and 2014. The first breeding week was defined as the week 4 weeks prior to hatching, when nest-building took place. The last breeding week was defined as 2 weeks after hatching, the last week in which nestlings were in the nest. Weeks are numbered according to week one representing 1 January to 7 January. Vertical bars represent final weeks of vegetation burning and first weeks of Bracken control.

week interquartile ranges (Figure 3.5) further highlight that the timing and length of the core breeding periods differ between species. The core period for Stonechat during which 50% of all nests hatched was the longest; from week 17 to week 24. For Meadow Pipit this period was from week 19 to 24, and Whinchat from week 23 to 25.

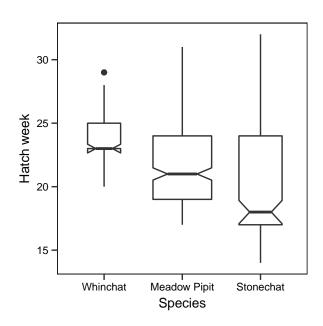


Figure 3.5: Boxplots showing hatch weeks for Stonechat, Meadow Pipit, and Whinchat nests. Weeks are numbered based on week one representing 1 January to 7 January. Whiskers show the highest and lowest value within 1.5 times the interquartile range. Notches represent a 95% confidence interval for the medians.

### 3.4.2 Vegetation management

Figure 3.4 shows the active breeding weeks from the first onset of building to the last nest fledging (for all years combined) by species, as well as showing weeks of overlap with vegetation management.

### Burning

Table 3.1 shows the percentage of nests (for all years combined) across the entire study area that showed potential overlap with burning. Stonechat showed the greatest overlap in all three scenarios, whereas Whinchat was not affected by burning management under any scenario. Under the week 15 burning scenario, matching current regulations, Stonechat breeding activity overlapped with permitted burning by 6 weeks. In week 15, when most burning would take place, 6% of all nests were at the nest building stage, 13% at laying stage, 41% at incubation stage and 1% at the nestling stage; summing up to a total of 61% of all nests being active. Meadow Pipit breeding activity across all years combined overlapped with week 15 burning by 3 weeks or 29% of nests, with 14% of all birds nest building, 11% laying and 4% incubating at week 15.

Both Stonechat and Meadow Pipit still showed overlap under the week 13 burning scenario; 4 weeks or 41% of all nests for Stonechat (28% building, 10% laying and 3% incubating), and 1 week or 4% of all nests (all at the building stage) for Meadow Pipit. Under the week 11 scenario, Meadow Pipit no longer showed overlap, and Stonechat overlap was reduced to 2 weeks or 3% of all nests. Under the week 11 scenario on onset of breeding (Figure 3.4) Stonechat would only be affected in years in which the onset of breeding is early.

Table 3.1: Percentage of monitored nests which are active during the final week in which vegetation burning is allowed. Percentages are split by nest stage. Three different final burning week deadlines are shown: week 15 (15 April), week 13 (31 March) and week 11 (15 March).

		Percentage of nests active during final burning week			
		Week 15	Week 13	Week 11	
Meadow Pipit					
	Building	14	4	0	
	Laying	11	0	0	
	Incubation	4	0	0	
	Nestling	0	0	0	
	Total potentially affected	29	4	0	
Stonechat					
	Building	6	28	2	
	Laying	13	10	1	
	Incubation	41	3	0	
	Nestling	1	0	0	
	Total potentially affected	61	41	3	
Whinchat					
	Building	0	0	0	
	Laying	0	0	0	
	Incubation	0	0	0	
	Nestling	0	0	0	
	Total potentially affected	0	0	0	

	Percentage of nests active			
	Week 26	Week 31		
Meadow Pipit	29	3		
Stonechat	28	9		
Whinchat	49	2		

**Table 3.2:** Percentage of nests active during or after the commencement of Bracken control. Two starting week scenarios for Bracken control are shown: week 26 (1 July) and week 31 (1 August).

### Bracken control

The final week of breeding activity was week 34 for Stonechat, week 33 for Meadow Pipit and week 31 for Whinchat (Figure 3.4). Bracken control commencing in week 26 would result in 9 weeks overlap with Stonechat breeding activity potentially affecting 28% of nests, 8 weeks with Meadow Pipit potentially affecting 29% of nests and 6 weeks overlap with Whinchat potentially affecting 49% of nests (Table 3.2). Commencing Bracken control in week 31 would result in 4 weeks overlap with Stonechat (potentially affecting 9% of nests), 3 weeks with Meadow Pipit (3%) and 1 week with Whinchat (2%).

### 3.5 Discussion

In this study we set out to record the timing of breeding for three upland groundnesting bird species; Meadow Pipit, Stonechat and Whinchat, and to assess the overlap in timing with two widespread upland vegetation management approaches; land burning and mechanical Bracken control.

### 3.5.1 Phenology

Our results show that there is substantial overlap in the breeding weeks of Meadow Pipit, Whinchat and Stonechat, but results also show clear differences in onset of breeding, core breeding period and the length of the breeding season. These findings are consistent with previous studies on BTO NRS data for these species (Fuller and Glue, 1977; Joys and Crick, 2004). The interannual variability in onset of breeding (by 2-4 weeks) for the three species is similar to other passerine species. For example, in a long-term study on Woodlark (*Lullula arborea*) onset of breeding varied by 25 days (Wright et al., 2009), and Hušek et al. (2012) found a maximum of 22 days of variation in first hatch date in Red-backed Shrike (*Lanius collurio*) in a study spanning over four decades.

It needs to be acknowledged that nest finding effort was variable throughout this study, resulting in less monitoring in certain weeks and years. This means that although general trends across years are provided, there could be some inaccuracies in the exact estimates of the core breeding period and length of the breeding seasons. A further limitation is that onset of breeding is derived from nest observations later in the nesting cycle, and earlier nests (especially those which failed early) might have been missed. However, this is a common limitation of nest-recording studies, and as we can assume that the probability of missing a nest will be similar between years and species, and the patterns presented here are the closest approximation of onset of breeding we can provide in this study. Late nests are unlikely to have been missed in this study, as nest recording at the end of the season was only reduced when breeding activity was ending, and ended when no further pairs and nests were found after comprehensive monitoring of the site.

### 3.5.2 Vegetation burning

Our study showed overlap with breeding activity of Stonechat and Meadow Pipit in all three burning scenarios. In the last permitted week of breeding (as per the 15 April deadline prescribed in the DEFRA (2007b) Heather and Grass Burning Code), over 60% of Stonechat and nearly 30% of Meadow Pipit nests are active on the study site, with a large proportion of nests at the laying and incubation stages. This is reduced to 41% and 4% respectively if the last week of burning is in line with the Dartmoor National Park Authority (2011) recommendations (31 March deadline). Our earliest scenario (the week of 15 March) results in no overlap with Meadow Pipit breeding activity, and overlap with Stonechat is minimised to a maximum of 2 weeks (few nests in building and laying stages only) in years in which onset of breeding is early.

Whilst only three species are considered in this study due to limitations in time and expertise, a range of other species is also likely to be affected by the current UK timings of burning. For example, opportunistically recorded as part of this study (meaning that earlier, unrecorded, nests may have also been present on the study site), Skylark (*Alauda arvensis*) and Linnet (*Linaria cannabina*) nests were found hatching in week 19, and would have therefore commenced nest-building during the week 15 burning deadline.

These results highlight that current UK regulations regarding timing are impacting on the nesting success of breeding bird populations. Both Stonechat and Meadow Pipit are impacted if vegetation burning is carried out in the first weeks of April. The earlier deadline (31 March), whilst an improvement, does not fully address this conflict and is likely to still result in a considerable direct impact on Stonechat breeding, as well as likely disturbing territory settlement and nest building in Meadow Pipit.

### 3.5.3 Bracken control

The timing of Bracken control also overlapped substantially with breeding activity when it commenced in July, with between 6 and 9 weeks of the breeding season remaining for the three bird species. More than a quarter of Stonechat and Meadow Pipit nests and half of Whinchat nests are potentially affected by current recorded timings of bracken control. Although the breeding season has not been fully completed for any of the three species by 1 August, this later start date substantially reduces the potential conflict; by that date less than 10% of nests are still active. Only Meadow Pipit, Stonechat and Whinchat were considered in this study, but other ground-nesting species are also likely affected by Bracken control. For example, we have recorded Tree Pipit *Anthus trivialis* fledging as late as mid-July (week 29), highlighting other species in the area are also still active during current permitted Bracken control timings (Tree Pipit was only a minor focus of the wider study with few nests recorded, and therefore not included in data analyses in this chapter).

In order to quantify the conflict between management and bird breeding, the percentage of active nests during the management window was calculated. In the case of vegetation burning, it is reasonable to assume that all those nests which are active in the area burnt would be destroyed. However, in the case of mechanical Bracken control, patches of non-Bracken vegetation might be left untouched. This means that birds breeding in patches with low Bracken cover in wider Bracken-rich areas could breed successfully despite these vegetation management interventions taking place in their vicinity. This is more likely to be the case for e.g. Stonechat and Meadow Pipit than for Whinchat, as Whinchat are known to show a breeding preference for Bracken-rich areas (Stillman, 1994; Pearce-Higgins and Grant, 2006). Therefore, decision-making regarding permitted timings in areas where Bracken control is desired, should take into account in particular the presence of species with known affinity for Bracken-rich habitats, as those species are likely to be the most highly impacted by mechanical Bracken control when timing of breeding and timing of control overlaps.

Information from the wider scientific literature on nest loss resulting from Bracken control is limited, but comparisons can be made with the similar practice of mowing. Evidence shows substantial impacts of such practices on nest success. For example, Grüebler et al. (2012) showed that Whinchat nest survival in Swiss alpine meadows increased from less than 10% to over 70% when mowing was carried out later in the season. For Corn Bunting (*Emberiza calandra*) on Scottish farm meadows, Perkins et al. (2013) showed that delaying mowing to 1 August could increase breeding productivity by 20%.

Whilst this study focuses on the period during which nesting takes place, it is important to consider that there is likely to be further negative impacts, which are not considered here, due to an overlap between Bracken control and the post-fledging period. In a study on Whinchat in Slovenia, it was found that at 8 days after fledging, half of fledglings respond to threat by remaining still, rather than attempting to escape (Tome and Denac, 2012). The authors also found direct evidence of fledglings killed by mowers. Therefore, whilst a start date of Bracken control of e.g. 1 August may mean that only a small proportion of all nests are still active, the area can still contain large numbers of young fledglings which are likely to not survive mechanical Bracken control activities.

### 3.5.4 Limitations of this study

There are some limitations of the data presented that need to be acknowledged. Firstly, inaccuracies in the survey methods mean that there could be slight inaccuracies in the calculated estimates of weeks of overlap and percentage nest activity. For example, due to restricted survey time, Stonechat monitoring is reduced later in the season in some study years, which might have led to a slight overestimate in the percentage of nests active during burning weeks, and an underestimate in the percentage of nests active during Bracken control weeks. Additionally, Meadow Pipit and Stonechat are double-brooded species on this study site. As birds were not marked and could not be followed individually through the season, each nest was considered to be independent, and therefore the effects on repeated breeding attempts were not considered here. For early-breeding pairs which lose a nest very early in the season due to burning, replacement broods may still be produced without constricting the opportunity of producing a second clutch. This would mean that the total number of offspring produced per season may not be reduced for all pairs, therefore potentially resulting in less pronounced population-level effects resulting from nest loss from land burning. However, further research on actual nest losses and the frequency of double-brooding would be needed to properly understand these population dynamics.

It is important to note that timing of breeding is not set, but can vary between years and show long-term change (Crick and Sparks, 1999). This study looks at overlap in timing by considering all study years combined. Whilst this is appropriate and informative for informing decision-making by providing evidence on potential conflict between vegetation management and breeding in future years (when onset of breeding is unknown), it means that the conflict in any individual year could be smaller than the percentages presented here. For example, in years with a late onset, conflict with vegetation burning may be lower, but conflict with late-summer Bracken control may be higher.

Furthermore, this study provided only an estimate on percentages of nests potentially impacted by Bracken control and vegetation burning. Numbers of destroyed nests, and therefore impacts on local (sub)-populations, will be highly variable due to differences in breeding densities and variation in the amount of land actively managed through burning and bracken control. In order to evaluate impacts on local populations, or to scale up findings to a regional or national scales, it would be necessary to calculate the numbers of nests affected, using reliable estimates of population densities across the entire area of interest, as well as records of the dates and spatial extents of burning and bracken control.

Lastly, it is important to note that using the results from this local observational study it is not possible to link nest failure caused by land management to the overall species population trends, which can be driven by other factors such as predation and post-fledging or adult survival. Further studies are needed to determine whether the current timings and landscape scale levels of vegetation management are directly affecting bird numbers.

### 3.5.5 Recommendations

Based on 8 years of phenological data, we find substantial overlap in the timing of existing Dartmoor land management practices and the breeding seasons of Meadow Pipit, Stonechat and Whinchat. These findings illustrate that there is a likely conflict between bird breeding and current vegetation management practices, resulting in potentially substantial nest losses both at the onset of the breeding season through vegetation burning, and the end of the breeding season through Bracken control.

We acknowledge the historical and conservation importance of land management for UK upland landscapes, but recommend that wherever possible, the prescribed dates for management are set to take into account the breeding phenology of the entire upland breeding bird community, particularly in areas where high breeding densities of birds are present. In order to minimise direct impacts on the groundnesting bird community, we would suggest that burning is avoided in late March. A revised burning deadline of no later than 15 March would, at this study site, prevent any overlap with the Whinchat and Meadow Pipit breeding season and would minimise conflict with Stonechat breeding. Additionally, we advise that Bracken control is delayed to late summer (preferably not earlier than August) wherever possible. We appreciate that due to the ecology of Bracken, effectively managing growth whilst completely avoiding bird breeding seasons can be challenging, especially in the first year of mechanical control (Scotland's Environmental and Rural Services, 2008). We would therefore recommend that if Bracken control needs to be carried out before August, sites are monitored to record local breeding hotspots which can then be avoided during Bracken management in order to facilitate the successful fledging of active nests. In order to achieve highest effectiveness, we would recommend selecting cutting over crushing, as crushing has been shown to be ineffective in an 8-year experimental study in the Peak District (Milligan et al., 2016). Where possible, manual cutting, e.g. with scythes rather than motorised vehicles, could help reduce impacts.

Whilst this chapter focused in particular on bracken control and burning, as timing information for these practices was available, this information can be used more broadly in land management planning. In addition to influencing the timing of bracken control and burning on certain Dartmoor moors through provision of this evidence to the Dartmoor National Park Authority and local commoners group, this research has also aided other local land management decision-making. For example, the nest record datasets underpinning this work were used to provide Dartmoor and Exmoor conservationists with estimates of how timing of mowing of *Molinia* (moor grass) for winter bedding may affect Meadow Pipit and Cuckoo. Information on nesting dates was also provided to peatland managers to better understand optimal start dates for peatland restoration in relation to ground-nesting bird breeding seasons. These examples illustrate how local nest recording studies and a comprehensive dataset of nest timings for moorland species can be used to inform a wide range of land management decisions, thereby positively influencing wildlife-friendly management practices in upland areas.

In terms of applicability of these findings beyond Dartmoor, geographical effects need to be considered. Timing of breeding is known to differ depending on geographical factors such as elevation and latitude (see for example Sanz (1998); Mainwaring et al. (2012)), therefore potential impacts of land management are likely to differ between regions, which needs to be considered when extrapolating results. However, as discussed above, the peaks of breeding recorded in this study are similar to those found in a previous study using data from across England (Joys and Crick, 2004). Therefore, whilst there may be some regional variation, the land management dates suggested in this study could be considered as a management recommendation beyond the upland Dartmoor area in which this study was carried out.

### 3.5.6 Future research and conclusions

Further research would be helpful in building a better understanding of the conflicts between land management practices and ground-nesting bird breeding. To our knowledge, there are no peer-reviewed studies quantifying nest loss resulting from current UK burning regimes. A better understanding of actual nest losses would be highly valuable in understanding the extent of the management-wildlife conflict in UK upland burning. This study only estimates the percentage of nests active during the permitted management windows; no estimate of affected nests could be made due to a lack of data on the annual management extents and management dates. It is unknown, for example, how much of the planned land burning on Dartmoor took place in the weeks in which nests were active. Therefore, additional work is needed to quantify the actual number of nests impacted, which relies on accurate recording of historical management dates and extents. We therefore recommend that land managers keep comprehensive records of the locations, extents, dates and methods of completed management interventions.

Furthermore, long-term changes in timing of breeding need to be considered. For example, earlier breeding due to shifts in response to rising temperatures could result increased overlap between land management timings and bird breeding seasons (Both et al., 2004; Carey, 2009). Therefore, timing of breeding should be periodically monitored for change, and recommended timings reviewed in accordance.

In order to apply vegetation management in a sustainable way that benefits both wildlife and ecosystem services in the UK uplands, it is necessary to keep working towards finding the correct balance of land uses and management regimes (Reed et al., 2009). Optimising vegetation management for ecosystem services such as livestock grazing or game bird production, should be permitted only if the benefits of such management outweigh the wider ecological and societal costs. For example, management for Red Grouse through burning and predator control can benefit a range of breeding birds and brings economic benefits through hunting activities (Thompson et al., 2016). However, it also comes with associated costs in terms of negative effects on other wildlife, reduced Carbon storage and increased water treatment costs (Thompson et al., 2016). An emerging field of research which may aid such upland management decision-making is the Natural Capital Approach, which can be employed to understand and quantify the costs and benefits of alternative management choices and land use changes (Guerry et al., 2015). From a conservation perspective, any management options which result in a net loss of species or biodiversity should be avoided. Therefore, burning, Bracken control and other land management practices should only be permitted during the nesting season if there is "no net loss" or "net gain" of both species populations and biodiversity. Unless new evidence emerges which shows that the employed timing of management practices and resulting nest losses do not result in negative population level effects, any nest losses through anthropogenic management should be considered unacceptable. We acknowledge that quantifying all costs, benefits and population-level effects of management options is a challenging and time-consuming task, which cannot realistically be completed in all situations. Therefore, as a general rule, in order to ensure that a wide diversity of wildlife continues to be encouraged, we would recommend that land managers look to minimise management-wildlife timing conflicts as much as possible, and employ their range of vegetation management practices in a way that creates a wide diversity of habitats, which will help create suitable habitat for a broad range of species with different ecological requirements (Buchanan et al., 2017).

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### References

- Alday, J. G., Cox, E. S., Pakeman, R. J., Harris, M. P. K., Leduc, M. G., & Marrs, R. H. Overcoming resistance and resilience of an invaded community is necessary for effective restoration: A multi-site bracken control study. *Journal of Applied Ecology*, 50:156–167, 2012.
- Allred, B. W., Fuhlendorf, S. D., Engle, D. M., & Elmore, R. D. Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution*, 1(2):132–144, 2011.
- Annett, R., Habibi, H. R., & Hontela, A. Impact of glyphosate and glyphosatebased herbicides on the freshwater environment. *Journal of Applied Toxicology*, 34:458–479, 2014.
- Ausden, M. Habitat management for conservation: A handbook of techniques. Oxford University Press, 2007.
- Bai, S. H. & Ogbourne, S. M. Glyphosate: environmental contamination, toxicity and potential risks to human health via food contamination. *Environmental Science and Pollution Research*, 23(19):18988–19001, 2016.
- Bargmann, T., Hatteland, B., & Grytnes, J. Effects of prescribed burning on carabid beetle diversity in coastal anthropogenic heathlands. *Biodiversity and Conservation*, 24:2565–2581, 2015.

- Bergman, E., Bishop, C., Freddy, D., White, G., & Doherty Jr, P. Habitat management influences overwinter survival of mule deer fawns in colorado. *The Journal* of Wildlife Management, 78:448–455, 2014.
- Both, C. & te Marvelde, L. Climate change and timing of avian breeding and migration throughout europe. *Climate Research*, 35:93–105, 2007.
- Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V., Jarvinen, A., Metcalfe, N. B., Nyholm, N. E. I., Potti, J., Ravussin, P.-A., Sanz, J. J., Silverin, B., Slater, F. M., Sokolov, L. V., Torok, J., Winkel, W., Wright, J., Zang, H., & Visser, M. E. Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society B: Biological Sciences*, 271:1657–1662, 2004.
- Bubova, T., Vrabec, V., Kulma, M., & Nowicki, P. Land management impacts on european butterflies of conservation concern: a review. *Journal of Insect Conser*vation, 19:805–821, 2015.
- Buchanan, G., Pearce-Higgings, J., Douglas, D., & Grant, M. Quantifying the importance of multi-scale management and environmental variables on moorland bird abundance. *Ibis*, 159:744–756, 2017.
- Burge, M. N. & Kirkwood, R. C. The control of Bracken. Critical Reviews in Biotechnology, 12(4):299–333, 1992.
- Butchart, S., Stattersfield, A., & Collar, N. How many bird extinctions have we prevented? Oryx, 40:266–278, 2006.
- Carey, C. The impacts of climate change on the annual cycles of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364:3321–3330, 2009.
- Chapman, D., Termansen, M., Quinn, C., Jin, N., Bonn, A., Cornell, S., Fraser, E., Hubacek, K., Kunin, W., & Reed, M. Modelling the coupled dynamics of moorland management and upland vegetation. *Journal of Applied Ecology*, 46: 278–288, 2009.
- Charmantier, A., McCleery, R., Cole, L., Perrins, C., Kruuk, L., & Sheldon, B. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, 320:800–803, 2008.
- Crick, H. Q., Baillie, S. R., & Leech, D. I. The UK Nest Record Scheme: Its value for science and conservation. *Bird Study*, 50(3):254–270, 2003.

- Crick, H. Q. P. & Sparks, T. H. Climate change related to egg-laying trends. Nature, 399:423–423, 1999.
- Crow, P. & Moffat, A. The management of the archaeological resource in uk wooded landscapes: An environmental perspective. *Conservation and Management of Archaeological Sites*, 7:103–116, 2005.
- Dartmoor National Park Authority. Dartmoor National Park Swaling Code of Conduct. http://www.dartmoor.gov.uk/lookingafter/laf-landmanagement/lafswaling/swaling-code-of-conduct, 2011.
- Davies, S. & Deviche, P. At the crossroads of physiology and ecology: Food supply and the timing of avian reproduction. *Hormones and Behavior*, 66(1):41–55, 2014.
- DEFRA. The Heather and Grass Burning Code 2007, Best Practice Guide 7: Burning in the uplands of south-west England, 2007a.
- DEFRA. The Heather and Grass Burning Code (2007 version), 2007b.
- Douglas, D. J. T., Buchanan, G. M., Thompson, P., Amar, A., Fielding, D. A., Redpath, S. M., & Wilson, J. D. Vegetation burning for game management in the UK uplands is increasing and overlaps spatially with soil carbon and protected areas. *Biological Conservation*, 191:243–250, 2015.
- Douglas, D. J. T., Beresford, A., Selvidge, J., Garnett, S., Buchanan, G. M., Gullett, P., & Grant, M. C. Changes in upland bird abundances show associations with moorland management. *Bird Study*, 64(2):242–254, 2017.
- Erwin, W. J. & Stasiak, R. H. Vertebrate mortality during the burning of a reestablished prairie in Nebraska. *The American Midland Naturalist*, 101(1):247–249, 1979.
- Ferreira, C., Touza, J., Rouco, C., Diaz-Ruiz, F., Fernandez-de Simon, J., Rios-Saldana, C., Ferreras, P., Villafuerte, R., & Delibes-Mateos, M. Habitat management as a generalized tool to boost european rabbit Oryctolagus cuniculus populations in the iberian peninsula: a cost-effectiveness analysis. Mammal Review, 44:30–43, 2014.
- Fletcher, K., Aebischer, N. J., Baines, D., Foster, R., & Hoodless, A. N. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecology*, 47:263–272, 2010.

- Fuller, R. J. & Glue, D. E. The breeding biology of the Stonechat and Whinchat. Bird Study, 24(4):215–228, 1977.
- Grüebler, M. U., Schuler, H., Horch, P., & Spaar, R. The effectiveness of conservation measures to enhance nest survival in a meadow bird suffering from anthropogenic nest loss. *Biological Conservation*, 146:197–203, 2012.
- Guerry, A., Polasky, S., Lubchenco, J., Chaplin-Kramer, R., Daily, G., Griffin,
  R., Ruckelshaus, M., Bateman, I., Duraiappah, A., Elmqvist, R., Feldman,
  M., Folke, C., Hoekstra, J., Kareiva, P., Keeler, B., Li, S., McKenzie, E., Ouyang,
  Z., Reyers, B., Ricketts, T., Rockstrom, J., Tallis, H., & Vira, B. Natural capital
  and ecosystem services informing decisions: From promise to practice. *PNAS*,
  112:7348–7355, 2015.
- Gurr, G., Wratten, S., Landis, D., & You, M. Habitat management to suppress pest populations: Progress and prospects. Annual Review of Entomology, 62:91–109, 2017.
- Hayhow, D., Conway, G., Eaton, M., Grice, P., Hall, C., Holt, C., Kuepfer, A., Noble,
  D., Oppel, S., Risely, K., Stringer, C., Stroud, D., Wilkinson, N., & Wotton, S.
  The state of the UK's birds 2014. *RSPB*, *BTO*, *WWT*, *JNCC*, *NE*, *NIEA*, *NRW* and SNH, Sandy, Bedfordshire., 2014.
- Henderson, I. G., Fuller, R. J., Conway, G. J., & Gough, S. J. Evidence for declines in populations of grassland-associated birds in marginal upland areas of Britain. *Bird Study*, 51:12–19, 2004.
- Hušek, J., Weidinger, K., Adamík, P., & Slagsvold, T. Impact of nesting mortality on avian breeding phenology: A case study on the Red-Backed Shrike (*Lanius collurio*). *Plos One*, 7(8):e43944, 2012.
- Jongsomjit, D., Jones, S., Gardali, T., Geupel, G., & Gouse, P. A guide to nestling development and aging in altricial passerines. U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication, FWS/BTP-R6008-2007, 2007.
- Joys, A. C. & Crick, H. Q. P. Breeding periods for selected bird species in England. BTO Research Report No. 352, 2004.

- Kruse, A. D. & Piehl, J. L. The impact of prescribed burning on ground-nesting birds. Proceedings of the Ninth North American Prairie Conference, pages 153– 156, 1984.
- Lambert, M., Quy, R., Smith, R., & Cowan, D. The effect of habitat management on home-range size and survival of rural norway rat populations. *Journal of Applied Ecology*, 45:1753–1761, 2008.
- Mainwaring, M. C., Hartley, I. R., Bearhop, S., Brulez, K., du Feu, C. R., Murphy, G., Plummer, K. E., Webber, S. L., James Reynolds, S., & Deeming, D. C. Latitudinal variation in Blue Tit and Great Tit nest characteristics indicates environmental adjustment. *Journal of Biogeography*, 39:1669–1677, 2012.
- Maren, I. E., Vandvik, V., & Ekelund, K. Restoration of bracken-invaded Calluna vulgaris heathlands: Effects on vegetation dynamics and non-target species. Biological Conservation, 141:1032–1042, 2008.
- Milligan, G., Cox, E., Alday, J., Santana, V., McAllistar, H., Pakeman, R., Le Duc, M., & Marrs, R. The effectiveness of old and new strategies for the long-term control of *Pteridium aquilinum*, an 8-year test. Weed Research, 56:247–257, 2016.
- Morales Fernaz, J., Schifferli, L., & Gruebler, M. Ageing nestling barn swallows *Hirundo rustica*: an illustrated guide and cautionary comments. *Ringing & Mi*gration, 27:65–75, 2012.
- Müller, M., Spaar, R., Schifferli, L., & Jenni, L. Effects of changes in farming of subalpine meadows on a grassland bird, the Whinchat (*Saxicola rubetra*). Journal of Ornithology, 146:14–23, 2005.
- Myers, J. P., Antoniou, M. N., Blumberg, B., Carroll, L., Colborn, T., Everett, L. G., Hansen, M., Landrigan, P. J., Lanphear, B. P., Mesnage, R., Vandenberg, L. N., Vom Saal, F. S., Welshons, W. V., & Benbrook, C. M. Concerns over use of glyphosate-based herbicides and risks associated with exposures: A consensus statement. *Environmental Health*, 15:1–13, 2016.
- Natural England. Bracken management: Ecological, archaeological and landscape issues and priorities (TIN047), 2008a.
- Natural England. Bracken management and control (TIN048), 2008b.
- Natural England. Agri-environment schemes in England 2009 (NE194), 2009.

- Natural England. Higher Level Stewardship: Environmental Stewardship Handbook (NE350). 2013.
- Natural England. SB5: Mechanical Bracken Control. https://www.gov.uk/ countryside-stewardship-grants/mechanical-bracken-control-sb5 - Accessed April 2017, 2015.

Natural England. Countryside Stewardship Higher Tier Manual, 2016.

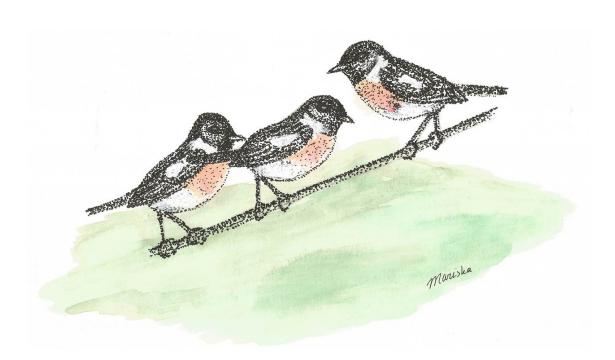
- Pakeman, R., Le Duc, M., & Marrs, R. A review of current bracken control and associated vegetation strategies in great britain. Web Ecology, 3:6–11, 2001.
- Pearce-Higgins, J. W. & Grant, M. C. Relationships between bird abundance and the composition and structure of moorland vegetation. *Bird Study*, 53:112–125, 2006.
- Pearce-Higgins, J. W., Dennis, P., Whittingham, M. J., & Yalden, D. W. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Global Change Biology*, 16(1):12–23, 2010.
- Perkins, A., Maggs, H., Wilson, J., & Watson, A. Delayed mowing increases corn bunting *Emberiza calandra* nest success in an agri-environment scheme trial. Agriculture, Ecosystems & Environment, 181:80–89, 2013.
- Powell, A. & Busby, W. Effects of grassland management on breeding birds at the western edge of the tallgrass prairie ecosystem in kansas. *Natural Areas Journal*, 33:130–138, 2013.
- R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2015.
- Reed, M. S., Bonn, A., Slee, W., Beharry-Borg, N., Birch, J., Brown, I., Burt, T. P., Chapman, D., Chapman, P. J., Clay, G. D., Cornell, S. J., Fraser, E. D., Glass, J. H., Holden, J., Hodgson, J. A., Hubacek, K., Irvine, B., Jin, N., Kirkby, M. J., Kunin, W. E., Moore, O., Moseley, D., Prell, C., Price, M. F., Quinn, C. H., Redpath, S., Reid, C., Stagl, S., Stringer, L. C., Termansen, M., Thorp, S., Towers, W., & Worrall, F. The future of the uplands. Land Use Policy, 26:S204–S216, 2009.
- Regulation (EC) No 1107/2009. http://eur-lex.europa.eu/legalcontent/EN/TXT/?uri=celex%3A32009R1107, 2009.

- Regulation (EU) No 1045/2011. https://eur-lex.europa.eu/legalcontent/EN/TXT/?uri=CELEX%3A32011R1045, 2011.
- Robertson, G., Newborn, D., M., R., & D., B. Does rotational burning increase red grouse abundance and breeding success on moors in northern england? *Wildlife Biology*, page SP1, 2017.
- Sanz, J. J. Effects of geographic location and habitat on breeding parameters of Great Tits. *The Auk*, 115(4):1034–1051, 1998.
- Scotland's Environmental and Rural Services. Bracken control, a guide to best practice, 2008.
- Sim, I. M. W., Gregory, R. D., Hancock, M. H., & Brown, A. F. Recent changes in the abundance of British upland breeding birds. *Bird Study*, 52:261–275, 2005.
- Sim, I. M. W., Ludwig, S. C., Grant, M. C., Loughrey, J. L., Rebecca, G. W., & Reid, J. M. Postfledging survival, movements, and dispersal of Ring Ouzels (*Turdus torquatus*). *The Auk*, 130(1):69–77, 2013.
- Stewart, G., Cox, E., Le Duc, M., Pakeman, R., Pullin, A., & Marrs, R. Control of *Pteridium aquilinum*: Meta-analysis of a multi-site study in the UK. Annals of Botany, 101:957–970, 2008.
- Stillman, R. A. Population sizes and habitat associations of upland breeding birds in the South Pennines, England. *Biological Conservation*, 69:307–314, 1994.
- Strebel, G., Jacot, A., Horch, P., & Spaar, R. Effects of grassland intensification on Whinchats Saxicola rubetra and implications for conservation in upland habitats. *Ibis*, 157:250–259, 2015.
- Tharme, A., Green, R., Baines, D., Bainbridge, I., & O'Brien, M. The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland. *Journal of Applied Ecology*, 38:439–457, 2001.
- Thompson, P., Douglas, D., Hoccom, D., Knott, J., Roos, S., & Wilson, J. Environmental impacts of high-output driven shooting of red grouse *Lagopus lagopus scotica*. *Ibis*, 158:446–452, 2016.
- Tome, D. & Denac, D. Survival and development of predator avoidance in the postfledging period of the whinchat (*Saxicola rubetra*): consequences for conservation measures. *Journal of Ornithology*, 153:131–138, 2012.

- Vickery, J. A., Tallowin, J. R., Feber, R. E., Asteraki, E. J., Atkinson, P. W., Fuller, R. J., & Brown, V. K. The management of lowland neutral grassland in Britain: effects of agricultural practice on birds and their food resources. *Journal of Applied Ecology*, 38:647–664, 2001.
- Visser, M. E., Caro, S. P., van Oers, K., Schaper, S. V., & Helm, B. Phenology, seasonal timing and circannual rhythms: Towards a unified framework. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365:3113–3127, 2010.
- Webb, N. R. The traditional management of European heathlands. Journal of Applied Ecology, 35:987–990, 1998.
- Wright, L. J., Hoblyn, R. A., Green, R. E., Bowden, C. G. R., Mallord, J. W., Sutherland, W. J., & Dolman, P. M. Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark *Lullula arborea*. *Journal of Animal Ecology*, 78(6):1191–1202, 2009.
- Yallop, A. R., Thacker, J. I., Thomas, G., Stephens, M., Clutterbuck, B., Brewer, T., & Sannier, C. A. D. The extent and intensity of management burning in the English uplands. *Journal of Applied Ecology*, 43:1138–1148, 2006.

## Chapter 4

# Nest site choice and breeding success in three co-occurring ground-nesting bird species on an upland moor in southern Britain



"There is nothing in which the birds differ more from man than the way in which they can build and yet leave a landscape as it was before" - Robert W Lynd

### Nest site choice and breeding success in three co-occurring ground-nesting bird species on an upland moor in southern Britain

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Short title: Nest site choice in ground-nesting birds

**Keywords:** microclimate - Dartmoor - altitude - Meadow Pipit - Stonechat - Whinchat - nest-site selection

### 4.1 Abstract

Conservation management often relies on a detailed knowledge of the breeding ecology of target species. In avian systems, nest site selection is an important component of breeding ecology. Here, we examined nest site choice at an upland study site in southwest England for three co-occurring species of ground-nesting passerines; the Meadow Pipit (Anthus pratensis), European Stonechat (Saxicola rubicola) and Whinchat (Saxicola rubetra). The nest characteristics studied were two topographical components of microclimate; altitude and solar coefficient (solar coefficient being a proxy for nest site temperature). We investigated whether any of the species select specific altitudes or solar coefficients, tested for associations between these nest characteristics and breeding success, and assessed interspecific differences in nest site use. We compared the altitude and solar coefficients of nest sites with random control sites and showed potential selection for higher altitudes and lower solar coefficient levels in Whinchat, but found no evidence for such selection in the two other species. We also found no associations between nest failure and altitude or solar coefficient. Significant interspecific differences in nest altitude and solar coefficient were observed between the three species, despite substantial overlap between species in both variables. In the context of local conservation management, when knowledge on the nesting ecology of co-occurring bird species is incomplete or lacking, conservation efforts which focus on areas with a high degree of variability in topography and vegetation types would aid in maximising the diversity of potential nest sites.

### 4.2 Introduction

Nest site selection is a key component of the ecology of a wide range of animal groups, including insects, fish, birds and mammals (Mol, 1996; Potts and Willmer, 1997; De Vere et al., 2011). It is driven by an underlying evolutionary process; better nest sites can result in higher reproductive success or survival, in turn resulting in a selective pressure to select optimal nest sites (Clark and Shutler, 1999). Refsnider and Janzen (2010) reviewed the ecological and evolutionary hypotheses for oviposition site choice across a broad range of species, and discussed how factors such as embryo and maternal survival explain site choice. For example, oviposition site selection in amphibians and reptiles can be determined by optimal thermal conditions and perceived egg predation risk, and that some insects select suboptimal oviposition sites, with host plants instead chosen to maximise maternal fecundity (Refsnider and Janzen, 2010). A study of a nest-building fish (Three-spined Stickleback *Gasterosteus aculeatus*) has shown that male breeding success is linked to nest depth, and that females display sexual selection for the depth of nests (which are built by the males in this species) (Bolnick et al., 2015). In Black-and-white Ruffled Lemurs (Varecia variequata), a species in which gestating females build multiple nests, it has been shown that microhabitat characteristics (such as altitude, slope and canopy cover) had no effect on nest site selection, but that infant survival was higher when nest sites were closer to their conspecifics, highlighting that social factors such as communal infant-rearing are also of importance in nest building behaviour in social species (Baden, 2019).

In birds, a broad range of environmental characteristics, including vegetation, predator abundance, altitude, and ectoparasite presence have been shown to be relevant in nest site selection (Oppliger et al., 1993; Hoover and Brittingham, 1998; Liebezeit and George, 2002; Forstmeier and Weiss, 2004; Sasvári and Hegyi, 2005). Nest-cavity excavators, such as woodpeckers, have been shown to select nest sites based on the wood hardness of trees (Lorenz et al., 2015), and a study on beachnesting California Least Tern (*Sternula antillarum browni*) appears to show nest site selection for, amongst other factors, specific vegetation heights and the absence of sand mounds in the landscape (Swaisgood et al., 2018). Another example of an abiotic factor of importance for some bird species is illumination. Podkowa and Surmacki (2017) showed that in the cavity-nesting Great Tit (*Parus major*), nest boxes with experimentally increased illumination were twice as likely to be selected, and birds breeding in darker nest boxes built higher nests (which was hypothesised

to compensate for low light).

A thorough understanding of breeding ecology and the environmental characteristics which determine nest site selection is essential for effective conservation. For example, a study in areas of post-fire timber harvest in the United States demonstrated that nesting woodpeckers nest in dead trees which are surrounded by a higher density of other dead trees, compared with random locations, showing that maintaining clumps of dead trees when logging post-fire habitats can help maintain breeding habitat (Saab et al., 2009). In another study on felling and forest birds, Bergmanis et al. (2019) suggest that forest management and felling regimes should safeguard the availability of mature stands near open areas to match the nest preferences of Lesser Spotted Eagle (*Clanga pomarina*). A study on the only remaining colony of South Georgia Diving-petrels (*Pelecanoides georgicus*) in New Zealand showed the birds have a preference for nesting on steep and fragile mobile foredunes (Fischer et al., 2017). The authors therefore suggest conservation action, such as chick translocation to establish a new colony, is needed to protect this population against the risk of the destructive effects of extreme whether events such as storms.

To support bird conservation it is also of importance to know how these different nest characteristics may affect breeding success. Previous studies have explored the relationship between breeding success and various nest characteristics, including nest site slope, vegetation and nest concealment (see for example Liebezeit and George (2002); Whittingham et al. (2002); Gjerdrum et al. (2005)). In a study on breeding birds in woodlands in their early succession in Pennsylvania (US), Schill and Yahner (2009) showed that daily nest success, mostly determined by nest predation in this study, was linked to nest characteristics such as stem density and the amount of vegetation concealment. In an urban environment, Eurasian Kestrel (Falco tinnunculus) has shown higher hatch rates and fledgling brood sizes for nests located closer to green gardens, likely due to the better foraging grounds these areas provided (Sumasgutner et al., 2014). Such information on nest site choice and its effect on breeding success can be used to inform conservation strategies. For example, work on Rusty Blackbird (*Euphagus carolinus*) found that daily nest survival rate increased with wetland vegetation, but was low in recently logged areas; the authors thus suggest implementing no-logging buffer zones around wetland perimeters to improve nest survival (Powell et al., 2010). Olah et al. (2014) found there was no significant difference in nest success between natural nest sites, wooden nest boxes and PVC nest tubes for Scarlet Macaws (Ara macao macao) in Peru, illustrating that artificial nest sites are a valuable conservation strategy in this species.

Consideration also needs to be given to the fact that bird species do not occur in isolation, but rather share habitats with other species and have overlapping breeding areas. Such differences in nest site selection between co-occurring species have been explored for a wide range of bird communities, including ducks, cavity nesters and grassland passerines (Sedgwick and Knopf, 1990; Clark and Shutler, 1999; Davis, 2005). As an example, a study on eight shorebird species in the Canadian Arctic found that the presence of geese affects both the selected location and habitat cover for shorebird nest sites (Flemming et al., 2019). In Blackbird (*Turdus merula*), Fieldfare (*Turdus pilaris*) and Song Thrush (*Turdus philomelos*), significant interspecific differences in nest site choice were shown in urban environments, whilst breeding success and predation rates were similar across the three species (Mikula et al., 2014).

Understanding how co-occurring species differ in their optimal requirements for nesting can be a key conservation consideration. Different woodpecker and bluebird species varied in whether they prefer unlogged or partially logged habitats, highlighting that appropriate post fire logging can be used to help breeding habitats for a range of species (Saab et al., 2009). A recent study on Piping Plover (*Charadrius melodus*) and American Oystercatcher (*Haematopus palliatus*) identified differences in the selected substrates on which the co-occurring species nested, and suggested that substrate manipulation could be used to reduce spatial overlap between the two nesting species, thereby potentially reducing antagonistic interactions which could negatively affect fitness (Hogan et al., 2018; Grant et al., 2019).

To effectively protect a breeding site or breeding bird community as a whole, the following key pieces of information regarding nest site selection are highly informative in aiding conservation decision-making: (i) the environmental characteristics used in nest site selection; (ii) the association between nest site characteristics and success; and (iii) the differences in nest site selection between co-occurring species. With this information, appropriate conservation areas which contain optimal nest sites for the focal species can be identified, and/or changes in landscape management to optimise breeding success can be implemented (see for example Suarez et al. (2000); Pasinelli (2007)).

In this study we investigated topoclimatic characteristics used in nest site selection, the association between nest site characteristics and success, and the differences in nest site selection between several co-occurring bird species in a habitat of conservation importance; the UK uplands. The uplands are highly vulnerable to climatic change and are under further threat from extensive habitat degradation

caused by factors such as intense vegetation management and high grazing pressures (Thompson and Macdonald, 1995; UK Biodiversity Group, 1999; Orr et al., 2008). Upland birds have shown stronger decreases in range size than other UK species, and in recent decades many upland bird species have shown severe population declines (Henderson et al., 2004; Sim et al., 2005; Goodenough and Hart, 2013). The species selected for this study were three ground-nesting songbirds frequently found breeding within the same upland habitats: the Meadow Pipit (Anthus pratensis), European Stonechat (Saxicola rubicola, hereafter referred to as "Stonechat") and Whinchat (Saxicola rubetra). These species were selected because they co-occur on the same breeding sites, and moreover, both Meadow Pipit and Whinchat have shown substantial UK declines (17% and 55% respectively since the mid-1990's,Hayhow et al. (2014)). A more detailed understanding of nest site selection in this ground-nesting bird community could therefore aid in the decision-making process for local upland moorland conservation. Local land managers, including land owners and the Dartmoor National Park Authority, have expressed an interest in understanding breeding site requirements of these and other key species breeding in the National Park. Therefore, an improved understanding of nest site selection in Meadow Pipit, Stonechat and Whinchat could potentially be used to target habitat management and wider protection to areas which are known to be preferred by these species.

The nest characteristics studied here are altitude and solar coefficient; two topographic components of microclimate. These topoclimatic factors were selected because they have been shown to be important for a wide range of bird species, and could affect breeding through both abiotic (e.g. physiological optima) and biotic (e.g. predation) mechanisms (Martin, 2001). Selection for optimal altitude has been widely studied, and has recently been illustrated in for example Greater Sage-Grouse (*Centrocercus urophasianus*), Egyptian Vulture (*Neophron percopterus*) and Peregrine Falcon (*Falco peregrinus*) (Lockyer et al., 2015; Sen et al., 2017; Peck et al., 2018). Whilst those studies focused on large geographic areas and/or broad altitudinal ranges, selection for altitude is also shown to be relevant in nest site selection at a local scale. For example, Hanane (2018) showed that Turtle Dove (Streptopelia turtur) select for lower altitudes in an area  $(32.8 \text{km}^2)$  with an elevation range of 450-649m. Similarly, in a  $4 \text{km}^2$  study area which ranged from 1500-1800m in altitude, Macdonald et al. (2016) found interspecific differences in the altitudes of nest sites of Horned Larks (Eremophila alpestris) and Savannah Sparrows (Passerculus sandwichensis). At an even smaller scale, for species nesting in or near aquatic environments, studies have also illustrated selection for small differences in elevation relative to the water level, such as in Clapper Rail (*Rallus crepitans*) and Piping Plover (Valdes et al., 2016; Baasch et al., 2017).

Solar coefficient, the other topoclimatic variable included in this study, is a proxy for the thermal microclimate of a site; it represents the amount of solar radiation on a surface, calculated based on solar irradiance, slope and aspect, thereby taking into account topographic shading. Solar radiation and other microclimatic factors have, for example, been linked to nest site choice, incubation behaviour and nest survival in a range of bird species. For example, Wachob (1996) estimated, among other factors, solar radiation at Mountain Chickadee (*Poecile gambeli*) nest boxes, and found that successful boxes had higher daily solar radiation and air temperatures compared with unoccupied boxes, therefore indicating selection for optimal thermal conditions. A study on South Island Saddleback (Philesturnus carunculatus carunculatus) in New Zealand showed similar selection for optimal microclimatic conditions, with birds selecting breeding cavities which were insulated from the cold and stable in temperature (Rhodes et al., 2009). Other cavity-nesters, such as Darkeyed Junco (Junco hyemalis), have been shown to have similar nest site selection for optimal thermal conditions (Robertson, 2009). Microclimatic conditions were also found to affect the breeding behaviour of Cape Barren geese (*Cereopsis no*vaehollandiae), where incubation recesses were generally held when solar radiation was stronger (Wagner and Seymour, 2001). These authors also showed a significant difference in nest temperature between exposed and more protected nests, but did not find a relationship with hatching success. However, a relationship between solar radiation and breeding success was shown in a study in Greater Prairie-Chickens (Tympanuchus cupido), although it needs to be noted that solar radiation was not measured or modelled for each nest site, but rather included as a weather variable in statistical models. (Hovick et al., 2015). In another study, microclimatic conditions (nest site temperature and humidity) were measured directly at the nest sites of Lesser Prairie-Chickens (Tympanuchus pallidicinctus) across a large area of its range, and a clear relationship with daily nest survival probability was shown (Grisham et al., 2016). Parasitism is another factor which has been linked to nest microclimate. In a study on Great Reed Warbler (Acrocephalus arundinaceus) nests with lower solar radiation levels, measured at the nest with light sensors, were shown to have lower risk of Cuckoo parasitism (*Cuculus canorus*), likely due to links between between low light levels and increased concealment (Muñoz et al., 2007).

The studies outlined above illustrate the importance of topoclimatic factors in

avian breeding. Such factors could be particular relevant in the nesting of the ground-nesting moorland species focused upon in this study, as they might be relatively sensitive to microclimatic factors due to the fact that they breed in habitats that are much more open and exposed compared to, for example, woodland-nesting species. Additionally, topoclimatic factors could be informative in understanding the breeding requirements in the context of climate warming and range shifts, for example in order to identify potential refuge sites or identify likely future ranges (see for example Ashcroft et al. (2012)). In this study, we test whether Meadow Pipit, Stonechat and Whinchat show possible selection for altitude and/or solar coefficient, as well as testing for associations with breeding success. Additionally, we test for interspecific differences in these two topographic components of microclimate.

### 4.3 Methods

### 4.3.1 Study site and species

The study was carried out with a 4.3km<sup>2</sup> area within Dartmoor (50° 31' 20"N, -3° 51' 30"W), a National Park in the southwest of England. The vegetation of the study site is typical of UK upland moorlands, and includes low gorse, heather, grasses and bracken with some high shrub and few scattered trees. The study site ranges from 211 to 457 meters above sea level. The centre of the study area is varied, with many fluctuations in altitude and a large number of banks, ditches, small streams and leats. This study focused on three of the most abundant breeding birds on the study site; Meadow Pipit, Stonechat and Whinchat. All three breed in close proximity of one another, nesting near the ground in low- to medium-height grasses and low shrubs (mostly gorse).

### 4.3.2 Nest data

Nests of Meadow Pipit, Stonechat and Whinchat were monitored for this study between 2011 and 2015. Nests were located by observing parental behaviours, and nest locations were recorded by handheld GPS (Garmin eTrex H). This device (from the manufacturer's specifications) has a digital GPS position accuracy of less than 3 meters. Nests were visited between one and eight times throughout the breeding period to record breeding progress and nest success. Breeding attempts were recorded as "failed" when dead chicks or signs of predation (destroyed nest, feather remains) were found. Nests were recorded as "successful" when nests were found empty and intact at the end of the breeding period, when adults were seen alarming or carrying food around or just after the predicted date for fledging, or when fledglings were sighted near the nest.

Two topographic nest site characteristics were used in this study; nest altitude and solar coefficient, which are both major components of nest microclimate. Nest altitude was extracted from the Tellus Digital Terrain Model (DTM) dataset. Tellus DTM is a LiDAR data collected in the southwest of England, providing 1 metre resolution surface height data at an average vertical accuracy of 25cm (Ferraccioli et al., 2014). Tellus data was chosen as it is more accurate than the altitude provided by the handheld GPS devices used in this study to determine horizontal nest position (as the manufacturer states) these only have a vertical accuracy of 3 metres. Solar coefficient, the proportion of direct beam radiation intercepted by a surface, is shown to be an effective proxy of thermal microclimate (Keating et al., 2007). Solar coefficient was modelled throughout the study area as the proportion of potential direct solar irradiance intercepted by a flat surface, influenced by its elevation, slope, aspect and shading from surrounding topography (Hofierka and Šúri, 2002), using a 5m x 5m Digital Elevation Model (DEM) and the computational method described in Bennie et al. (2008). For each DEM grid cell, the data on topography and solar radiation are combined to compute the solar coefficient for each location on the study site. Sites with a greater solar coefficient generally achieve higher daily mean and maximum temperatures than lower solar coefficient sites at equivalent geographic positions in terms of latitude, longitude, elevation or distance from the sea (see Maclean et al. (2017)).

### 4.3.3 Control site data

To assess whether the species select for topographic components of microclimate we tested whether known nest sites and randomly generated control sites differed in altitude or solar coefficient. For each known nest, a random control site was generated within the study area boundaries using the "Create Random Points" tool in ArcMap (ArcGIS 10.4.1). The centre of the study area, consisting of a reservoir with surrounding conifers, is unsuitable nesting habitat for the three species and this area was therefore excluded when generating the random control sites. For each control site, its corresponding altitude and solar coefficient were extracted. Solar coefficient was obtained from the DEM-derived dataset described above. Tellus DTM data (Ferraccioli et al. (2014), described above) were used to obtain altitude (surface height) data for each control site.

### 4.3.4 Statistical analyses

Altitude and solar coefficient were found not to be correlated (Spearman's rank correlation, p=0.403, rho=-0.03) and were therefore both included in the analysis. Mann Whitney U tests were used to test for differences in altitude and solar coefficient between nest sites and random control sites. Each of the three species was tested separately.

To test for associations between nest success and altitude and solar coefficient, a generalised linear modelling approach was used. Only nests with known outcome were included in this analysis. As nests that fail early in the breeding cycle have a lower chance of being recorded, and not all nests were observed for the same period of time, using binary failures and successes would likely lead to an overestimate of nest success. We therefore used the Mayfield method; deriving the number of observation days (see Chapter 2), rounding to the nearest day, and using this to calculate a daily failure rate (dfr) for each nest (see for example Hazler (2004)) through dividing binomial nest outcome (1=fail, 0=success) by the number of observation days:

$$dfr = (\frac{binomial \ outcome}{number \ of \ observation \ days})$$

We then fitted a logistic generalised linear model with logit link function, separately for each species, using the "glm" command in R version 3.3.1, using dfr as the dependent variable, and altitude, solar coefficient and year as explanatory variables. Year was included as an explanatory variable in order to test whether associations between the nest characteristics and success differed between years. Altitude and solar coefficient data were centred and standardised, following Gelman (2008); Schielzeth (2010), by substracting the sample mean from each data point, and dividing this by 2\*Standard Deviation. The interactions between altitude, solar coefficient and year were also included in the model, as the effect of altitude on success could vary depending on solar coefficient (and vice versa), and effects could vary by year. The "dredge" functionality of the R package MuMIn, (Barton, 2016), was used to automatically select models based on corrected AIC (AICc). When alternative models had a difference of AICc ( $\Delta AIC$ ) of <2 compared to the model with the lowest AIC, it was concluded that there was no single optimal model. In this case, the "model.avg" MuMIn function was used to obtain average parameter estimates, calculated from all models with  $\Delta AIC$  of <2.

To test for interspecific differences in nest altitude and solar coefficient, Kruskal Wallis Rank Sum tests were used. When these tests revealed a significant difference (p<0.05), Mann Whitney U tests with Bonferroni corrections were used as post hoc tests to test for pairwise differences between species. All data were analysed using R version 3.3.1 (R Core Team, 2015).

### 4.4 Results

### 4.4.1 Nest site selection

The locations of nest sites are shown in Figure 4.1. Altitude and solar coefficient were obtained for a total of 692 nests (399 Meadow Pipit, 194 Stonechat and 99 Whinchat). The altitudes and solar coefficients at nest and random control sites are shown in Figure 4.2. Test results for differences in these topographic components of microclimate between the nest sites and the random control sites are shown in Table 4.1. No difference in altitude or solar coefficient was found between nest sites and control sites in Meadow Pipit and Stonechat. In contrast, Whinchat nest sites were significantly higher in altitude (median=347m) than control sites (median=336m, Mann Whitney U test, p=0.006). Nest site solar coefficient was significantly lower than control sites, 0.155 vs. 0.165, respectively (Mann Whitney U test, p=0.005).

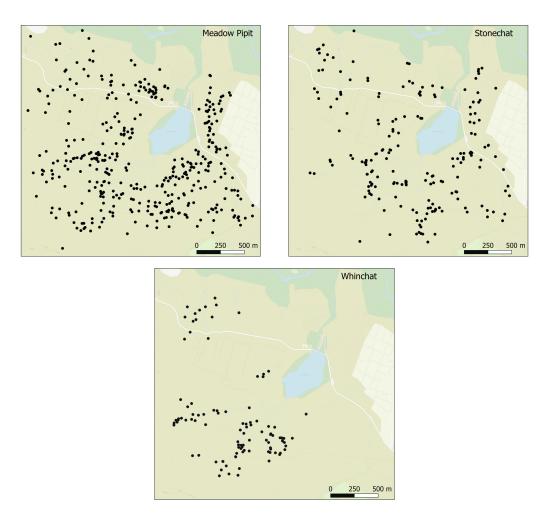


Figure 4.1: Study site map showing nest site locations of Meadow Pipit, Stonechat and Whinchat between 2011 and 2015 (Dartmoor National Park, UK). Created in QGIS using OpenStreetMap basemap.

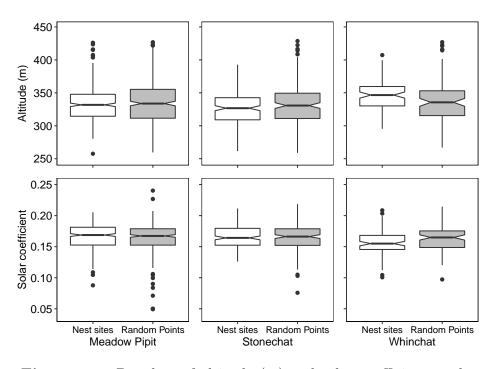


Figure 4.2: Boxplots of altitude (m) and solar coefficient at the nest sites of three breeding bird species on a study site in Dartmoor National Park (UK), and at randomly selected control sites. The species studied are Meadow Pipit, Stonechat and Whinchat. Whiskers show the highest and lowest value within 1.5 times the interquartile range. Notches represent a 95% confidence interval for the medians.

**Table 4.1:** Results of Mann Whitney U tests performed to test for differences in two ecological characteristics (solar coefficient (SC) and altitude) between nest sites and randomly selected control sites. The species tested were Meadow Pipit, Stonechat and Whinchat. Columns indicate: the ecological nest characteristic for which the test was performed; the medians and interquartile ranges for nest and control groups, the U statistic from Mann-Whitney U tests, and the p-value. Significant p-values (p<0.05) are indicated with a star.

Species	Ecological characteristic	Nest median	$egin{array}{c} { m Nest} \ { m IQR} \end{array}$	Control site median	Control site IQR	U statistic	p-value
Meadow Pipit	Altitude	332	33	334	44	78048	0.634
	SC	0.169	0.029	0.167	0.026	81878.5	0.484
Stonechat	Altitude	327	34	331	38	16950	0.091
	$\mathbf{SC}$	0.164	0.027	0.166	0.027	19226	0.712
Whinchat	Altitude	347	29	336	38	6018.5	$0.006^{*}$
	SC	0.155	0.023	0.165	0.027	3766	0.005*

#### 4.4.2 Breeding success and nest characteristics

A total 350 Meadow Pipit nests, 148 Stonechat nests and 94 Whinchat nests with both known outcome and exposure days were included in the generalised linear models testing for associations between dfr and solar coefficient, altitude and year (see Figure 4.3).

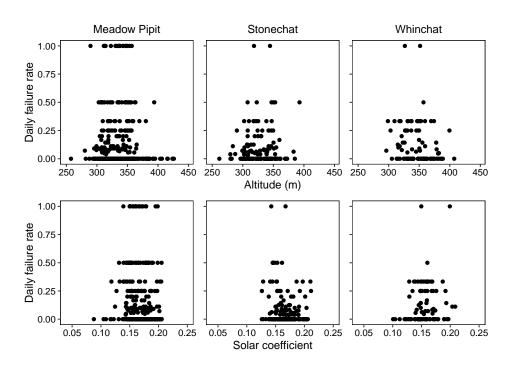


Figure 4.3: Plots showing altitude (m) and solar coefficient against nest daily failure rate for three breeding bird species on a study site in Dartmoor National Park (UK); Meadow Pipit, Stonechat and Whinchat. Each datapoint represents one nest site.

GLM model results for all three species are shown in Table 4.2, with corresponding model averaging results found in Table 4.3. The results show that for all three species, the null model had the lowest AIC, and no single optimal model could be identified as  $\Delta$ AIC was <2 for multiple models in all three species. In addition, residual deviance was high, suggesting that altitude, solar coefficient and year do not explain much of the variation in nest daily failure rate. Findings suggest that there is no discernible relationship between nest daily failure rate and the investigated variables. **Table 4.2:** Results of logistic generalised linear models testing for associations between daily failure rate (dfr) and the centred and standardised explanatory variables of solar coefficient (SC), altitude and study year for the nests of three bird species; Meadow Pipit, Stonechat and Whinchat. Columns indicate the species for which the model was constructed, model type, corrected Akaike Information Criterion (AICc), the difference in AIC ( $\Delta$ AIC) and null and residual deviances.  $\Delta$ AIC represents the difference between the model with the lowest AIC and other models. Only models with  $\Delta$ AIC of <2 compared with the model with the lowest AICc are shown.

Species	Model	AICc	$\Delta AICc$	Null deviance	Residual deviance
Meadow Pipit	Null	174.0	0	160.73	160.73
	$\mathrm{Dfr}\sim\mathrm{Year}$	174.1	0.07	160.73	150.76
	$\mathrm{Dfr}\sim\mathrm{SC}+\mathrm{Year}$	175.6	1.56	160.73	149.60
	$\rm Dfr \sim SC$	175.7	1.68	160.73	159.81
Stonechat	Null	40.7	0	44.15	44.15
	$\rm Dfr \sim SC$	42.2	1.50	44.15	42.79
	Dfr $\sim$ Altitude	42.7	1.98	44.15	42.63
Whinchat	Null	35.6	0	27.39	27.39
	$\rm Dfr \sim SC$	36.9	1.39	27.39	26.73
	$\mathrm{Dfr}\sim\mathrm{Altitude}$	37.6	2.00	27.39	26.46

Table 4.3: Model averaging results for logistic generalised linear models testing for associations between daily failure rate (dfr) and the centred and standardised explanatory variables of solar coefficient (SC), altitude and study year for the nests of three bird species; Meadow Pipit, Stonechat and Whinchat. Only models with  $\Delta$ AIC of <2 compared with the model with the lowest AICc are included in model averaging.

Species	Parameter	Estimate	SE (unconditional)	Relative importance
Meadow Pipit	Year (2012)	-0.34	0.60	
	Year (2013)	0.16	0.45	0.50
	Year (2014)	-0.12	0.51	
	Year (2015)	0.37	0.52	
	$\mathbf{SC}$	-0.10	0.22	0.31
Stonechat	$\mathbf{SC}$	-0.18	0.43	0.26
	Altitude	0.08	0.29	0.20
Whinchat	$\mathbf{SC}$	0.13	0.39	0.27
	Altitude	-0.12	0.38	0.20

### 4.4.3 Interspecific differences in nest characteristics

Figure 4.4 shows nest altitude and solar coefficient for the nests of the three study species. A Kruskal Wallis Rank Sum test showed significant variation in nest altitude between species ( $\chi^2$ =38.37, p<0.001). Mann Whitney U post hoc tests indicated that the median altitude of Whinchat nests (347m) was significantly higher than both Meadow Pipit (median=332, p<0.001) and Stonechat (median=327, p<0.001) nests. Meadow Pipit and Stonechat nest altitude also differed significantly (p=0.001).

Significant differences in solar coefficient between species were also found ( $\chi^2 = 25.57$ , p<0.001). Post hoc tests revealed that nest solar coefficient in Whinchat (median=0.155) was significantly lower than in Meadow Pipit (median=0.169, p<0.001) and Stonechat (median=0.164, p<0.001). Meadow Pipit and Stonechat did not differ significantly in nest solar coefficient.

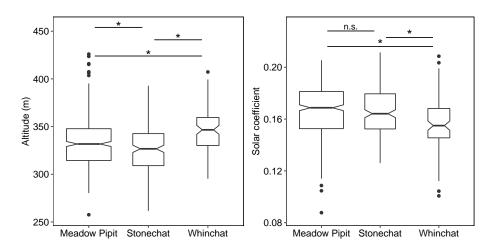


Figure 4.4: Boxplots of altitude (m) and solar coefficient for the nests of three breeding bird species on a study site in Dartmoor National Park (UK). The species studied are Meadow Pipit, Stonechat and Whinchat. Stars indicate species which differed significantly (p<0.05) in the measured variable (Kruskal Wallis Rank Sum tests, using Mann Whitney U tests with Bonferroni correction as post hoc tests). Box width represents relative sample size for each species. Whiskers show the highest and lowest value within 1.5 times the interquartile range. Notches represent a 95% confidence interval for the medians. Study site elevation range was 211 to 457 meters.

# 4.5 Discussion

#### 4.5.1 Nest site selection and breeding success

Whinchat at this study site thus appear to preferentially choose nest sites with a cooler microclimate (i.e. higher altitudes and lower solar coefficient levels) compared to the wider landscape on the study site. This difference between Whinchat breeding sites and the available nesting areas on the study site as a whole, suggests possible selection for these topographic components of microclimate in nest site choice for this species. The ultimate drivers for the selection of sites with higher altitudes and lower solar coefficients cannot be inferred from this study, but are likely to be related to optimal thermoregulatory requirements, food availability and/or predation pressures (e.g. Blomqvist and Johansson (1995); Martin (2001)). For example, D'Alba et al. (2009) showed that nest site selection for optimal microclimates was linked to better environments for egg development and subsequent hatching success, as well as affecting adult female mass loss during incubation. Similarly, a study in Northern Bobwhite (*Colinus virginanus*) showed that the species selected nest sites which showed less fluctuation in temperature than random locations, and that cooler nests were more successful (Carroll et al., 2015).

Whinchat are not solely an upland species and are found widespread across Europe, breeding also in lowland habitats across their range (Hagemeijer and Blair, 1997). Altitudinal preferences can therefore not be considered independently from regional and latitudinal trends, as local temperature conditions are affected by both factors. For example, Calladine and Bray (2012) show that Whinchat territories in Scotland tended to be at lower altitudes than those in north Wales. The mapping of Whinchat territories at a Scottish study site  $(8.8 \mathrm{km}^2)$  over an altitude range of 225-610m above sea level revealed a strong preference for both lower altitudes and south and east facing slopes. Another Scottish study, carried out altitudes between 250 and 900m, found that Whinchat abundance was greatest at altitudes of less than 400m (Brown and Stillman, 1993). In a study conducted on Whinchat in the Pennines, in northern England, abundance was also significantly greater at lower (<300m) altitudes (Stillman, 1994). In our study, we find a preference for breeding at higher altitudes than randomly expected in an area in the south of England with an altitude range of 211 to 457m. This could be related to latitudinal trends, with local temperatures at the same altitude differing depending on the region of the country. However, a study on Salisbury Plain, which is located at a similar latitude to Dartmoor, found a preference for lower altitudes at study site altitudes ranging

from 70-237m (Border et al., 2017). In addition to latitudinal differences, other confounding factors, for example regional differences in factors such as vegetation cover, interspecific competition and food availability, could explain these differences in altitudinal preferences between these various studies.

If Whinchat are selecting for optimal topographical or microclimatic conditions, driven by an underlying process of natural selection, we would expect this nest site choice to affect breeding success (Clark and Shutler, 1999). However, we found no evidence that topographic components of microclimate affected nest failure in Whinchat on our study site. It is important to note that our study used only one measure of success; daily failure rate. Previous work has highlighted that other measures of breeding success, such as nestling weight and post-fledging survival, might show different trends and are worth investigating. For example, Dawson et al. (2005) showed that in nests with experimentally increased temperatures, nestling Tree Swallows (*Tachycineta bicolor*) had a significantly higher growth rate and pre-fledging mass compared to those in control nests. In Black Skimmer (Rynchops niger), it was found that the elevation of nests relative to the high-tide line affected both daily nest success rate as well as hatching success, with the main causes of failure being predation, flooding and competition (Owen and Pierce, 2013). Therefore, nest site selection for higher altitude and lower nest site temperatures in Whinchat, as observed in this study, may be linked to success measures other than daily failure rate.

In Meadow Pipit and Stonechat, no evidence for nest site selection or associations between success and nest altitude or nest solar coefficient were found. Few other studies have explored nest site selection in Stonechat and Meadow Pipit, and the literature on topoclimatic factors for nest-site selection in these species is particularly scarce. To our knowledge, no studies on the relationship between nest site choice and breeding success have been conducted in European Stonechat. However, the importance of other nest site characteristics has been explored in the closely related Canary Island Stonechat (*Saxicola dacotiae*), where slope was shown to be an important factor in nest site selection (Illera et al., 2010). To our knowledge, no peer-reviewed studies on nest site selection for altitude, nest temperature or solar coefficient have been carried out for Meadow Pipit, but some studies have emphasised the importance of microclimate in the nesting of related species. For example, Richard's Pipit (*Anthus novaeseelandiae*) nests are oriented so they are away from cold winds (Norment and Green, 2004).

Predation was the main cause of nest failure for all three species on our study

site (pers.obs.), with predation observed from Carrion Crows (Corvus corone) and Adder (Vipera berus), as well as strongly suspected from foxes (Vulpes vulpes), stoats (Mustela erminea) and other avian and mammalian predators (see introductory chapter). Therefore, the relationship between nest characteristics and the predation risk from different types of predators warrants further investigation. As mentioned previously, altitude and solar coefficient, as investigated here, are measures derived from the topography of the landscape. Previous studies have shown that nest predation risk can be linked to topographic variables such as altitude (O'Connor et al., 2010; Ims et al., 2019). Using artificial nests in trees and on the ground, Delgado et al. (2013) found that rat predation rates varied with slope and vegetation type. Furthermore, Boyle (2008) demonstrated that both predation risk and predator type varied across altitudes for artificial nests placed across an elevation range of 2740m. Studies on natural nests at local scales have found similar results. For example in a study on Tawny Owl (Strix aluco) in nestboxes over an altitudinal range of 560m, predation risk was lower at higher elevations, which was due to density-dependence in the predation risk, with breeding densities differing by altitude (Sasvari and Hegyi, 2011). Nest placement and vegetation cover, which are not addressed in this study, are likely to be important additional factors in determining predation risk. A previous Meadow Pipit study showed that nest placement within grassy tussocks affected nest success due to differences in predation rates between nests placed on top or below tussocks (Halupka, 1998). Although nest site selection was not explicitly investigated in that study, the authors suggest that nest sites with higher predation rates might not have been selected against due to a trade-off between moisture levels and predation risk. The effect size of potential relationships between vegetation characteristics and nest success also needs to be considered. To illustrate this, Bellamy et al. (2018) found a significant but small effect of vegetation on predation rates in Wood Warbler (*Phylloscopus sibilatrix*), and emphasise that from a management perspective, vegetation manipulation is unlikely to strongly influence predation rates. To better understand the factors affecting predation rates, as well as the feasibility of potential management interventions, in Meadow Pipit, Stonechat and Whinchat, we suggest that further studies are needed to investigate predation risk in the context of factors such as nest placement and vegetation, alongside topographic variables.

A microclimatic factor which was not considered in this study is nest orientation. Previous work has shown that ground-nesting passerines can exhibit preferences for specific nest orientations, and this preference can vary intraspecifically depending on breeding latitude (Burton, 2007). Painted Honeyeater (*Grantiella picta*), for example, preferentially orientate their nest to the North-East to reduce afternoon sun exposure (Barea, 2008). An association between nest orientation and breeding performance has also been shown; for example in Tree Pipit (*Anthus trivialis*) where higher hatching success occurs in nests with preferred nest orientations (Burton, 2006). Thus, while no selection for altitude and solar coefficient was shown for Meadow Pipit and Stonechat, topoclimatic factors may still be important, and variables such as nest orientation might allow ground-nesting birds to modify the microclimatic conditions experienced in the nest. For example, Long et al. (2009) showed a seasonal shift in the orientation of Grasshopper Sparrow (*Ammodramus savannarum*) and Eastern Meadowlark (*Sturnella magna*) nests, which the authors proposed was to create an optimal nesting environment in a trade-off between factors such as wind and solar radiation. Therefore, incorporating nest orientation in future studies on nest-site selection of these species would be worthwhile.

### 4.5.2 Interspecific differences

Our results reveal interspecific differences in both altitude and solar coefficient, although substantial overlaps in both topographical components of microclimate are seen among the three species. Whinchat nest altitude was found to be higher, and nest solar coefficient lower compared with Stonechat and Meadow Pipit. Additionally, Stonechat nest site altitude was lower than in both other study species. This suggests that while these three species co-occur and breed within the same local area, their nesting requirements are likely to be different. It does, however, have to be noted that the mean altitudinal difference between Stonechat and Meadow Pipit, whilst significant, was only 5 meters, and therefore may be of only limited relevance. The difference between the nest altitude of Whinchat and the other two species was more substantial (15m and 20m with Meadow Pipit and Stonechat respectively), and this result is therefore highly unlikely to be due to random variation in the data.

To our knowledge, no other studies have explored differences in topographical components of microclimate between these three species. Interspecific differences in nest site microclimatic characteristics for other co-occurring breeding bird species, however, have been shown. For example, Gloutney and Clark (1997) found no difference in air temperature and relative humidity of Mallard (*Anas platyrhynchos*) and Blue-winged Teal (*Anas discors*) nests, but found a significant difference in "operative temperature", a measure combining air temperature with solar insolation

and heat flow. Interspecific differences in altitude have been observed in several other local-scale studies (see e.g. Macdonald et al. (2016), also discussed in the introduction). For example, on a 10 km2 study site with an elevation range of 1,400-2,200m, Wilson and Martin (2008) found differences in slope and altitude between White-tailed, Rock and Willow Ptarmigan (*Lagopus leucura*, *L. muta* and *L. lagopus*, respectively).

A possible driving factor which could explain the differences in nest microclimate between species is interspecific competition. It could be hypothesised that Whinchat may prefer similar altitudes to the other two species, but that a competitive disadvantage forces them to breed at higher altitudes; as Whinchat begin breeding later in the season than the other two species (see 3), sites at lower altitudes could already be occupied with territories of Meadow Pipit, Stonechat and other species. If this were the case, we could then expect Whinchat to to select sites that receive higher levels of solar insolation, in order to ensure the cooler, higher altitudes are compensated for by selecting a warmer solar microclimate. However, our study shows the opposite; Whinchat preferentially use sites with lower insolation levels, suggesting that they are selecting for relatively cool or topographically enclosed conditions rather than compensating for the lack of availability of warm, low-altitude sites and choosing the warmest locations left at high elevations. Furthermore, anecdotal observations at the site suggest that sufficient unoccupied areas would likely be available as potential territories at the lower altitudes of the study site when Whinchat commence breeding, suggesting a preferential selection of higher altitudes. The difference in mean altitude and solar coefficient therefore appears to reflect a true difference in the breeding preferences of Whinchat, rather than displacement driven by interspecific competition. An alternative explanation for the observed higher altitudes and lower solar coefficient levels in Whinchat relates to timing of breeding: As Whinchat on our study site start breeding later in the season (late April) compared to Stonechat (late March) and Meadow Pipit (early April; median onset of nest building between 2008-2014, unpublished data), when average air temperatures are higher, it is possible that the actual nest microclimate selected for is in fact similar across all three species. This theory is supported by for example Brambilla and Rubolini (2009) who showed that as the breeding season progresses, Woodlark (Lullula arborea) territories shift to higher altitudes.

Studying a wider range of nest site characteristics could help better understand differences in nest preference between these species. In this study, we were only able to investigate the topographic components of microclimate, but we hypothesise that microhabitat preferences and the vegetation component of microhabitat could be of crucial importance. Several studies have explored bird-habitat associations in these species. Pearce-Higgins and Grant (2006) showed associations with Heather (*Calluna vulgaris*) for both Stonechat (positive association) and Meadow Pipit (curvilinear relationship), and a positive association with Bracken (*Pteridium aquilinum*) in Whinchat. Brown and Stillman (1993) also showed an association between Whinchat and Bracken, whereas Meadow Pipit showed no association with any of the studied habitat characteristics. The importance of Bracken for Whinchat was confirmed by several other studies (for example Stillman (1994); Conway and Fuller (2010)), with Stillman (1994) showing a further association with *Juncus* spp. A further study on these three species which looks to collect a wider range of topoclimatic information, alongside information on predation risk and vegetation around the nest site, could help clarify microclimatic and microhabitat preferences, and the relationship between these two factors and success rates.

### 4.5.3 Limitations

This work was carried out on a study site of a relatively small spatial extent, and the results presented here are therefore likely to be of limited relevance for landscape scale or distribution-wide issues. This is partly due to the fact that the nest altitudes and solar coefficients used here represent only a subset of the available nest conditions in the wider landscape. Additionally, interspecific differences and relationships between nest site choice and breeding success could become more pronounced at larger spatial scales, and drivers of nest site selection can differ depending on the scale of observation (Mayor et al., 2009; McGill, 2010). For example, Border et al. (2017) showed that the importance of slope and vegetation characteristics for Whinchat habitat selection differed between landscape and territory scales.

Although we did not find any evidence for selection for topographic components of microclimate for Meadow Pipit and Stonechat at this local scale, these variables could be important drivers of nest site choice or abundance at larger spatial extents and when a broader range of altitudes and solar coefficients are represented. For example, a study on Meadow Pipit across Scotland showed that the mean altitude of 2km<sup>2</sup> study plots was significantly related with Meadow Pipit abundance on those plots (Pearce-Higgins and Grant, 2006). A UK-wide Meadow Pipit study showed that in areas where macroclimatic conditions are less suitable, microclimate (solar coefficient) becomes a more important predictor of Meadow Pipit occurrence (Suggitt et al., 2014). This scale-dependence of different factors highlights the importance of choosing appropriate study scales and ecological variables, informed by the end goals of the study. We emphasise that the findings presented here are suitable for identifying local patterns, for example in conservation decision-making when looking to locate or protect nearby sites with optimal nesting conditions for the three species. The information could potentially also be extrapolated for regional use in areas with similar environmental characteristics, however, more extensive information is needed for larger-scale issues, and potential range shifts due to climatic change need to be taken into consideration (Goodenough and Hart, 2013; Gillings et al., 2015).

Two further limitations in this work should be acknowledged. Firstly, whilst the both the altitude and solar coefficient data used in this study are high resolution and high accuracy, some error is likely to be introduced due to inaccuracies in the position of nest sites as estimated by handheld GPS (see methods). Altitude and solar coefficient were extracted based on the GPS-derived position, and therefore an incorrect GPS reference could lead to an inaccuracy in the derived altitude and solar coefficient. However, the manufacturer states the GPS position has a derived accuracy of within 3m (from the manufacturer specifications), and in-field experience of use of the handheld GPS devices to revisit nests during breeding progress checks showed a very high accuracy in pinpointing previously recorded nest locations (pers. obs.). Any inaccuracies are therefore likely minimal, with the exception of some nests located near or at very abrupt changes in topography, such as in or near steep sides of gullies. This limitation is widespread in such ecological studies, and can only be minimised by using higher-accuracy GPS devices as they become available (and affordable). A second limitation which needs to be acknowledged is that both Stonechat and Meadow Pipit are double-brooded. Furthermore, the same male and female may also nest together in multiple years. Some of the nests in this study are therefore likely to come from the same pair, adding some pseudo-replication in this study on nest site selection. Whilst the authors acknowledge this as a limitation, measures to overcome this, for instance the use of identifiable markers such as coloured leg rings on adult birds, were not feasible (nor desirable) in this study.

### 4.5.4 Conclusion

This study explored three interlinked aspects of nesting ecology; nest site selection, associations between nest sites and breeding success, and interspecific differences in nest sites. Whilst no associations between topographic components of microclimate and breeding success were found, we showed interspecific differences in nest site choice, as well as potential nest site selection for topographic components of microclimate in Whinchat. Our findings and discussions highlight that various insights can be gained from studying these various aspects of nesting ecology, but that wider work on other factors such as different metrics of breeding success, nest concealment and predation risk are needed to provide a full picture of the relationships between nest site selection and breeding performance. From the findings presented in this study, no particular management recommendations can be provided, but more generally, we suggest that when comprehensive information on nesting ecology of co-occurring species is not available, it is desirable to focus conservation efforts on sites with a diverse range of topographic features and vegetation types. This will ensure a diversity of available nest sites, which is especially important in the context of climatic change and local range shifts.

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# References

- Ashcroft, M., Gollan, J., Warton, D., & Ramp, D. A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology*, 18:1866–1879, 2012.
- Baasch, D., Farrell, P., Farnsworth, J., & Smith, C. Nest-site selection by Interior Least Terns and Piping Plovers at managed, off-channel sites along the Central Platte River in Nebraska, USA. *Journal of Field Ornithology*, 88:236–249, 2017.
- Baden, A. A description of nesting behaviors, including factors impacting nest site selection, in black-and-white ruffed lemurs (*Varecia variegata*). Ecology and Evolution, 9:1010–1028, 2019.

- Barea, L. Nest-site selection by the Painted Honeyeater (*Grantiella picta*), a mistletoe specialist. *Emu - Austral Ornithology*, 108:213–220, 2008.
- Barton, K. MuMIn: Multi-Model Inference, 2016. R package version 1.15.6.
- Bellamy, P., Burgess, M., Mallord, J., Cristinacce, A., Orsman, C., Davis, T., Grice, P., & Charman, E. Nest predation and the influence of habitat structure on nest predation of Wood Warbler *Phylloscopus sibilatrix*, a ground-nesting forest passerine. *Journal of Ornithology*, 159:493–506, 2018.
- Bennie, J., Huntley, B., Wiltshire, A., Hill, M. O., & Baxter, R. Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling*, 216(1):47–59, 2008.
- Bergmanis, U., Amerika, K., Vali, U., & Treinys, R. Nest site selection and turnover patterns in support of conservation decisions: Case study of the lesser spotted eagle in the core area of its global population. *Forest Ecology and Management*, 448:67–75, 2019.
- Blomqvist, D. & Johansson, O. C. Trade-offs in nest-site selection in coastal populations of Lapwings Vanellus vanellus. Ibis, 137:550–558, 1995.
- Bolnick, D., Shim, K., & Brock, C. Female stickleback prefer shallow males: Sexual selection on nest microhabitat. *Evolution*, 69:1643–1653, 2015.
- Border, J. A., Henderson, I. G., Redhead, J. W., & Hartley, I. R. Habitat selection by breeding Whinchats *Saxicola rubetra* at territory and landscape scales. *Ibis*, 159(1):139–151, 2017.
- Boyle, W. A. Can variation in risk of nest predation explain altitudinal migration in tropical birds? *Oecologia*, 155:397–403, 2008.
- Brambilla, M. & Rubolini, D. Intra-seasonal changes in distribution and habitat associations of a multi-brooded bird species: implications for conservation planning. *Animal Conservation*, 12:71–77, 2009.
- Brown, A. F. & Stillman, R. A. Bird-habitat associations in the Eastern highlands of Scotland. *Journal of Applied Ecology*, 30:31–42, 1993.
- Burton, N. H. K. Nest orientation and hatching success in the Tree Pipit Anthus trivialis. Journal of Avian Biology, 37:312–317, 2006.

- Burton, N. H. K. Intraspecific latitudinal variation in nest orientation among ground-nesting passerines: A study using published data. *The Condor*, 109:441– 446, 2007.
- Calladine, J. & Bray, J. The importance of altitude and aspect for breeding Whinchats Saxicola rubetra in the uplands: Limitations of the uplands as a refuge for a declining, formerly widespread species? Bird Study, 59:43–51, 2012.
- Carroll, J. M., Davis, C. A., Elmore, R. D., & Fuhlendorf, S. D. A ground nesting galliform's response to thermal heterogeneity: implications for ground dwelling birds. *PLoS ONE*, 10(11), 2015.
- Clark, R. G. & Shutler, D. Avian habitat selection: Pattern from process in nest-site use by ducks? *Ecology*, 80(1):272–287, 1999.
- Conway, G. J. & Fuller, R. J. Multi-scale relationships between vegetation pattern and breeding birds in the upland margins (ffridd) of North Wales. *BTO Research Report No. 566*, 2010.
- D'Alba, L., Monaghan, P., & Nager, R. G. Thermal benefits of nest shelter for incubating female Eiders. *Journal of Thermal Biology*, 34:93–99, 2009.
- Davis, S. K. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *The Condor*, 107(3):605–616, 2005.
- Dawson, R. D., Lawrie, C. C., & O'Brien, E. L. The importance of microclimate variation in determining size, growth and survival of avian offspring: Experimental evidence from a cavity nesting passerine. *Oecologia*, 144:499–507, 2005.
- De Vere, R. A., Warren, Y., Nicholas, A., Mackenzie, M. E., & Higham, J. P. Nest site ecology of the cross river gorilla at the Kagwene Gorilla Sanctuary, Cameroon, with special reference to anthropogenic influence. *American Journal* of Primatology, 73(3):253–261, 2011.
- Delgado, J. D., Morales, G., Arroyo, N. L., Arévalo, J. R., & Fernández-Palacios, J. M. Logging and topography effects on artificial nest predation by rats in laurel forests. *Applied Ecology and Environmental Research*, 11(1):53–65, 2013.
- Ferraccioli et al. LiDAR based Digital Terrain Model (DTM) data for South West England. NERC Environmental Information Data Centre, 2014.

- Fischer, J., Debski, I., Taylor, G. A., & Wittmer, H. Nest site selection of South Georgia Diving petrels Pelecanoider georgicus on Codfish Island, New Zealand: Implications for conservation management. *Bird Conservation International*, 28: 216–227, 2017.
- Flemming, S., Nol, E., Kennedy, L., & Smith, P. Hyperabundant herbivores limit habitat availability and influence nest site selection of Arctic-breeding birds. *Jour*nal of Applied Ecology, 56:976–987, 2019.
- Forstmeier, W. & Weiss, I. Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos*, 104:487–499, 2004.
- Gelman, A. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine, 27:2865–2873, 2008.
- Gillings, S., Balmer, D. E., & Fuller, R. J. Directionality of recent bird distribution shifts and climate change in Great Britain. *Global Change Biology*, 21(6):2155– 2168, 2015.
- Gjerdrum, C., Elphic, C. S., & Rubega, M. Nest site selection and nesting success in saltmarsh breeding Sparrows: The importance of nest habitat, timing, and study site differences. *The Condor*, 107(4):849–862, 2005.
- Gloutney, M. L. & Clark, R. G. Nest-site selection by Mallards and Blue-Winged Teal in relation to microclimate. *The Auk*, 114(3):381–395, 1997.
- Goodenough, A. E. & Hart, A. G. Correlates of vulnerability to climate-induced distribution changes in European avifauna: Habitat, migration and endemism. *Climatic Change*, 118(3-4):659–669, 2013.
- Grant, D., Cohen, J., Stantial, M., & Linhart, R. Substrate-level nest site selection of sympatric Piping Plovers (*Charadrius melodus*) and American Oystercatchers (*Haematopus palliatus*) in New Jersey, USA. Waterbirds, 42:272–281, 2019.
- Grisham, B., Godar, A., Boal, C., & Haukos, D. Interactive effects between nest microclimate and nest vegetation structure confirm microclimate thresholds for Lesser Prairie-Chicken nest survival. *The Condor*, 118:728–746, 2016.
- Hagemeijer, E. & Blair, M. The EBCC Atlas of European Breeding Birds: their distribution and abundance. 1997.

- Halupka, K. Nest-site selection and nest predation in Meadow Pipits. Folia Zoologica, 47(1):29–37, 1998.
- Hanane, S. Multi-scale turtle dove nest habitat selection in a Mediterranean agroforestry landscape: implications for the conservation of a vulnerable species. *European Journal of Wildlife Research*, 64:1–9, 2018.
- Hayhow, D., Conway, G., Eaton, M., Grice, P., Hall, C., Holt, C., Kuepfer, A., Noble, D., Oppel, S., Risely, K., Stringer, C., Stroud, D., Wilkinson, N., & Wotton, S. The state of the UK's birds 2014. *RSPB*, *BTO*, *WWT*, *JNCC*, *NE*, *NIEA*, *NRW* and SNH, Sandy, Bedfordshire., 2014.
- Hazler, K. R. Mayfield Logistic Regression: A practical approach for analysis of nest survival. *The Auk*, 121(3):707–716, 2004.
- Henderson, I. G., Fuller, R. J., Conway, G. J., & Gough, S. J. Evidence for declines in populations of grassland-associated birds in marginal upland areas of Britain. *Bird Study*, 51:12–19, 2004.
- Hofierka, J. & Šúri, M. The solar radiation model for Open Source GIS: implementation and applications. Proceedings of the Open source GIS-GRASS users conference, 2002.
- Hogan, B., Grigione, M., Marconi, M., Thomas, R., & Sarno, R. Asymmetric antagonism between Piping Plovers (*Charadrius melodus*) and American Oystercatchers (*Haematopus palliatus*), New York, USA. Waterbirds, 41:443–448, 2018.
- Hoover, J. P. & Brittingham, M. C. Nest-site selection and nesting success of Wood Thrushes. Wilson Bulletin, 110(3):375–383, 1998.
- Hovick, T. J., Elmore, R., Fuhlendorf, S. D., & Dahlgren, D. K. Weather constrains the influence of fire and grazing on nesting Greater Prairie-Chickens. *Rangeland Ecology and Management*, 68(2):186–193, 2015.
- Illera, J. C., von Wehrden, H., & Wehner, J. Nest site selection and the effects of land use in a multi-scale approach on the distribution of a passerine in an island arid environment. *Journal of Arid Environments*, 74:1408–1412, 2010.
- Ims, R., Henden, J., Stromeng, M. A., Thingness, A., Garmo, M., & Jepsen, J. Arctic greening and bird nest predation risk across tundra ecotones. *Nature Climate Change*, pages 1–6, 2019.

- Keating, K. A., Gogan, P. J. P., Vore, J. M., & Irby, L. R. A simple solar radiation index for wildlife habitat studies. *Journal of Wildlife Management*, 71(4):1344– 1348, 2007.
- Liebezeit, J. R. & George, T. L. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed ponderosa pine forest. *The Condor*, 104:507–517, 2002.
- Lockyer, Z., Coates, P., Casazza, M., Espinosa, S., & Delehanty, D. Nest-site selection and reproductive success of Greater Sage-Grouse in a fire-affected habitat of Northwestern Nevada. *Journal of Wildlife Management*, 79:785–797, 2015.
- Long, A., Jensen, W., & With, K. Orientation of Grasshopper Sparrow and Eastern Meadowlark nests in relation to wind direction. *The Condor*, 111:395–399, 2009.
- Lorenz, T., Vierling, K., Johnson, T., & Fischer, P. The role of wood hardness in limiting nest site selection in avian cavity excavators. *Ecological Applications*, 25: 1016–1033, 2015.
- Macdonald, E. C., Camfield, A. F., Martin, M., Wilson, S., & Martin, K. Nest-site selection and consequences for nest survival among three sympatric songbirds in an alpine environment. *Journal of Ornithology*, 157:393–405, 2016.
- Maclean, I. M. D., Suggitt, A. J., Wilson, R. J., Duffy, J. P., & Bennie, J. J. Finescale climate change: Modelling spatial variation in biologically meaningful rates of warming. *Global Change Biology*, 23(1):256–268, 2017.
- Martin, T. E. Abiotic vs . biotic influences on habitat selection of coexisting species: Climate change impacts? *Ecology*, 82(1):175–188, 2001.
- Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. Habitat selection at multiple scales. *Ecoscience*, 16(2):238–247, 2009.
- McGill, B. J. Matters of scale. Science, 328:575–576, 2010.
- Mikula, P., Hromada, M., Albrecht, T., & Tryjanowski, P. Nest site selection and breeding success in three *Turdus* thrush species coexisting in an urban environment. *Acta Ornithologica*, 49:83–92, 2014.
- Mol, J. H. Reproductive seasonality and nest-site differentiation in three closely related armoured catfishes (Siluriformes: Callichthyidae). *Environmental Biology* of Fishes, 45:363–381, 1996.

- Muñoz, A. R., Altamirano, M., Takasu, F., Nakamura, H., & Briskie, J. V. Nest light environment and the potential risk of Common Cuckoo (*Cuculus canorus*) parasitism. *The Auk*, 124(2):619–627, 2007.
- Norment, C. & Green, K. Breeding ecology of Richard's Pipit (Anthus novaeseelandiae) in the Snowy Mountains. Emu - Austral Ornithology, 104:327–336, 2004.
- O'Connor, J., Dudaniec, R., & Kleindorfer, S. Parasite infestation and predation in Darwin's small ground finch: contrasting two elevational habitats between islands. *Journal of Tropical Ecology*, 26:285–292, 2010.
- Olah, G., Vigo, G., Heinsohn, R., & Brightsmith, D. Nest site selection and efficacy of artificial nests for breeding success of Scarlet Macaws Ara macao macao in lowland Peru. Journal for Nature Conservation, 22:176–185, 2014.
- Oppliger, A., Richner, H., & Christe, P. Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the Great Tit (*Parus major*). *Behavioral Ecology*, 5(2):130–134, 1993.
- Orr, H., Wilby, R., McKenzie Hedger, M., & Brown, I. Climate change in the uplands: A UK perspective on safeguarding regulatory ecosystem services. *Climate Research*, 37:77–98, 2008.
- Owen, T. & Pierce, A. Hatching success and nest site characteristics of Black Skimmer (*Rynchops niger*) on the Isles Dernieres Barrier Island Refuge, Louisiana. *Waterbirds*, 36:342–347, 2013.
- Pasinelli, G. Nest site selection in middle and great spotted woodpeckers *Dendro-copos medius & D. major*: implications for forest management and conservation. *Biodiversity & Conservation*, 16:1283–1298, 2007.
- Pearce-Higgins, J. W. & Grant, M. C. Relationships between bird abundance and the composition and structure of moorland vegetation. *Bird Study*, 53:112–125, 2006.
- Peck, K., Franke, A., Lecomte, N., & Bety, J. Nesting habitat selection and distribution of an avian top predator in the Canadian Arctic. Arctic Science, 4:499–512, 2018.
- Podkowa, P. & Surmacki, A. The importance of illumination in nest site choice and nest characteristics of cavity nesting birds. *Scientific Reports*, 7:1329, 2017.

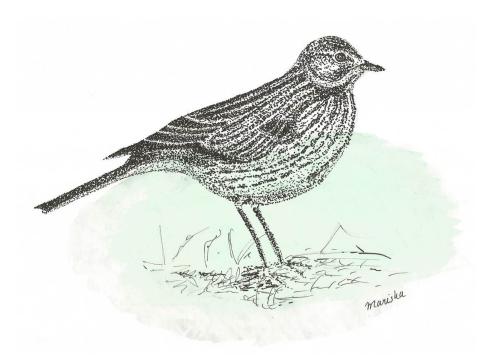
- Potts, S. & Willmer, P. Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. *Ecological Entomology*, 22: 319–328, 1997.
- Powell, L., Hodgman, T., Glanz, W. E., Osenton, J., & Fisher, C. Nest-site selection and nest survival of the Rusty Blackbird: Does timber managament adjacent to wetlands create ecological traps? *The Condor*, 112:800–809, 2010.
- R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2015.
- Refsnider, J. & Janzen, F. Putting eggs in one basket: Ecological and evolutionary hypotheses for variation in oviposition-site choice. Annual Review of Ecology, Evolution and Systematics, 41:39–57, 2010.
- Rhodes, B., O'Donnel, C., & Jamieson, I. Microclimate of natural cavity nests and its implications for a threatened secondary cavity-nesting passerine of New Zealand, the South Island Saddleback. *The Condor*, 111:462–469, 2009.
- Robertson, B. Nest-site selection in a post-fire landscape: Do parents make tradeoffs between microclimate and predation risk? *The Auk*, 500-510:500–510, 2009.
- Saab, V., Russell, R., & Dudley, J. Nest-site selection by cavity-nesting birds in relation to postfire salvage logging. *Forest Ecology and Management*, 257:151– 159, 2009.
- Sasvári, L. & Hegyi, Z. Effects of breeding experience on nest-site choice and the reproductive performance of Tawny Owls (*Strix aluco*). *Journal of Raptor Research*, 39(1):26–35, 2005.
- Sasvari, L. & Hegyi, Z. Predation risk of Tawny Owl Strix aluco nests in relation to altitude, breeding experience, breeding density and weather conditions. Ardea, 99:227–232, 2011.
- Schielzeth, H. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution, 1:103–113, 2010.
- Schill, K. & Yahner, R. Nest-Site Selection and Nest Survival of Early Successional Birds in Central Pennsylvania. . The Wilson Journal of Ornithology, 121:476–484, 2009.

- Sedgwick, J. A. & Knopf, F. L. Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains. *Journal of Wildlife Management*, 54(1):112–124, 1990.
- Sen, B., Tavares, J., & Bilgin, C. Nest site selection patterns of a local Egyptian Vulture Neophron percnopterus population in Turkey. Bird Conservation International, 27:568–581, 2017.
- Sim, I. M. W., Gregory, R. D., Hancock, M. H., & Brown, A. F. Recent changes in the abundance of British upland breeding birds. *Bird Study*, 52:261–275, 2005.
- Stillman, R. A. Population sizes and habitat associations of upland breeding birds in the South Pennines, England. *Biological Conservation*, 69:307–314, 1994.
- Suarez, S., Balbontin, J., & Ferrer, M. Nesting habitat selection by booted eagles *Hieraaetus pennatus* and implications for management. *Journal of Applied Ecology*, 37:215–223, 2000.
- Suggitt, A., Wilson, R., August, T., Beale, C., Bennie, J., Dordolo, A., Fox, R., Hopkins, J. J., Isaac, N. J. B., Jorieux, P., MacGregor, N., Marcetteau, J., Massimini, D., Morecroft, M., Pearce-Higgins, J., Walker, K., & Maclean, I. Climate change refugia for the flora and fauna of England. *Natural England Commissioned Reports, Number 162*, 2014.
- Sumasgutner, P., Schulze, C., Krenn, H., & Gamauf, A. Conservation related conflicts in nest-site selection of the Eurasian Kestrel (Falco tinnunculus) and the distribution of its avian prey. *Landscape and Urban Planning*, 127:94–103, 2014.
- Swaisgood, R., Nordstrom, L., Schuets, J., Boylan, J., Fournier, J., & Shemai, B. A management experiment evaluating nest-site selection by beach-nesting birds. *The Journal of Wildlife Management*, 82:192–201, 2018.
- Thompson, D. B. A. & Macdonald, A. J. Upland heather moorland in Great Britain: A review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation*, 71:163–178, 1995.
- UK Biodiversity Group. Tranche 2 action plans: terrestrial and freshwater species and habitats. 1999.
- Valdes, K., Hunter, E., & Nibbelink, N. Salt marsh elevation is a strong determinant of nest-site selection by Clapper Rails in Georgia. *Journal of Field Ornithology*, 87:65–73, 2016.

- Wachob, D. A microclimate analysis of nest-site selection by Mountain Chickadees. Journal of Field Ornithology, 67(4):525–533, 1996.
- Wagner, K. & Seymour, R. Nesting climate and behaviour of Cape Barren geese (*Cereopsis novaehollandiae* Latham). Australian Journal of Zoology, 49(2):155– 170, 2001.
- Whittingham, M. J., Percival, S. M., & Brown, A. F. Nest-site selection by Golden Plover: Why do shorebirds avoid nesting on slopes? *Journal of Avian Biology*, 33:184–190, 2002.
- Wilson, S. & Martin, K. Breeding habitat selection of sympatric White-tailed, Rock and Willow Ptarmigan in the southern Yukon Territory, Canada. *Journal of Ornithology*, 149:629–637, 2008.

# Chapter 5

# Foraging habitat and breeding performance in Meadow Pipit (Anthus pratensis)



"But oh! the furze, the bonny furze, - it braves the winter cold, The tempest's roar has passed it o'er; it has not quitted hold, -It still lifts high its golden eye, from midst the barren wold." The Furze - Emily F. A. Sergeant

# Foraging habitat and breeding performance in Meadow Pipit (Anthus pratensis)

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Short title: Meadow Pipit foraging habitat and breeding performance

**Keywords:** growth rate - Mayfield - vegetation - Dartmoor - nest record scheme - upland - success

# 5.1 Abstract

Bird populations are showing alarming rates of decline. Habitat management can be used as a tool in conservation to help protect declining bird populations, but to do so effectively it is crucial to understand associations between habitat characteristics and reproductive performance. In this study, we investigate whether the characteristics of the habitat surrounding the nest site (vegetation type, vegetation height and vegetation diversity) are associated with breeding performance in a declining UK upland ground-nesting passerine; the Meadow Pipit (Anthus pratensis). The study was conducted in the 2015 and 2016 breeding seasons on a  $4.3 \mathrm{km}^2$  upland moorland study site in Dartmoor National Park (UK). Habitat characteristics were classified at a 100m radius around the nest to reflect the foraging area around the nest. Breeding performance was assessed by calculating Mayfield daily nest failure rate, as well as average daily nestling growth. Habitat data were collected for a total of 60 nests. Nest daily failure rates were available for 56 of these nests, and nestling daily growth rates for 27 nests. No relationship between these measures of breeding performance and habitat characteristics were found in this study. To better understand the complex interactions between habitat, food resources and reproductive performance, a wider range of spatial scales, further vegetation characteristics and other potential confounding factors need to be investigated. As this study did not find a distinguishable effect of vegetation structure on breeding success and growth rates, we cannot derive specific advice on managing moorland vegetation for optimising breeding performance in Meadow Pipit. As many other factors, such as food availability and human disturbance, could also potentially affect breeding success, a broad focus in local management plans is desirable in the absence of further information. We recommend ensuring a rich diversity of habitats, a minimisation of anthropogenic disturbance and measures to promote insect populations.

# 5.2 Introduction

Anthropogenic changes have caused a global conservation crisis, with declines in diversity and abundance across animal groups world-wide. For example, between 21% and 36% of the world's mammals are at risk of extinction (Schipper et al., 2008), and a mean 45% decline has been shown for 67% of monitored insect populations (Dirzo et al., 2014). The causes of these declines are often multifactorial, but many are driven by man-made changes. Examples include drivers such as climatic shifts, land use change and the introduction of invasive species (Brook et al., 2008; Hof et al., 2011).

Conservationists use a wide range of *in-situ* and *ex-situ* interventions in attempts to halt or reverse declines, depending on the underlying proximate and ultimate cause(s). For example, to improve individual survival and breeding success, supplementary feeding can be used to overcome shortages in food availability (e.g. González et al. (2006)), and predator or pest control can be used to manage invasive species (see, for example Zavaleta et al. (2001) and O'Donnell and Hoare (2012)). Captive breeding programmes can be used to increase population numbers (e.g. Griffiths and Pavajeau (2008)). Furthermore, vegetation management is widely applied to improve habitat quality or food availability for declining and threatened species (e.g. Davies et al. (2005); Forrester et al. (2005); Delibes-Mateos et al. (2009)). Selecting and applying successful management techniques relies on an underlying knowledge of species ecology and the underlying causes of declines.

In the UK, birds are declining at alarming rates. Between 2009 and 2015, the UK red list grew by 15 species, resulting in a total of 27.5% of the UK's birds now being red-listed (Eaton et al., 2015). Declines in species associated with uplands have been particularly severe. For example, Curlew (*Numenius arquata*) have shown a 48% decrease in numbers between 1995 and 2014, and Whinchat (*Saxicola rubetra*) have declined by 53% over the same period (Harris et al., 2016; Hayhow et al., 2016). In recent years, these and other upland species, such as Dotterel (*Charadrius morinel-lus*), Merlin (*Falco columbarius*) and Grey Wagtail (*Motacilla cinerea*) have moved to the red-list and are considered to be of urgent conservation concern (Hayhow et al., 2016).

The UK uplands are a landscape highly shaped by human activity, for example through livestock grazing and vegetation burning (Yallop et al., 2006; Britton and Fisher, 2007; Medina-Roldán et al., 2012). Many of these anthropogenic changes to the landscape are part of the traditional management and have been used for hundreds of years (Simmons, 1990; Webb, 1998). However, starting in the twentieth century, the landscape has been changed significantly due to changes in grazing pressures and management techniques (Thompson and Macdonald, 1995; Douglas et al., 2017). These changes in habitat, as well as other contributing factors such as climatic change, are thought to underlie the declines in the UK's upland bird populations (Beale et al., 2006; Pearce-Higgins, 2010; Douglas et al., 2017).

Unlike factors such as climatic change, vegetation structure and habitats can be manipulated on a local scale, making it possible to reverse land use changes and/or to improve habitat quality for declining species (see for example O'Brien et al. (2006); Jeffs et al. (2016)). Habitat management can also aid conservation by improving breeding success and survival indirectly, for example by reducing predation rates (e.g. Dunn et al. (2016); Laidlaw et al. (2017)). In order to use habitat management as a conservation tool, it is therefore of crucial importance to understand how breeding success and survival are affected by habitat characteristics.

In this study, we investigate the association between breeding performance and upland vegetation type and diversity (hereafter referred to as "habitat characteristics") in a widespread UK upland moorland species, the Meadow Pipit (*Anthus pratensis*). This species is of conservation concern as it has shown UK population declines of 35% since the 1970s (Hayhow et al., 2016). The Meadow Pipit is of additional interest as it is the main upland host of the Common Cuckoo (*Cuculus canorus*), which has declined by 43% in just 20 years (Hayhow et al., 2016).

We investigate the relationship between habitat characteristics and nest success (daily nest failure rate) and nestling growth (daily growth rate). We studied the habitat at the scale of the Meadow Pipit foraging area, as previous studies have shown that differences in food availability or food quality can explain the link between habitat characteristics and reproductive success (see for example Burke and Nol (1998); Mägi et al. (2009)). In Meadow Pipit, the majority of adult foraging trips have been shown to take place within approximately 100m of the nest (Douglas et al., 2008; Vandenberghe et al., 2009; van Klink et al., 2014). Douglas et al. (2008) showed that on intensively grazed moorland, Meadow Pipit forage at up to 120m distance from the nest, with 89% of foraging trips being within 80m distance from the nest. van Klink et al. (2014) found that in grazed coastal salt marshes, 76% of all foraging locations were less than 75m from the nest (with a maximum foraging location at 208m from the nest). Based on these previous studies, we therefore selected a 100m radius as an appropriate scale at which to study habitat characteristics around the nest site, as based on the previous studies we can be confident the majority of foraging trips take place within this distance. From previous studies, we know that habitat characteristics at comparable spatial scales have the potential to affect breeding performance. For example, Hinsley et al. (2008) showed that differences in tree structure at a 30m radius around the nest were linked to differences in fledging success in Great Tits (*Parus major*). Similarly, successful and unsuccessful nests in Sage Sparrow (Amphispiza belli) differed significantly in percentage cover of the type of ground cover, canopy, and substrate at the territory (1-2ha) scale (Misenhelter and Rotenberry, 2000). A historical study on heathlands also suggested a link between the number of young and the amount of gorse cover in Dartford Warbler (Sylvia undata) territories (Catchpole and Phillips, 1992). In this study, we focused on vegetation diversity, as well as two of the most extensive vegetation types on upland moors; grass and gorse (*Ulex* spp.). Grass habitats of low vegetation height have been shown previously to be important for Meadow Pipit foraging (Vandenberghe et al., 2009). Based on this previous work, it could therefore be hypothesised that the available vegetation structure around the nest site, at the scale of typical foraging distances, may affect Meadow Pipit breeding performance. The extent and height of grass and gorse are heavily affected by upland vegetation management through grazing and gorse burning, therefore understanding the optimal gorse and grass conditions for Meadow Pipit breeding success would therefore be of particular relevance for conservation decision-making.

# 5.3 Methods

In order to investigate the association between habitat characteristics and breeding performance, nests of Meadow Pipit were monitored in the field. Nestlings were measured in order to be able to calculate growth rates, and the nest outcome was determined in order to calculate the nest daily failure rates. After breeding was complete, the habitat in a 100m radius around the nest was classified in order to test for associations between habitat characteristics and nestling growth and breeding success.

### 5.3.1 Breeding performance

Meadow Pipit nests were monitored in 2015 and 2016 on a 4.3km<sup>2</sup> upland moorland study site in Dartmoor National Park, UK (50° 31' 20", -3° 51' 30"). Nests were found by observing the behaviour of breeding pairs, and the locations of nests were recorded by handheld GPS (Garmin eTrex H). Nests were visited between one and eight times to record breeding progress and nest success. Surviving nestlings were weighed twice (using a Pesola LightLine Spring Scale 20g) between the ages of four and 10 days old. These ages were chosen to prevent nest abandonment due to early disturbance, and to prevent early fledging due to late disturbance (Meadow Pipit fledge between the ages of 12 and 14 days old (Robinson, 2017)). The interval between weighing visits ranged from two to four days. A nest was considered to have failed when dead chicks or feather remains were observed, or when the nest cup was found to have been destroyed. Nests were considered successful when fledglings were observed near the nest, when adults were seen alarming or carrying food, or when the nest was found intact after the projected end of the breeding period.

### 5.3.2 Habitat characteristics

The characteristics of habitats around nests were recorded after fledging or nest failure to avoid nest disturbance, and within four weeks of breeding season completion to minimise vegetation change. The habitat was recorded for 12 squares, each 50m<sup>2</sup> in size, to approximate an area representing a 100m radius around the nest (see Figure 5.1). The following foraging habitat characteristics were recorded for each nest: average cover scores for the four main vegetation types on the study site (low grass, low gorse, medium gorse and mixed low gorse & grass), and a measure of habitat diversity. All average cover scores were calculated by estimating percentage cover for each square using the Braun-Blanquet (BB) scale (see Figure 5.1 and Wikum and Shanholtzer (1978)), and averaging BB score across all 12 squares. BB scores of + and r (see Figure 5.1) were excluded from this calculation as they were considered not to significantly contribute to ground cover. Based on observations of the flora across the entire study site, 14 main vegetation types were distinguished (see Table 5.1 for a description of all vegetation types). Habitat diversity was a count of the total number of vegetation types present across all 12 squares.

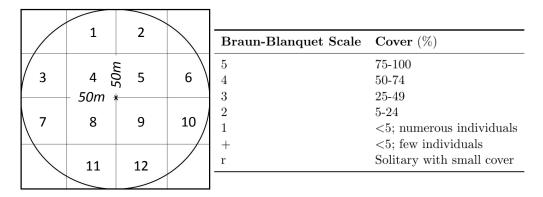


Figure 5.1: Vegetation characteristics around Meadow Pipit nest sites ( $\times$ ) were measured in 12 50m<sup>2</sup> squares to represent an adult foraging area of a 100m radius around the nest (left figure). The right table shows Braun-Blanquet scale classes used to estimate percentage cover of vegetation types around Meadow Pipit (*Anthus pratensis*) nests. Table adapted from Wikum and Shanholtzer (1978).

### 5.3.3 Statistical analyses

A total of 243 Meadow Pipit nests were monitored during the field study of this project. However, due to limitations in field time, habitat data and growth rate data could not be collected for all these nests (breeding results for all nests can be viewed in Chapter 2). Foraging habitat data were collected for a total of 60 nests. Nest daily failure rates could be calculated for a total of 56 of these nests, and repeated growth rate measurements could be collected for a total of 27 of these nests.

R version 3.3.1 was used for all analyses (R Core Team, 2015). Daily failure rate was used as a measure of nest success. The Mayfield method was used to calculate daily failure rates (dfr) of nests (see Chapter 4 and Mayfield (1975); Hazler (2004)). Average daily growth rate (dgr) was calculated by averaging nestling mass per visit for each nest, and dividing by the interval between the two nest visits. As nestling growth in Meadow Pipit has been shown to be linear between day 4 and day 10 (Seel and Walton, 1979; van Oosten, 2016), this provides an accurate approximation

Vegetation type	Description
Low gorse $(<75cm)$ Medium corse $(75.150cm)$	Gorse ( <i>Ulex</i> spp.) less than 75cm in height Gorse ( <i>Illex</i> spn.) 75, 15,0cm in height
High gorse (>150cm)	Gorse bushes or stands of gorse greater than 150cm in height
Trees	Individual trees on open moor, any spp
Mixed low gorse & grass	Areas where low gorse and grass grow intertwined
Grass (< 10cm)	Low (often heavily grazed) patches of grass
Homogeneous grass (>10cm)	Homogeneous areas of grass taller than 10cm
Tussock $(>10 \text{cm})$	Tufty grass and/or sedges, e.g. Purple Moor-grass (Molinia caerulea), Cotton-grass (Eriophorum angustifolium)
Dead gorse twigs & low grass	Grass growing around dead gorse stems, typical where patches were burnt in recent years
Bracken	Bracken (Pteridium aquilinum)
Dead Bracken	Dead Bracken ( $Pteridium \ aquilinum$ )
Heather	Heather $(Calluna vulgaris)$
Mosses	Mosses (e.g. <i>Sphagnum</i> spp.)
Coniferous trees	Stands of coniferous plantation forest
Bare rock/road	Areas of rock and/road with no vegetation cover
Other	Any other cover, e.g. open water, bare ground, Bilberry (Vaccinium myrtillus)

**Table 5.1:** Description of vegetation types used to classify habitats in 100m radius around Meadow Pipit (Anthus

of daily growth. Nests in which the number of nestlings declined between visits (presumably caused by predation), as well as one nest with a negative growth rate (loss in mass) were excluded from the analysis. Intra-brood variability in growth rates was explored, with a Bartlett's test for homogeneity of variance used to test for differences in variance in growth rates between individual nests.

To test for associations between foraging habitat characteristics and breeding success a binomial logistic generalised linear model with logit link function was used, using the "glm" command in R version 3.3.1. A binomial logistic glm was selected as it has previously been demonstrated to be appropriate for analysing Mayfield nest survival data as collected in this study (Hazler, 2004). The dependent variable was dfr, the explanatory variables were low grass cover, low gorse cover, medium gorse cover, mixed grass/gorse cover, habitat diversity and year (to test for differences between 2015 and 2016). As it is conceivable that there is an interaction between habitat diversity and the other habitat variables (i.e. the effects of the individual habitat cover on success varying depending on the total diversity of the habitat explanatory values was included in the model. It is also possible that the importance of habitat to breeding success differs between year (e.g. in years with abundant insect food across the area, habitat type may be less important in predicting success), and therefore year was also included as an interaction term in the model.

To test for associations between foraging habitats and nestling growth, a gaussian glm was used with dgr as the dependent variable. A gaussian glm was selected because the dependent variable, dgr, was normally distributed (Shapiro-Wilk normality test, W=0.97, p=0.49). As outlined above, the effect of individual habitat covers may be affected by the habitat diversity around the nest sites, and there may be different effects between years. Therefore, habitat diversity and year were included as in interaction with all other habitat variables. Brood size was added as an additional explanatory variable to test for any effects of brood size on daily growth rate, and an interaction between brood size and all habitat variables was included as the effect of habitat on growth rate could differ depending on brood size. As Chapter 2 showed no significant differences in brood size between 2015 and 2016, no interaction term was included between year and brood size.

For both these glm analyses, all input variables were centred and standardised (by subtracting the variable mean from each input variable value, and dividing by two times the standard deviation), following Gelman (2008); Schielzeth (2010). Model selection was done using Akaike Information Criterion (AIC). The "dredge" function from the MuMIn R package was used for automated model selection based on AICc (corrected AIC) (Barton, 2016). A difference in AICc ( $\Delta$ AICc) of <2 between the model with the lowest AICc and subsequent models meant that no single optimal model could be selected. To account for this uncertainty, the model.avg function in the MuMIn package was used to average the parameter estimates for the models with a  $\Delta$ AICc of <2.

# 5.4 Results

Minimum, maximum and mean Braun-Blanquet scores for the five foraging habitat characteristics (low grass, low gorse, medium gorse, mixed low gorse & grass and habitat diversity) are shown in Table 5.2. Mixed low gorse and grass was the most common habitat type around nests (mean BB score of 2.82), followed by low grass (mean BB score of 2.24). Habitat diversity in the foraging area ranged from 8 to 15 habitat types (from a total of 16, see Table 5.1).

**Table 5.2:** Minimum, maximum and mean Braun-Blanquet (BB) and diversity (div) scores for five foraging habitat characteristics measured in a 100m radius around Meadow Pipit (*Anthus pratensis*) nests.

Habitat characteristics	Min	Max	Mean
Low gorse (BB)	0	2.83	0.67
Medium gorse (BB)	0	2.67	0.66
Mixed low gorse & grass (BB)	0	5.00	2.82
Grass (BB)	0.42	4.17	2.24
Habitat diversity (div)	8	15	12.42

Results for glm models testing for associations between daily failure rate and foraging habitat are shown in Table 5.3, with model averaging results shown in Table 5.4. The null model was the optimal model according to the AICc score, although no single best model could be identified as  $\Delta$ AICc was <2 for five other models, and residual deviance was very high. These results indicate the explanatory variables (and their interactions) explain the variation in the data poorly, therefore suggesting that there is no association between dfr and the foraging habitat characteristics of low gorse, medium gorse, mixed gorse & grass and habitat diversity.

Model	AICc	$\Delta AICc$	Null deviance	Residual deviance
Null	27.7	0	23.47	23.47
Dfr $\sim$ Habitat diversity + Year	28.4	0.7	23.47	21.74
Dfr ~ Medium gorse	28.5	0.8	23.47	22.78
$\mathrm{Dfr} \sim \mathrm{Year}$	29.0	1.3	23.47	23.28
Dfr $\sim$ Habit at diversity	29.4	1.7	23.47	22.96
Dfr $\sim$ Low gorse	29.7	2	23.47	23.37

**Table 5.3:** GLM model results testing for associations between nest daily failure rate (dfr) and five habitat characteristics & year. Only models with  $\Delta$ AICc of <2 compared with the lowest AICc model are shown.

**Table 5.4:** Model averaging results (estimates for centred and standardised parameters) after GLMs testing for associations between nest daily failure rate (dfr) and five habitat characteristics & year. Only models with  $\Delta$ AICc of <2 compared with the lowest AICc model were included in model averaging.

Parameter	Estimate	SE (unconditional)	Relative importance
(Null)	-2.00	0.49	
Habitat diversity	0.38	0.93	0.31
Year	-0.29	0.75	0.33
Medium gorse	0.12	0.42	0.19
Low gorse	0.02	0.27	0.10

Brood sizes ranged from one to four nestlings (mean=3.33). Average daily growth rates ranged from 0.42 to 3.19 grams/day (mean=1.72±0.76, see Figure 5.2). In Figure 5.3, average nestling growth rate per nest is displayed. A Bartlett's test showed that variance in growth rate is not significantly different between nests (Bartlett's test for homogeneity of variance,  $K^2=37.503$ , p=0.05169), therefore the relationship between variance in growth rate and habitat variables was not explored further.

GLM results for the relationship between growth rate and habitat variables are shown in Table 5.5, and model averaging results are shown in 5.6. Results were similar to the dfr models; the null model had the lowest AICc, and high residual deviances and no significant explanatory variables were seen in competing models

( $\Delta AICc < 2$ ). This suggests that dgr is also not associated with the habitat characteristics investigated.

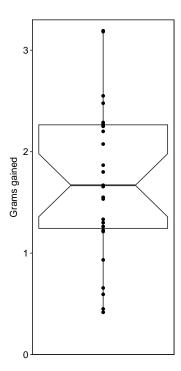
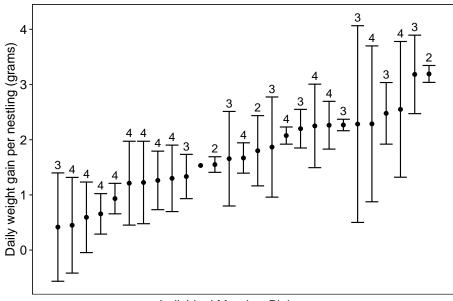


Figure 5.2: Boxplot of average nestling growth rates (grams gained per day) calculated for 27 Meadow Pipit (*Anthus pratensis*) broods. Nestlings were weighed twice between the ages of 4 and 10 days.



Individual Meadow Pipit nests

Figure 5.3: Mean and standard deviation in nestling growth rates (grams gained per day) for 27 Meadow Pipit (*Anthus pratensis*) broods. Nestlings were weighed twice between the ages of four and 10 days. Brood size is displayed for each nest. X-axis is ordered by increasing average daily weight gain.

**Table 5.5:** GLM model results testing for associations between average nestling daily growth rate (dgr) and five habitat characteristics, brood size & year. Only models with  $\Delta$ AICc of <2 compared with the lowest AICc model are shown.

Model	AIC	$\Delta AIC$	Null	Residual
Model			deviance	deviance
Null	65.1	0	14.91	14.91
Dgr $\sim$ Brood size	65.6	0.5	14.91	13.84
Dgr $\sim$ Low gorse	66.6	1.5	14.91	14.34

**Table 5.6:** Model averaging results (estimates for centred and standardised parameters) after GLMs testing for associations between nestling daily growth rate (dfr), five habitat characteristics, brood size & year. Only models with  $\Delta$ AICc of <2 compared with the lowest AICc model were included in model averaging.

Parameter	Estimate	SE (unconditional)	Relative importance	
(Null)	1.72	0.14		
Brood size	-0.14	0.26	0.34	
Low gorse	0.06	0.18	0.21	

# 5.5 Discussion

In this study, we found no relationship between habitat characteristics within a 100m radius of Meadow Pipit nest sites and breeding success or nestling growth rate. This suggests that the habitat characteristics, at the spatial scale and resolution at which they were studied here, are not factors in determining nest success and nestling growth at this study site. Meadow Pipits have been shown to have a broad diet, feeding on for example on Tipulidae and other Diptera, as well as Lepidoptera, Coleoptera, Arachnidae and more (Evans et al., 2005a; Douglas et al., 2008). It is therefore possible that on this study site, all selected habitats were relatively suitable, providing all necessary food resources resources. A study site with a wider range of vegetation types or characteristics may reveal different results. For example, (Vandenberghe et al., 2009) found that Meadow Pipit select foraging locations which have heterogeneity in the height of the vegetation. However, habitat factors at the current site may still be of relevance for breeding performance at different scales or through different mechanisms. For instance, the habitat around the nest site may affect other components of breeding performance, such as post-fledging survival, as we know from field observations (pers. obs.) that young Meadow Pipit remain close to the nest in the days after fledgling.

It is also possible that the method of habitat type designation in this study was not detailed enough, or that a different methodology in classifying vegetation types may show a different result. For example, Chalfoun and Martin (2007) showed that depending on the focal area (territory vs. nest patch), Brewer's Sparrow (*Spizella breweri*) preferred different habitat characteristics. This indicates that habitat characteristics may need to be measured differently depending on the scale of observation, and therefore a different classification methodology for the 100m radius around Meadow Pipit nests may be needed to fully understand the effects of habitat differences on breeding performance. A further improvement to the current study would be to measure food availability rather than habitat characteristics, and conduct invertebrate prey sampling to better understand the relationship between Meadow Pipit feeding and reproductive success (see for example Boulton et al. (2008)).

The radius around the nest at which vegetation was studied here was chosen to reflect the foraging area. However, only one of the two studies on which the selection of the 100m foraging radius was based, was conducted in upland grasslands. It is therefore possible that the 100m radius was not appropriate, and foraging trips take place at much smaller or larger distances at this study site. A follow-up study on this is currently being undertaken in another PhD study, through which the foraging distances at this study site, and improved information on Meadow Pipit foraging behaviour in this Dartmoor habitat, will be available in the near future. It is possible that habitat factors are important at a different spatial resolution.

Furthermore, nest predation is one of the main reasons for nest failure on the study site; Mayfield nest success rate was 0.22 for Meadow Pipit over a 9-year period at this study site (*unpubl. data*), and we suspect the far majority of nests failed due to predation. This suggests that the habitat in the 100m radius around the nest may not be a major limiting factor. Instead, the vegetation structure directly around the nest site may impact breeding performance by affecting nest concealment. This has been shown in a wide range of ground- and shrub-nesting species, such as Blackcap (*Sylvia atricapilla*), Hermit Thrush (*Catharus guttatus*), Dusky Flycatcher (*Empidonax oberholseri*) and Clay-coloured Sparrow (*Spizella pallida*) (Flaspohler et al., 2000; Liebezeit and George, 2002; Remeš, 2005; Winter et al., 2005). Links between nest success and the vegetation structure in the direct vicinity of the nest site may therefore be worthwhile exploring in a future study.

Other studies have explored the relationships between habitat characteristics and Meadow Pipit breeding performance. For example, Pedroli (1978) indicated that nest sites situated further away from a habitat rich in food resources had nestlings with a lower body weight. Halupka (1998b) found that although nest success rates were comparable across studies in different habitat types across Europe, the relative importance of predation as a cause of nest failure varied between sites; it is not possible however, to distinguish whether this is due to a direct effect of habitat differences, for example through concealment, or due to a difference in predator densities between the different sites or habitat types. In another study, Halupka (1998a) showed that nest placed on top of grassy tussocks had higher predation rates than nests positioned at lower levels in the vegetation. Therefore, in addition to considering the vegetation around the nest, the placement of nests within the vegetation needs to also be considered. To fully understand the associations between breeding performance and habitat on Dartmoor, further studies should focus on assessing habitat characteristics at various scales, and across multiple study sites. The association between vegetation and food availability also needs to be clarified, and a better understanding of nest site selection relative to the wider available habitat is needed.

The growth rates reported in this study fall within the range of those reported in other studies on Meadow Pipit nestlings. Figures in Seel and Walton (1979) and van Oosten (2016) both show a mean growth rate of approximately two grams per day (compared to a mean of 1.72 grams per day reported here). These studies did not investigate differences between nests in intra-brood variability in growth rates, and it is therefore unknown whether the wider Meadow Pipit population also show no significant differences between nests in intra-brood variability in growth rates, as was shown in this study.

In addition to studying habitat characteristics in more detail, it is crucial to consider other factors which may be driving breeding performance. As mentioned in earlier parts of this thesis, predation patterns need to be studied in more detail. Breeding density is another factor which may have significant effects on breeding performance. An effect of breeding density on success has been illustrated in a range of studies on simulated ground nests (Sugden and Beyersbergen, 1986; Keyser et al., 1998; Larivière and Messier, 1998). Furthermore, nestling growth could be driven by, for example, parental quality or parental experience. For example, Saino et al. (2005) showed that Kittiwake (*Rissa tridactyla*) nestlings grew faster when the female parent was an experienced breeder and in Great Tit (*Parus major*) males with larger black breast stripes produce heavier fledglings (Norris, 1990). Parental quality can be affected by other relevant ecological factors. For example, Saino et al. (2005) showed that female Barn Swallows (*Hirundo rustica*) which were exposed to predators during laying produced lower quality offspring.

Another factor which may affect breeding performance is grazing intensity. Evans et al. (2005b) showed that higher sheep grazing levels resulted in smaller egg sizes in Meadow Pipit. Although no effect on fledging success was found, the authors highlight that effects on post-fledging survival are currently unknown. Anthropogenic disturbance also needs to be taken into consideration, particularly for landscapes such as Dartmoor, where visitor pressures in some areas are intense and are likely to increase under ever-growing human populations. Previous studies have shown that human disturbance can affect breeding success in moorland bird species such as the Dartford Warbler (*Sylvia undata*, Murison et al. (2007)) and a wide range of other species, e.g. Mourning Dove (*Zenaida macroura*), Bearded Vulture (*Gypaetus barbatus*), including even nocturnal species such as European Storm Petrel (*Hydrobates pelagicus*)(Westmoreland and Best, 1985; Arroyo and Razin, 2006; Watson et al., 2014). Studying such additional factors will aid in further understanding the relative importance of habitat characteristics in the context of other drivers of breeding success and nestling growth.

Determining the factors which affect breeding performance is essential for better

understanding the ecology of declining species such as the Meadow Pipit. However, it needs to be acknowledged that looking for improved nestling body condition is not necessarily a successful conservation strategy, as it is not necessarily related to other success measures. Nestling weight has been shown to correlate with survival in for example Blackbird (Turdus merula, Magrath (1991)), Great Tit and Coal Tit (Parus ater, Naef-Daenzer et al. (2001)). However, this is not found across all species and/or populations. For example, no such association was shown in Stonechat (Saxicola rubicola, Greig-Smith (1985)), and Guillemot (Uria aalqe, Hedgren (1981)). Associations can also vary temporally. Nur (1984), for example, found an association between nestling weight and survival in only one out of two study years in Blue Tit (*Cyanistes caeruleus*). These findings show that improved nestling body condition does not guarantee improved nestling survival. Additionally, targeted habitat improvements do not necessarily succeed in improving population numbers nationally. For example, Vickery et al. (2004) showed that despite substantial nationwide habitat management practices within agri-environment schemes, many farmland bird populations have continued to decline. The authors of the study highlight that detailed evaluation and adaptation is needed in order to ensure management schemes meet the target species' resource requirements.

It is clear that further research is needed to disentangle the complex relationships between habitat characteristics, food resources, reproductive success and population numbers. This study did not reveal a relationship between breeding performance and habitat conditions at the scale of the foraging area. We can therefore not provide specific recommendations on how to manage moorland vegetation for optimising Meadow Pipit breeding success. Until further research builds more detailed knowledge, we would recommend that the local management has a broad focus in order to cover a range of potential factors. We would recommend that local management plans i) ensure a rich diversity of habitats, ii) work to minimise anthropogenic disturbance, and iii) promote insect populations to ensure sufficient food availability for breeding birds, for example through reduced pesticide use and encouraging optimal vegetation for insects.

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# References

- Arroyo, B. & Razin, M. Effect of human activities on bearded vulture behaviour and breeding success in the French Pyrenees. *Biological Conservation*, 128:276–284, 2006.
- Barton, K. MuMIn: Multi-Model Inference, 2016. R package version 1.15.6.
- Beale, C. M., Burfield, I. J., Sim, I. M. W., Rebecca, G. W., Pearce-Higgins, J. W., & Grant, M. C. Climate change may account for the decline in British ring ouzels *Turdus torquatus. Journal of Animal Ecology*, 75:826–835, 2006.
- Boulton, R., Richard, Y., & Armstrong, D. Influence of food availability, predator density and forest fragmentation on nest survival of New Zealand robins. *Biological Conservation*, 141:580–589, 2008.
- Britton, A. J. & Fisher, J. M. Interactive effects of nitrogen deposition, fire and grazing on diversity and composition of low-alpine prostrate *Calluna vulgaris* heathland. *Journal of Applied Ecology*, 44:125–135, 2007.
- Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, 23(8):453–460, 2008.
- Burke, D. M. & Nol, E. Influence of food abundance nest site habitat and forest fragmentation on breeding Ovenbirds. *The Auk*, 115(1):96–104, 1998.
- Catchpole, C. & Phillips, J. Territory quality and reproductive success in the Dartford warbler Sylvia undata in Droset, England. Biological Conservation, 61:209– 215, 1992.
- Chalfoun, A. D. & Martin, T. E. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology*, 44: 983–992, 2007.
- Davies, Z., Wilson, R., Brereton, T., & Thomas, C. The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. *Biological Conservation*, 124:189–198, 2005.
- Delibes-Mateos, M., Ferreras, P., & Villafuerte, R. European rabbit population trends and associated factors: A review of the situation in the Iberian Peninsula. *Mammal Review*, 39(2):124–140, 2009.

- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. Defaunation in the Anthropocene. *Science*, 345(6195):401–406, 2014.
- Douglas, D. J., Evans, D. M., & Redpath, S. M. Selection of foraging habitat and nestling diet by Meadow Pipits Anthus pratensis breeding on intensively grazed moorland. Bird Study, 55:290–296, 2008.
- Douglas, D. J. T., Beresford, A., Selvidge, J., Garnett, S., Buchanan, G. M., Gullett, P., & Grant, M. C. Changes in upland bird abundances show associations with moorland management. *Bird Study*, 64(2):242–254, 2017.
- Dunn, J. C., Gruar, D., Stoate, C., Szczur, J., & Peach, W. J. Can hedgerow management mitigate the impacts of predation on songbird nest survival? *Journal* of Environmental Management, 184:535–544, 2016.
- Eaton, M., Aebischer, N., Brown, A., Hearn, R., Lock, L., Musgrove, A., Noble, D., Stroud, D., & Gregory, R. Birds of conservation concern 4: The population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds*, 108:708–746, 2015.
- Evans, D. M., Redpath, S. M., & Evans, S. A. Seasonal patterns in the productivity of Meadow Pipits in the uplands of Scotland. *Journal of Field Ornithology*, 76(3): 245–251, 2005a.
- Evans, D. M., Redpath, S. M., Evans, S. A., Elston, D. A., & Dennis, P. Livestock grazing affects the egg size of an insectivorous passerine. *Biology Letters*, 1:322– 325, 2005b.
- Flaspohler, D. J., Temple, S. A., & Rosenfield, R. N. Relationship between nest success and concealment in two ground-nesting passerines. *Journal of Field Ornithology*, 71(4):736–747, 2000.
- Forrester, J. A., Leopold, D. J., & Hafner, S. D. Maintaining critical habitat in a heavily managed landscape: Effects of power line corridor management on Karner blue butterfly (*Lycaeides melissa samuelis*) habitat. *Restoration Ecology*, 13(3): 488–498, 2005.
- Gelman, A. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine, 27:2865–2873, 2008.

- González, L. M., Margalida, A., Sánchez, R., & Oria, J. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (Aquila adalberti). Biological Conservation, 129:477–486, 2006.
- Greig-Smith, P. Weight differences, brood reduction, and sibling competition among nestling Stonechats Saxicola torquata (Aves: Turdidae). Journal of Zoology, 205 (3):453–465, 1985.
- Griffiths, R. A. & Pavajeau, L. Captive breeding, reintroduction, and the conservation of amphibians. *Conservation Biology*, 22(4):852–861, 2008.
- Halupka, K. Nest-site selection and nest predation in Meadow Pipits. Folia Zoologica, 47(1):29–37, 1998a.
- Halupka, K. Nest predation in Meadow Pipits Anthus pratensis nesting in natural conditions. Ornis Fennica, 75:139–143, 1998b.
- Harris, S. J., Massimino, S., Newson, S. E., Eaton, M. A., Marchant, J. H., Balmer, D. E., Noble, D. G., Gillings, S., Procter, D., & Pearce-Higgins, J. W. The Breeding Bird Survey 2015. BTO Research Report 687, British Trust for Ornithology, Thetford, 2016.
- Hayhow, D., Bond, A., Douse, A., Eaton, M., Frost, T., Grice, P., Hall, C., Harrist, S., Havery, S., Hearn, R., Noble, D., Oppel, S., Williams, J., Win, I., & Wotton, S. The state of the UK's birds 2016. *RSPB, BTO, WWT, DAERA, JNCC, NE, NRW and SNH, Sandy, Bedfordshire.*, 2016.
- Hazler, K. R. Mayfield Logistic Regression: A practical approach for analysis of nest survival. *The Auk*, 121(3):707–716, 2004.
- Hedgren, S. Effects of fledging weight and time of fledging on survival of Guillemot Uria aalge chicks. Ornis Scandinavica, 12(1):51–54, 1981.
- Hinsley, S., Hill, R., Bellamy, P. E., Harrison, N., Speakman, J., Wilson, A., & Ferns, P. Effect of structural and functional habitat gaps on breeding woodland birds: working harder for less. *Landscape Ecology*, 23:615–626, 2008.
- Hof, C., Araújo, M. B., Jetz, W., & Rahbek, C. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, 480:516–521, 2011.

- Jeffs, C., Davies, M., Carter, I., Gregson, J., Sainsbury, A., & Lister, J. Reintroducing the Cirl Bunting to Cornwall. *British Birds*, 109:374–388, 2016.
- Keyser, A. J., Hill, G. E., & Soehren, E. C. Effects of forest fragment size, nest density and proximity to edge on the risk of predation to ground-nesting passerine birds. *Conservation Biology*, 12(5):986–994, 1998.
- Laidlaw, R. A., Smart, J., Smart, M. A., & Gill, J. A. Scenarios of habitat management options to reduce predator impacts on nesting waders. *Journal of Applied Ecology*, 54:1219–1229, 2017.
- Larivière, S. & Messier, F. Effect of density and nearest neighbours on simulated waterfowl nests: Can predators recognize high-density nesting patches? Oikos, 83(1):12–20, 1998.
- Liebezeit, J. R. & George, T. L. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed ponderosa pine forest. *The Condor*, 104:507–517, 2002.
- Mägi, M., Mänd, R., Tamm, H., Sisask, E., Kilgas, P., & Tilgar, V. Low reproductive success of great tits in the preferred habitat: A role of food availability. *Ecoscience*, 16(2):145–157, 2009.
- Magrath, R. D. Nestling weight and juvenile survival in the Blackbird, Turdus merula. Journal of Animal Ecology, 60(1):335–351, 1991.
- Mayfield, H. F. Suggestions for calculating nest success. The Wilson Bulletin, 87 (4):456–466, 1975.
- Medina-Roldán, E., Paz-Ferreiro, J., & Bardgett, R. D. Grazing exclusion affects soil and plant communities, but has no impact on soil carbon storage in an upland grassland. Agriculture, Ecosystems and Environment, 149:118–123, 2012.
- Misenhelter, M. & Rotenberry, J. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology*, 81:2892–2901, 2000.
- Murison, G., Bullock, J. M., Underhill-Day, J., Langston, R., Brown, A. F., & Sutherland, W. J. Habitat type determines the effects of disturbance on the breeding productivity of the Dartford Warbler Sylvia undata. Ibis, 149(Suppl. 1): 16–26, 2007.

- Naef-Daenzer, B., Widmer, F., & Nuber, M. Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging data. *Journal of Animal Ecology*, 70:730–738, 2001.
- Norris, K. J. Female choice and the quality of parental care in the Great Tit *Parus* major. Behavioral Ecology and Sociobiology, 27:275–281, 1990.
- Nur, N. The consequences of brood size for breeding Blue Tits II. Nestling weight, offspring survival and optimal brood size. *Journal of Animal Ecology*, 53:479–517, 1984.
- O'Brien, M., Green, R. E., & Wilson, J. D. Partial recovery of the population of Corncrakes *Crex crex* in Britain, 1993-2004. *Bird Study*, 53:213–224, 2006.
- O'Donnell, C. F. J. & Hoare, J. M. Quantifying the benefits of long-term integrated pest control for forest bird populations in a New Zealand temperate rainforest. *New Zealand Journal of Ecology*, 36(2):131–140, 2012.
- Pearce-Higgins, J. W. Using diet to assess the sensitivity of northern and upland birds to climate change. *Climate Research*, 24:119–130, 2010.
- Pedroli, J.-C. Breeding success of the Meadow Pipit Anthus pratensis in the Swiss Jura. Ornis Scandinavica, 9(2):168–171, 1978.
- R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2015.
- Remeš, V. Birds and rodents destroy different nests: A study of Blackcap *Sylvia atricapilla* using the removal of nest concealment. *Ibis*, 147:213–216, 2005.
- Robinson, R. A. BirdFacts: Profiles of birds occurring in Britain & Ireland. BTO Research Report 407, 2017.
- Saino, N., Romano, M., Ferrari, R. P., Martinelli, R., & Møller, A. P. Stressed mothers lay eggs with high corticosterone levels which produce low-quality offspring. *Journal of Experimental Zoology*, 303A:998–1006, 2005.
- Schielzeth, H. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution, 1:103–113, 2010.
- Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A. S. L., Stuart, S. N., Temple, H. J., Baillie,

J., Boitani, L., Lacher Jr, T. E., Mittermeier, R. A., Smith, A. T., Absolon, D., Aguiar, J. M., Amori, G., Bakkour, N., Baldi, R., Berridge, R. J., Bielby, J., Black, P. A., Blanc, J. J., Brooks, T. M., Burton, J. A., Butynski, T. M., Catullo, G., Garshelis, D. L., Gates, C., Gimenez-dixon, M., Gonzalez, S., Gonzalez-Maya, J. F., Good, T. C., Hammerson, G., Hammond, P. S., Happold, D., Happold, M., Hare, J., Harris, R. B., Hawkins, C. E., Haywood, M., Heaney, L. R., Hedges, S., Helgen, K. M., Hilton-taylor, C., Hussain, S. A., Ishii, N., Jefferson, T. A., Jenkins, R. K. B., Johnston, C. H., Keith, M., Kingdon, J., Knox, D. H., Kovacs, K. M., Langhammer, P., Leus, K., Lewison, R., Lichtenstein, G., Lowry, L. F., Macavoy, Z., Medellín, R. A., Medici, P., Mills, G., Moehlman, P. D., Molur, S., Mora, A., Nowell, K., Oates, J. F., Olech, W., Oliver, W. R. L., Oprea, M., Patterson, B. D., Perrin, W. F., Polidoro, B. A., Pollock, C., Powel, A., Protas, Y., Racey, P., Ragle, J., Ramani, P., Rathbun, G., Reeves, R. R., Reilly, S. B., Reynolds III, J. E., Rondinini, C., Rosell-ambal, R. G., Rulli, M., Rylands, A. B., Savini, S., Schank, C. J., Sechrest, W., Self-sullivan, C., Shoemaker, A., Sillero-zubiri, C., Silva, N. D., Smith, D. E., Taylor, B. L., Timmins, R., Tirira, D. G., Tognelli, M. F., Tsytsulina, K., Veiga, L. M., Vié, J.-C., Williamson, E. A., Wyatt, S. A., Xie, Y., & Young, B. E. The status of the world's land and marine mammals: Diversity, threat and knowledge. Science, 322: 225-230, 2008.

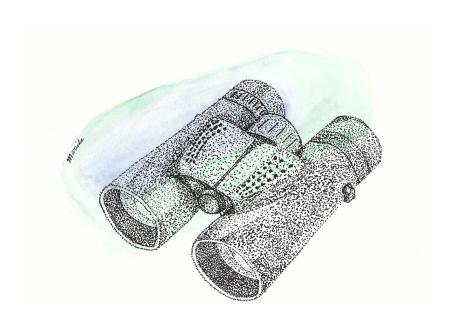
- Seel, D. C. & Walton, K. C. Numbers of Meadow Pipits Anthus pratensis on mountain farm grassland in North Wales in the breeding season. *Ibis*, 121:147– 164, 1979.
- Simmons, I. G. The mid-Holocene ecological history of the moorlands of England and Wales and its relevance for conservation. *Environmental Conservation*, 17(1): 61–69, 1990.
- Sugden, L. G. & Beyersbergen, G. W. Effect of density and concealment on American Crow predation of simulated duck nests. *The Journal of Wildlife Management*, 50(1):9–14, 1986.
- Thompson, D. B. A. & Macdonald, A. J. Upland heather moorland in Great Britain: A review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation*, 71:163–178, 1995.
- van Klink, R., Mandema, F. S., Bakker, J. P., & Tinbergen, J. M. Foraging site

choice and diet selection of Meadow Pipits *Anthus pratensis* breeding on grazed salt marshes. *Bird Study*, 61(1):101–110, 2014.

- van Oosten, H. H. Comparative breeding biology of three insectivorous songbirds in Dutch dune grasslands. Ardea, 104(3):199–2012, 2016.
- Vandenberghe, C., Prior, G., Littlewood, N. A., Brooker, R., & Pakeman, R. Influence of livestock grazing on Meadow Pipit foraging behaviour in upland grassland. *Basic and Applied Ecology*, 10:662–670, 2009.
- Vickery, J. A., Bradbury, R. B., Henderson, I. G., Eaton, M. A., & Grice, P. V. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. *Biological Conservation*, 119:19–39, 2004.
- Watson, H., Bolton, M., & Monaghan, P. Out of sight but not out of harm's way: Human disturbance reduces reproductive success of a cavity-nesting seabird. *Biological Conservation*, 174:127–133, 2014.
- Webb, N. R. The traditional management of European heathlands. *Journal of Applied Ecology*, 35:987–990, 1998.
- Westmoreland, D. & Best, L. B. The effect of disturbance on Mourning Dove nesting success. The Auk, 102(4):774–780, 1985.
- Wikum, D. A. & Shanholtzer, G. F. Application of the Braun-Blanquet coverabundance scale for vegetation analysis in land development studies. *Environmental Management*, 2(4):323–329, 1978.
- Winter, M., Johnson, D., & Shaffer, J. Variability in vegetation effects on density and nesting success of grassland birds. *The Journal of Animal Ecology*, 69(1): 185–197, 2005.
- Yallop, A. R., Thacker, J. I., Thomas, G., Stephens, M., Clutterbuck, B., Brewer, T., & Sannier, C. A. D. The extent and intensity of management burning in the English uplands. *Journal of Applied Ecology*, 43:1138–1148, 2006.
- Zavaleta, E. S., Hobbs, R. J., & Mooney, H. A. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution*, 16(8):454–459, 2001.

# Chapter 6

# Cuckoo occurrences in Devon: Comparing findings from systematic volunteer surveys and opportunistic citizen science



"He isn't what you'd call a star, with such a basic repertoire. And yet, that simple two-note phrase, casts such a spell on summer days." Author unknown

# Cuckoo occurrences in Devon: Comparing findings from systematic volunteer surveys and opportunistic citizen science

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Short title: Comparing ornithological survey and Citizen Science findings

Keywords: outreach - engagement - science communication - Devon - distribution

Disclaimer: Some of the themes and findings presented in this chapter have been previously discussed in an online blog for the British Ornithology Union (BOU).

# 6.1 Abstract

In addition to using traditional ecological surveys conducted by professionals, citizen science initiatives are increasingly used to collect ecological data. In this study we explored whether different survey approaches produce similar results regarding the occurrences of Common Cuckoo (*Cuculus canorus*) across Devon. We compare two survey methods for mapping Cuckoo; a standardised distribution survey conducted by experienced volunteers (the Devon Bird Atlas), and a newly-created citizen science initiative which opportunistically collected 3,166 records over a four-year period. A comparison of the two survey methods shows that there are significant differences in the resulting occurrence maps, with the citizen science approach giving a larger proportion occupancy compared to the Devon Bird Atlas. We re-analyse the data after spatially aggregating the data to better reflect Cuckoo territory size, and find that whilst overall similarity between results from the two survey methods increases, findings remain significantly different. We find that the citizen science initiative may help identify Cuckoo hotspots which are overlooked by the shorter survey duration of the Devon Bird Atlas methodology, and the findings from this work can be usefully applied to locally target further studies and conservation on this declining species. Further work is needed, however, to establish the error associated with the different survey approaches. We conclude that the most suitable methodology is dependent on the envisaged applications of the work.

# 6.2 Introduction

A key starting point for the study of many species is mapping its distribution. It is necessary for determining a species' ecological niche and predicting future changes in populations. Distribution data has, for example, been used to illustrate that drought sensitivity drives tropical tree distribution (Engelbrecht et al., 2007), to show an altitudinal shift in plant species in response to climate change (Lenoir et al., 2008), and to determine that the "habitat types" on a human body drive the species of bacteria present (Costello et al., 2009). Distribution mapping is essential for the monitoring and conservation of declining species. It is needed to understand the importance of interspecific interactions in determining where species occur (Belmaker et al., 2015), it can help identify the threats species face (Schipper et al., 2008; Wich et al., 2012), and it can also be used to quantify the success of conservation interventions (Davies et al., 2005).

Collecting data on species presences or distributions is time-consuming, especially when working across large geographical areas. It is also often costly due to the considerable amounts of staff time and travel required. An appealing alternative is therefore to involve the general public, so-called "citizen scientist", in collecting data (Schmeller et al., 2008). Such citizen science-based projects have become increasingly popular in ecological studies (Silvertown, 2009). Dickinson et al. (2012) reviewed a broad range of citizen-science studies and illustrated that they have for example tracked disease spread, identified phenological shifts in flowering plants, and re-discovered species thought to be extinct. Some successful citizen science initiatives are thoroughly planned, systematic surveys where experienced volunteers are recruited to collect data using standardised methodology, much like a conventional ecological survey (McKinley et al., 2017; Peach et al., 1998; Silvertown, 2009). In the case of ornithological initiatives this includes Constant Effort Sites for bird ringing and volunteer bird transect surveys such as the US and UK Breeding Bird Surveys (Newson et al., 2005; Sauer et al., 2003). Many other citizen science project are open for participation by all members of the public rather than only selected volunteers, but are nonetheless surveys with a standardised methodology. This include monitoring initiatives such as the RSPB's Big Garden Birdwatch (www.rspb.org.uk) and Butterfly Conservation's Big Butterfly Count (www.butterfly-conservation.org), where all members of the public are invited to count birds and butterflies for a set time window on specific dates of the year. Other citizen science initiatives are less standardised, and collect opportunistic observational data year-round, for examples using websites such as eBird and iNaturalist, where amateur naturalists can record their observations (McKinley et al., 2017).

Traditional ecological surveys and the various types of citizen science initiatives each have their advantages and disadvantages. In data collection on species distributions, the use of professionals or highly experienced volunteers can minimise the risk of misidentification, and well-planned, standardised surveys reduce the likelihood of issues such as pseudo-replication or recording errors in the data (Crall et al., 2011; Ruttenberg et al., 2012). On the other hand, due to their prescribed nature, such surveys are often restricted to one or few survey visits a year, and are only carried out at a subset of selected or randomised locations (e.g. using transects). This reduces temporal and spatial coverage, and could mean that local species hotspots may be missed. Conversely, opportunistic citizen science projects facilitate the collection of species records across wide areas and over prolonged time periods, and large amounts of data can be generated using this method (McCaffrey, 2005; Snall et al., 2011). However, misidentification can be more likely than in standardised surveys with experienced volunteers or professionals (Kosmala et al., 2016). Furthermore, such opportunistic data is often restricted to presence-only records as absence data is typically not recorded (see for example Snall et al. (2011)). Sampling bias is also a concern when survey locations are not pre-determined, with higher survey effort likely to occur in, for example, areas with easy access (Dickinson et al., 2010).

These various approaches to species distribution monitoring raise the questions of whether different survey approaches can provide similar answers as to a species' distribution, and whether standardised survey methods carried out by ornithologists or experienced volunteers provide similar answers as opportunistic data collection by the general public.

In this study, we explore this issue for the Cuckoo (*Cuculus canorus*) in Devon. The Cuckoo is an obligate brood parasite. In the UK, its main hosts are the Meadow Pipit (*Anthus pratensis*), Reed Warbler (*Acrocephalus scirpaceus*) and Dunnock (*Prunella modularis*) (Brooke and Davies, 1987). The Cuckoo is red-listed in the UK, having shown a 43 % decline in just 20 years (Hayhow et al., 2016). The reasons underlying these sharp declines are poorly understood, but could include migratory conditions and shortages in food availability (Hewson et al., 2016; Conrad et al., 2006). To identify potential factors on the breeding ground which contribute to the declines of Cuckoos, it is essential to have an understanding of the locations at which Cuckoo occur. As a charismatic species with a widely known call, the Cuckoo is an ideal candidate for a citizen science project. Furthermore, a citizen science

initiative on Cuckoo provides an opportunity for outreach and awareness-raising about the decline of this species with the local public.

In this chapter, we discuss the development, promotion, public uptake and resulting data obtained from running this Devon Cuckoo citizen science project from 2014 to 2017. We then compare the findings on Cuckoo occurrences in Devon from the citizen science initiative, with results from the Devon Bird Atlas 2007-2013 (Beavan and Lock, 2016), a standardised bird distribution survey conducted in each Ordnance Survey tetrad (2km<sup>2</sup>) across Devon (see methodology for further details). We compare total Devon occupancy across Devon between both survey methods, and calculate similarity for the two Cuckoo maps.

On their breeding grounds, Cuckoos have been shown to have home ranges larger than  $2\text{km}^2$ , the tetrad scale at which the Devon Bird Atlas data is presented. Estimates of Cuckoo home ranges in the breeding ground vary widely; a study on females in a pond habitat in the Czech republic found a home range ranging from 0.33 to  $3.15\text{km}^2$  (Vogl et al., 2004), whereas a study on both males and females in Scandinavia found a mean home range of  $135\text{km}^2$  (Williams et al., 2016). We therefore replicate the analyses at a scale more representative of the mid-range of estimates of Cuckoo home-range size, by repeating the comparison between the Devon Atlas survey and citizen science initiative at the scale of Ordnance Survey hectads ( $10\text{km}^2$ ). This is similar to the size of the home range recorded in a study on Cuckoo in reedbeds and woodland in Hungary, where, using kernel density estimation, a mean home range of  $8.8\text{km}^2$  was found (Moskat et al., 2019).

Furthermore, research has shown that bird species have shifted their distributions and that the relative importance of different habitat types and regions are changing, with Cuckoo having shown the strongest declines in lowland agricultural areas and being increasingly associated with upland areas (Denerley et al., 2019; Gillings et al., 2015). By comparing the Devon Bird atlases of 1977-85 and 2007-13, we can see that Cuckoo are no longer recorded in many of the lowland survey tetrads in Devon (Beavan and Lock, 2016; Sitters, H.P., 1988). These findings suggest that the uplands may be becoming an increasingly important refuge for declining species like Cuckoo. The majority of Cuckoo presence sites in the Devon Bird Atlas 2007-13 are in the upland areas of Dartmoor National Park and the Devon portion of Exmoor National Park. We test whether the citizen science initiative is in line with the Devon Bird Atlas with regards to the relative importance of the uplands for Cuckoo sites. We do this by comparing the proportion of Devon Cuckoo occurrences found in the two upland National Parks between the two approaches.

# 6.3 Methods

#### 6.3.1 Citizen science project

A citizen science initiative was set up for members of the public to record observations of Cuckoos in Devon. The citizen science page was designed by the authors, and developed by and hosted on the website of Devon Birds; the county's birdwatching society. The page consisted of a web form (Figure 6.1) where the public were asked to log the details of any Cuckoo seen or heard across the county. Contributors were asked to record i) the grid reference of the location at which the Cuckoo was observed (with a web-link provided to a map where people could obtain the grid reference for any location visited with a simple mouse-click), ii) a description of the location, iii) the date and time of the observation, iv) the number of birds observed, v) whether the bird was seen, heard or both, and lastly, vi) a comment box in which further information could be recorded. All records fed into a live map where members of the public could view the location of all reports to date during that year. In addition to the online map, records were also collected manually from visitors at the main Dartmoor National Park Authority (DNPA) visitor centre. The project ran for four consecutive years; during the spring and summer of 2014, 2015, 2016 and 2017.

The web page was promoted extensively on the Devon Birds and DNPA websites, with regular updates being posted throughout the season on the Devon Birds website. In addition to this, the project was promoted regularly on social media (Twitter) by Devon Birds, DNPA and Sara Zonneveld. Press releases on the initiative were published by local newspapers, and flyers were distributed in the DNPA visitor centers (Figure 6.2). All reported records were collated into a spreadsheet by Devon Bird volunteers and the authors.

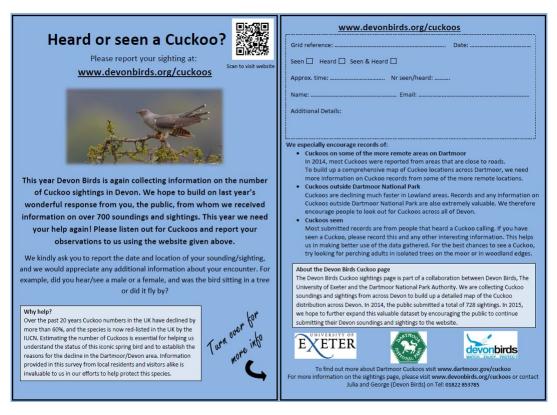
### 6.3.2 Atlas data

To test the similarity in findings from citizen science initiatives with systematic ornithological surveys, we compare the findings of the above-described Devon Cuckoo citizen science initiative to the data for Cuckoo from the Devon Bird Atlas (Beavan and Lock, 2016). The Devon Bird Atlas used surveys of every Ordnance Survey tetrad (2x2km square) in Devon to map the presences of all recorded bird species. Birds were surveyed by experienced volunteer birdwatchers using a standardised method; the Timed Tetrad Visit method, as used in the National BTO Atlas (Balmer

Grid Ref:	(must be SS, ST, SX, SY)
Place:	
Date:	/ / 2017 Now
Time:	
Number:	1 •
Additional Details:	Seen Heard
	E.g. male or female, juvenile or adult, flying or perching.
Name:	
Email:	
	w you are a human being and not a spam robot please answer ng question before submitting your sighting.
What anin	nal barks?

Figure 6.1: Screenshot of the web form of the Cuckoo citizen science project (www.devonbirds.org/cuckoos).

et al., 2013). Timed Tetrad Visits are one or two hour surveys along a route containing all the major habitats within a tetrad, where each tetrad is visited twice in a breeding season (between April and July), as well as twice in the winter (between November and February - not relevant for Cuckoo). Timed Tetrad Visits were completed between 2007 and 2013, with each Devon tetrad surveyed at least once during this seven-year period. Part of the tetrad survey data (a minimum of eight squares in each  $10 \text{km}^2$  hectad) were obtained directly from the national BTO atlas data (Balmer et al., 2013), the surveys for which were conducted between 2007 and 2011. The remainder of all tetrad surveys was organised directly by Devon Birds and were carried out in 2012 and 2013 using identical methodology. In addition to mapping the presences of birds using Timed Tetrad Visit data, the Devon Bird Atlas book also included a category for tetrads in which species were observed using anecdotal records (e.g. BTO Roving Records, Birdtrack) (Beavan and Lock, 2016). These anecdotal records were not included in this study, with only the presence data from standardised Timed Tetrad Visit considered, as the aim of this study was to compare standardised surveys with citizen science initiatives.



**Figure 6.2:** Promotional flyer for the Devon Cuckoo citizen science project.

#### 6.3.3 Analysis

All data were mapped and processed using QGIS (QGIS Development Team, 2009). The grid references at which Cuckoo were recorded as part of the citizen science initiative were converted into presences or absences within Ordnance Survey tetrads to allow comparability with the Devon Bird Atlas data. Statistical analyses were carried out in R (R Core Team, 2015). Chi-squared tests were used to compare total tetrad occupancy (the number of tetrad squares in Devon in which Cuckoo were recorded) between both approaches. To quantify the degree of similarity between the two Devon Cuckoo maps, the Jaccard similarity coefficient and the Baroni-Urbani & Buser coefficient were used (Jaccard, 1901; Baroni-Urbani and Buser, 1976). Jaccard similarity coefficient quantifies similarity in the recorded presences between the two approaches; it captures the extent to which the Devon Bird Atlas and citizen science project agree on where Cuckoos are present. It is calculated using the following formula:

$$J = \frac{c}{a+b-c}$$

where a is the number of tetrads in which Cuckoo were recorded in the Devon Bird Atlas survey, and b is the number of tetrads with Cuckoo records in the citizen science project. The variable c represents the number of tetrads in which both surveys recorded Cuckoo.

The Baroni-Urbani & Buser coefficient complements the Jaccard similarity coefficient by also considering absences in the data (Marcia Barbosa et al., 2012), thereby comparing the overall agreement between the two survey approaches regarding whether or not Cuckoos are present. It is calculated as follows:

$$B = \frac{\sqrt{cd} + c}{\sqrt{cd} + a + b - c}$$

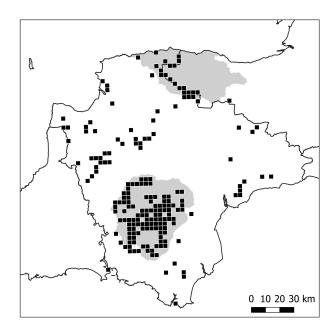
with the variable d indicating the number of tetrads in which Cuckoo records are absent in both the Devon Atlas and citizen science approach.

As previous research has shown that Cuckoo can roam across areas larger than a tetrad square (see introduction), we repeated these analyses after converting the data into Ordnance Survey hectads (10km<sup>2</sup> squares) to compare findings. Finally, we use a Chi-squared test to assess similarity in the relative importance of the upland National Parks (including only the Devon part of Exmoor) as a stronghold for Cuckoo between the Atlas survey and citizen science methods.

# 6.4 Results

#### 6.4.1 Atlas findings

Figure 6.3 shows the Cuckoo presence map based on the Devon Bird Atlas Timed Tetrad Visit data. Cuckoo were recorded in 195 out of Devon's 1858 tetrads, a proportion occupancy of 10% (See Table 6.1).



**Figure 6.3:** Ordnance survey tetrads in which Cuckoos were recorded to be present as part of the Devon Bird Atlas surveys. Grey shading shows Dartmoor and Exmoor National Parks.

Table 6.1: A comparison of the number of Devon tetrads  $(2\text{km}^2)$  in which Cuckoo were recorded through the two different survey methods. The table also shows the total number of tetrads with records (regardless of survey method), and the overlap between the two surveys. The last column shows the proportion of all tetrads in which Cuckoo were recorded, out of a total of 1858 Devon tetrads.

	No. of tetrads with records	Proportion of all tetrads
Devon Bird Atlas	195	0.10
Citizen science	406	0.22
Combined (either survey)	470	0.25
Overlap (both surveys)	131	0.07

#### 6.4.2 Citizen science findings

The citizen science initiative proved highly successful, receiving a substantial amount of attention in local newspapers, local magazines and on social media. A total of 3,166 records were submitted to the website over the four years by 1206 different individuals. The majority of records were for birds heard (58%) and birds both seen and heard (18%). Birds were seen but not heard in 11% of records, and the remaining 13% of records did not report whether birds were seen or heard. Data checks revealed that for 150 records a non-existent or incomplete grid reference was submitted, and 69 records were received for locations outside the boundaries of the county of Devon. These records were removed, resulting in a final count of 2,947 records (Figure 6.4).

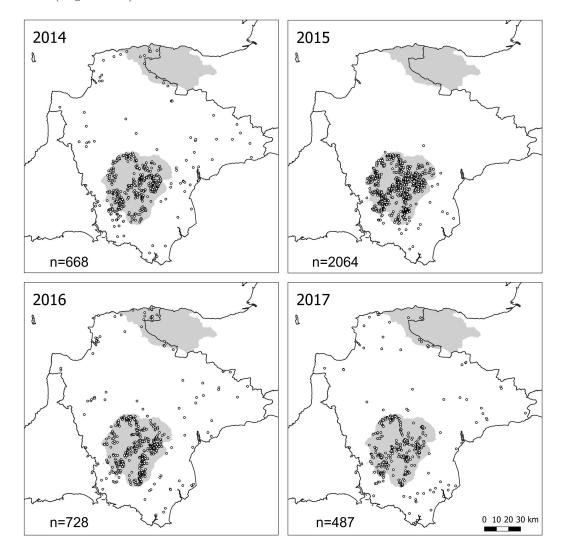


Figure 6.4: Locations of Cuckoos recorded in Devon between 2014 and 2017 as part of a citizen science survey. Each panel shows the recorded locations for an individual year; the citizen science survey was active from 2014 to 2017.

Figure 6.5 shows maps of the locations at which Cuckoos were recorded as part

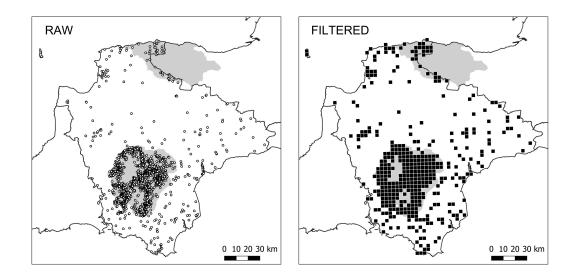


Figure 6.5: Locations of Cuckoos recorded in Devon between 2014 and 2017 as part of a citizen science survey. The left panel shows the locations at which a Cuckoo was reported to be observed (raw). The right panel shows these locations after conversion to presences in Ordnance Survey tetrads (filtered).

of the citizen science initiative across all four survey years, and the Ordnance survey tetrads in which these recordings were located. Cuckoo were reported in 406 tetrad, representing 22% of all Devon tetrads (see Table 6.1).

#### 6.4.3 Comparing survey method findings

Figure 6.6 shows the records from both survey methods and the overlap between them. Out of a total of 1858 tetrads, 470 had records of Cuckoo when both survey methods were included (25% of all tetrads). There was an overlap between methods for 131 tetrads, with Cuckoo recorded by both surveys in those squares (see Table 6.1).

The proportion of all Devon tetrads with Cuckoo records was significantly different between the Devon Bird Atlas and the citizen science initiative (Chi-squared test,  $\chi^2=87.6$ , p<0.001). The Jaccard similarity coefficient shows a similarity of 0.28, showing that in 28% of tetrads with Cuckoo records both survey methods are in agreement. When also taking into consideration tetrads with absences, the Baroni-Urbani & Buser coefficient shows a similarity of 0.62.

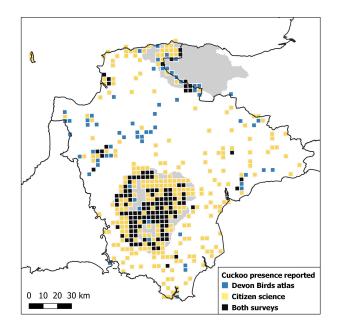


Figure 6.6: Devon Ordnance Survey tetrads with Cuckoos records based on two different survey methods. Blue squares represent tetrads in which Cuckoos were recorded as part of the Devon Bird Atlas survey, yellow squares represent tetrads in which Cuckoos were recorded through the citizen science initiative, and black squares show tetrads in which Cuckoo were recorded through both survey methods.

#### 6.4.4 Upscaling to hectads

Figure 6.7 show a map of Cuckoo presences from both survey methods after upscaling the data into Ordnance Survey hectads. Out of a total of 95 Devon hectads, 78 have Cuckoo records. The Devon Bird atlas records 49 hectads with Cuckoo, and the citizen science initiative records 73. In 44 hectads, both approaches record Cuckoo (Table 6.2.

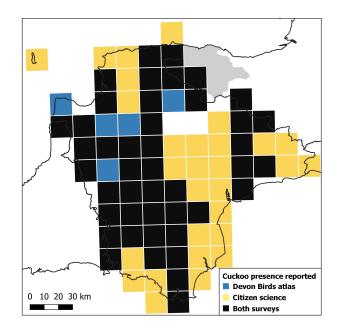


Figure 6.7: Devon Ordnance Survey hectads with Cuckoos recorded to be present based on two different survey methods. Blue squares represent hectads in which Cuckoos were recorded as part of the Devon Bird Atlas survey methods (which surveyed each Devon square), yellow squares represent hectads in which Cuckoos were opportunistically recorded through the citizen science initiative. Black squares show hectads in which Cuckoo were recorded in both survey methods.

Table 6.2: A comparison of the number of Devon hectads  $(10 \text{km}^2)$  in which Cuckoo were recorded through the two different survey methods. The table also shows the total number of hectads with records (regardless of survey method), and the overlap between the two surveys. The last column shows proportion of all hectads in which Cuckoo were recorded, out of a total of 95 Devon hectads.

	No. of hectads with records	Proportion of all hectads
Devon Bird Atlas	49	0.52
Citizen science	73	0.77
Combined (either survey)	78	0.82
Overlap (both surveys)	44	0.46

As was the case in the tetrad analyses, there was a significant difference between the two survey methods in the total proportion of hectads with Cuckoo records (Chisquared test,  $\chi^2=12.1$ , p<0.001). A Jaccard similarity coefficient of 0.56 shows that in 56% of tetrads with Cuckoo records, both approaches have recorded Cuckoo to be present. The Baroni-Urbani & Buser coefficient for the hectad data is 0.68.

## 6.4.5 Upland importance

The grey shading in Figure 6.6 shows the location of Exmoor and Dartmoor National Parks, and the tetrads with recorded Cuckoo located within the National Parks. When both approaches are considered, 258 out of 470 tetrads (55%) with Cuckoo records are fully or partly located in Dartmoor and Exmoor National Parks (Table 6.3). The Devon Bird Atlas records 69% of all records in the National Parks (134 out of 195 tetrads with Cuckoo), the citizen science initiative 59% (240 out of 406 records). There is a significant difference between the two survey methods in the proportion of occupied tetrads located in the National Parks (Chi-squared test,  $\chi^2=4.8$ , p<0.03).

**Table 6.3:** The number and proportion of Devon tetrads (2km<sup>2</sup>) with Cuckoo recorded (partially) inside and outside the boundaries of Dartmoor and Exmoor National Parks (NPs).

	Cuckoo tetrads in NPs	Cuckoo tetrads in Devon	Proportion
Devon Bird Atlas	134	195	0.69
Citizen science	240	406	0.59
Combined	258	470	0.55

## 6.5 Discussion

#### 6.5.1 Citizen science findings

The number of records for Cuckoo and the spatial distribution of these records varied across the study years in the citizen science initiative. For example, in 2015, very few records were submitted from outside Dartmoor National Park. We strongly suspect, however, that these differences are in the promotional activity of this initiative, rather than a true absence of Cuckoos in the lowland areas in that year. In 2015 promotion in Dartmoor visitor centres still took place, but wider promotional coverage in Devon media was limited, which skewed the number of records towards the Dartmoor area. As the citizen science initiative collects presence data only, not absence data, these differences in coverage across years do not limit the analyses regarding where Cuckoo are present (but absences cannot be inferred). However, this variation between years does illustrate the importance of extensive promotion of such opportunistic citizen science projects across the entire spatial area of interest, and emphasises the value of running initiatives over longer time periods (e.g. multiple seasons) to maximise data collection; it is likely that true distributions are more accurately represented when a larger number of data points are collected (Paul et al., 2014).

As outlined in the introduction, there are limitations in the use of opportunistically collected citizen science data. Mis-identifications could constitute part of the Cuckoo records. In addition, some records might be submitted with incorrect grid references. The risk of misidentification could not be mitigated, but this possibility was assumed to be minimal here given that both the Cuckoo's call and appearance are relatively distinct and therefore readily recognised by non-birders. This supposition was supported by a study on school pupils and university students, who successfully identified Cuckoo in 98% of cases when presented with its call and picture, in 89% of cases when presented with only its call, and in 37% of cases when presented with only its picture (Prokop and Rodak, 2009). This compared to an average identification success, for 25 other species tested in that study, of 45% for call/song+picture, 19% for call/song only, and 39% for picture only, illustrating that Cuckoo identification based on its call is relatively successful (Prokop and Rodak, 2009). The fact that the far majority of records in the Devon Cuckoo citizen science initiative were for Cuckoos heard or both seen and heard, gives confidence of correct identification in the majority of reports.

The risk of incorrect grid reference reporting was minimised by providing a link

to a map at which grid references for visited locations could be easily obtained. However, errors in map-reading mean that mistakes in grid references are possible. Further work on validating the location references with participants would be needed to quantify the error in location reporting, but such a test was not conducted in this study due to limitations in time and resources. Furthermore, as records are submitted across the entire spring and summer season, some records are likely to represent birds on passage, rather than Cuckoo territories. Whilst this limits the use of the data for certain applications, such as studies of Cuckoo breeding sites, this approach does help provide informative broader information of the range of areas and habitats used by Cuckoos throughout their time in Devon. Further data processing, such as excluding records from the migratory period, could be used to tailor the data to wider uses. Spatial bias is an additional limitation of the opportunistic data collection; coverage will inevitably be higher at sites nearer towns and hotspots for tourism and birdwatching, and false absences are therefore more likely in areas which are less frequented. This was illustrated across a range of taxa, including birds, by Mair and Ruete (2016), who showed that road access and population density can explain sampling bias in citizen science studies. Pseudo-replication is also likely to be high with a species as mobile as the Cuckoo, with the same birds potentially being reported in multiple Ordnance Survey tetrads across the season. Whilst this means that the records from this opportunistic citizen science initiative cannot be used to infer information on, for example, population size, this method can nonetheless be successfully used to inform on the areas and habitats which support Cuckoo.

All in all, the citizen science initiative was highly successful in collecting comprehensive information on potential Cuckoo presence sites in Devon, and as the locations of Cuckoo observations are recorded by grid reference, further groundtruthing could be used if future studies are desired; further visits could for example be used to confirm Cuckoo presences, identify breeding sites, and to study Cuckoo habitats and breeding sites in more detail.

#### 6.5.2 Comparisons between approaches

The citizen science initiative recorded Cuckoo presences in more than double the Devon tetrads compared to the Devon Bird Atlas. Although misidentification and misplaced grid references could lead to some false presence data in the opportunistic citizen science study (see discussion earlier in this section), it is likely that many of these additional occupied tetrads (compared to the Atlas approach) represent true Cuckoo presences that were not picked up by the Atlas approach. This is due to the fact that in the Atlas survey, tetrads were only visited twice for 1-2 hours per year (with many tetrads visited only once during the 2007-2013 survey period). In addition, only part of the tetrad was visited as a pre-planned route is used. These factors make it likely that the Devon Bird Atlas data contains numerous falsenegatives, with Cuckoo using tetrads, but not observed there during the brief survey visit (i.e. the Cuckoo may have been present near the survey route but not observed by the recorder, or the Cuckoo was present in a different area during the time of the survey). The issue of false-negatives in species detection is widely described, with studies showing that species are less likely to be recorded when they are, for example, low in density, small in size, or located further away from the survey route (Diefenbach et al., 2003; Lee and Barnard, 2017). Using a case study of 20-minute bird surveys on 2-hectare sites, Tyre et al. (2003) recommended that at least three visits are needed so that false-negatives rates can be accurately quantified. The fact that the citizen science initiative records Cuckoos in a significantly larger number of tetrads compared to the Atlas data, suggests that Cuckoo are likely more widespread across Devon than the Atlas data has indicated. Furthermore, when records from both approaches are combined, we find that Cuckoos may make use of a quarter of all Devon tetrads, although further verification of citizen science records, as well as a quantification of false absence rates in the Atlas survey, would be needed to provide further insights on this.

When considering tetrads with absences, the two approaches showed substantially greater similarity. As highlighted by Lewandowski and Specht (2015) and Aceves-Bueno et al. (2017), there is not currently a minimum level of similarity between citizen science and expert data at which results are considered adequate for further use, and furthermore, a wide range of different methods are used to compare opportunistic citizen science data with other survey methods (Aceves-Bueno et al., 2017), making it difficult to directly compare the findings from this study with others. However, previous studies suggest that recorded similarity in species distribution findings vary between opportunistic citizen science and expert surveys. For example, a study which compared standardised expert and opportunistic volunteer surveys in detecting mammals along a highway in Canada found agreement between the two methods as long as sample sizes were high enough (Paul et al., 2014). Similarly, in a study on White-tailed Ptarmigan (Lagopus leucura), Jackson et al. (2015) found that species distribution modelling using field survey data and citizen science data yielded comparable results. Conversely, a study comparing expert and layman citizen science initiatives for Bumblebee recording in the UK found that different spatial biases in the respective approaches led to different distribution results, although abundance data was comparable between the two survey methods (van der Wal et al., 2015). Meanwhile, a comparison of the US Breeding Bird Survey and eBird data (similar to Devon Atlas and Cuckoo citizen science project methodology respectively, albeit at much larger scale), found that the relative performance of the two approaches in determining distributional patterns differed depending on which species was considered (Munson et al., 2010).

From this study on Cuckoo surveys in Devon, we can conclude that whilst there are some similarities in the results obtained by the two different survey methods, the two approaches give statistically different results in terms of the occurrences of the Cuckoo in Devon. From this study, it is not possible to derive which survey method is better, and the usefulness of each approach will be dependent on the wider uses and applications. When, for example, a subset of Cuckoo habitats needs to be selected for further in-depth study, the Atlas approach with its use of experienced recorders, would give a more certain indication of sites with definite Cuckoo presences which would be suitable for further study. However, if there is an interest in finding out all the potential areas which may be of importance for Cuckoo conservation in Devon, the citizen science approach, or the use of both approaches in conjunction, is less likely to lead to key sites being overlooked. Such benefits of combining opportunistic citizen science surveys with expert data collection is confirmed by other studies conducting similar survey comparisons (van der Wal et al., 2015). For example, a study on butterflies across Canada found that phenology and species richness estimates were improved when combining professional and citizen science results (Soroye et al., 2018).

#### 6.5.3 Hectad analysis

When the analysis was upscaled to Ordnance Survey hectads, the spatial resolution should be more representative of Cuckoo territory size, and indeed we found much higher agreement between the two survey approaches than in the tetrad analysis (56% vs. 28% agreement in Cuckoo presence locations). However, we still found a significant difference in the proportion of tetrads with Cuckoo records between the two survey approaches at the hectad scale. The similarity between the two survey approaches when also considering absences shows good agreement between the hectad and tetrad analyses (0.68 vs. 0.62 similarity coefficients). The results suggest that whilst significantly different in proportion occupancy, the two different scales of analyses are nonetheless in agreement on Cuckoo presences and absences in the majority of areas in Devon. As Cuckoos likely roam over areas larger than a tetrad (see introduction), the comparison between survey approaches at the hectad level is more representative of true Cuckoo range size. However, it should be noted that investigating Cuckoo distributions at the coarser resolution is likely of limited relevance for further studies or management decision-making, as Cuckoos will not use all sites and habitats within the 10km<sup>2</sup> area. The tetrad approach is therefore deemed to have more relevance for informing future work, with a need to keep the wider Cuckoo range sizes in mind when designing follow-up work.

#### 6.5.4 Upland importance

The maps for both approaches show that by far the majority of records originated from Dartmoor. Another hotspot for Cuckoo was Exmoor, the other Devon National Park located in the north of the county (as well as in Somerset). The citizen science map and atlas broadly align with previous studies of Cuckoo distribution. For example, the BTO bird atlas for Britain and Ireland also indicates that Dartmoor and Exmoor are Cuckoo hotspots in Devon (Balmer et al., 2013). It should be emphasised however that the Devon Bird Atlas data consists partly of data from this national atlas, and the two are therefore not independent. When we compare the Devon Bird atlas and Citizen science initiative, we find a significant difference in the proportion of occupied tetrads located in the upland National Parks. In the Devon Bird Atlas work, significantly more of the occupied tetrads were located in the uplands compared to the citizen science approach (69% vs 59%). Whilst both approaches clearly illustrate that uplands are of key importance as habitat for Cuckoo, the citizen science work suggests that there may be more remaining lowland Cuckoo sites than appear to be the case when considering the Devon Atlas data alone. Findings from the citizen science initiative therefore suggests that the lowlands may still be of slightly more importance to Cuckoo than previously thought, and continuing to focus Devon Cuckoo research and conservation efforts in areas outside Exmoor and Dartmoor would be worthwhile.

## 6.5.5 Conclusions

In this study, we compared findings on Cuckoo occurrences in Devon between a systematic survey with experienced volunteers, and an opportunistic citizen science initiative. In the context of the Cuckoo in Devon, the value of the citizen science initiative has been the identification of potential additional hotspots of Cuckoo in Devon beyond the sites already mapped in the Devon Bird Atlas. This illustrates the need to protect a broad range of sites and habitats for avian conservation across the wider Devon landscape. In addition, the citizen science records map can be used in future studies to investigate potential, previously unknown, breeding sites and build on the ongoing study of Cuckoo breeding ecology in Devon. An added benefit of this citizen science initiative was the resulting outreach and awareness-raising on the Cuckoo in Devon through media coverage over the four years (see appendix for examples of media coverage).

More generally, we find that whilst there are some noticeable similarities in the resulting occurrence maps, the two different surveying approaches provide statistically different information on species presences. This work highlights the fact that the survey approach employed in species distribution surveys will affect the results obtained. We describe that the similarities in findings between opportunistic citizen science projects and standardised surveys vary between studies, and the studies described above illustrate the usefulness of cross-checking opportunistic citizen science findings with expert data when available. In addition, statistical approaches should be used to determine optimal sample sizes where possible (Guillera and Lahoz-Monfort, 2012). Other improvements, such as volunteer training and statistical methods for improving data processing, have been suggested to further improve data quality (Lewandowski and Specht, 2015).

Finally, when designing methods for species distribution studies, regardless of whether this is a traditional professional ecological survey, a volunteer-run standardised survey, or an opportunistic citizen-science based project, the advantages and limitations of each approach should be considered and made explicit. Only then can researchers design suitable follow-up studies, and can land managers make optimal use of the data for conservation and decision-making.

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## References

- Aceves-Bueno, E., Adeleye, A., Feraud, M., Huang, Y., Tao, M., Yang, Y., & Anderson, S. The Accuracy of Citizen Science Data: A Quantitative Review. *The Bulletin of the Ecological Society of America*, 98:278–290, 2017.
- Balmer, D., Gillings, S., Caffrey, B., Swann, R., Downie, I., & Fuller, R. Bird Atlas 2007-2011: The breeding and wintering birds of Britain and Ireland. *BTO*, *Thetford*, 2013.
- Baroni-Urbani, C. & Buser, M. Similarity of binary data. Systematic Biology, 25: 251–259, 1976.
- Beavan, S. & Lock, M. Devon Birds Atlas 2007-2013. Devon Birds, 2016.
- Belmaker, J., Zarnetske, P., Tuanmu, M., Zonneveld, S., Record, S., Strecker, A., & Beaudrot, L. Empirical evidence for the scale dependence of biotic interactions. *Global Ecology and Biogeography*, 24:750–761, 2015.
- Brooke, M. D. L. & Davies, N. B. Recent changes in host usage by Cuckoos Cuculus canorus in Britain. Journal of Animal Ecology, 56(3):873–883, 1987.
- Conrad, K. F., Warren, M. S., Fox, R., Parsons, M. S., & Woiwod, I. P. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, 132:279–291, 2006.
- Costello, E., Lauber, C., Hamady, M., Fierer, N., Gordon, J., & Knights, R. Bacterial Community Variation in Human Body Habitats Across Space and Time. *Science*, 326:1694–1697, 2009.
- Crall, A., Newman, G., Stohlgren, T., Holfelder, K., Graham, J., & Waller, D. Assessing citizen science data quality: and invasive species case study. *Conservation Letters*, 4:433–442, 2011.
- Davies, Z., Wilson, R., Brereton, T., & Thomas, C. The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. *Biological Conservation*, 124:189–198, 2005.
- Denerley, C., Redpath, S., van der Wal, R., Newson, S., Chapman, J., & Wilson, J. Breeding ground correlates of the distribution and decline of the Common Cuckoo *Cuculus canorus* at two spatial scales. *Ibis*, 161:346–358, 2019.

- Dickinson, J., Zuckerberg, B., & Bonter, D. Citizen Science as an Ecological Research Tool: Challenges and Benefits. Annual Review of Ecology, Evolution and Systematics, 41:149–172, 2010.
- Dickinson, J., Shirk, J., Bonter, D., Bonney, R., Crain, R., Martin, J., Phillips, T., & Purcell, K. The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment*, 10:291–297, 2012.
- Diefenbach, D., Brauning, D., & Mattice, J. Variability in grassland bird counts related to observer differences and species detection rates. *The Auk*, 120:1168– 1179, 2003.
- Engelbrecht, B., Comita, L., Condit, R., Kursar, T., Tyree, M., Turner, B., & Hubbell, S. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, 447:80, 2007.
- Gillings, S., Balmer, D. E., & Fuller, R. J. Directionality of recent bird distribution shifts and climate change in Great Britain. *Global Change Biology*, 21(6):2155– 2168, 2015.
- Guillera, G. & Lahoz-Monfort, J. Designing studies to detect differences in species occupancy: power analysis under imperfect detection. *Methods in Ecology and Evolution*, 3:860–869, 2012.
- Hayhow, D., Bond, A., Douse, A., Eaton, M., Frost, T., Grice, P., Hall, C., Harrist, S., Havery, S., Hearn, R., Noble, D., Oppel, S., Williams, J., Win, I., & Wotton, S. The state of the UK's birds 2016. *RSPB*, *BTO*, *WWT*, *DAERA*, *JNCC*, *NE*, *NRW and SNH*, *Sandy*, *Bedfordshire*., 2016.
- Hewson, C. M., Thorup, K., Pearce-Higgins, J. W., & Atkinson, P. W. Population decline is linked to migration route in the Common Cuckoo. *Nature Communications*, 7:12296, 2016.
- Jaccard, P. Étude comparative de la distribution florale dans une portion des Alpes et des Jura. Bulletin de la Societe Vaudoise des Sciences Naturelles, 37:547–579, 1901.
- Jackson, M., Gergel, S., & Martin, K. Citizen science and field survey observations provide comparable results for mapping Vancouver Island White-tailed Ptarmigan

(Lagopus leucura saxatilis) distributions. Biological Conservation, 181:162–172, 2015.

- Kosmala, M., Wiggins, A., Swanson, A., & Simmons, B. Assessing data quality in citizen science. Frontiers in Ecology and the Environment, 14:551–560, 2016.
- Lee, A. & Barnard, P. How well do bird atlas reporting rates reflect bird densities? Correlates of detection from the Fynbos biome, South Africa, with applications for population estimation. Ostrich, 88:9–17, 2017.
- Lenoir, J., Gegout, J., Marquet, P., de Ruffray, P., & Brisse, H. A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320: 1768–1771, 2008.
- Lewandowski, E. & Specht, H. Influence of volunteer and project characteristics on data quality of biological surveys. *Conservation Biology*, 29:713–723, 2015.
- Mair, L. & Ruete, A. Explaining Spatial Variation in the Recording Effort of Citizen Science Data across Multiple Taxa. PLOS ONE, 11:e0147796, 2016.
- Marcia Barbosa, A., Estrada, A., Marquez, A., Purvis, A., & Orme, C. Atlas versus range maps: robustness of chorological relationships to distribution data types in European mammals. *Journal of Biogeography*, 39:1391–1400, 2012.
- McCaffrey, R. Using citizen science in urban bird studies. *Urban Habitats*, 3:70–86, 2005.
- McKinley, D., Miller-Rushing, A., Ballard, H., Bonney, R., Brown, H., Cook-Patton, S., Evans, D., French, R., Parrish, J., Phillips, T., Ryan, S., Shanley, L., Shirk, J., Stepenuck, K., Weltzin, J., Wiggins, A., Boyle, O., Briggs, R.D.and Chapin III, S., Hewitt, D., Preuss, P., & Soukup, M. Citizen science can improve conservation science, natural resource management, and environmental protection. *Biological Conservation*, 208:15–28, 2017.
- Moskat, C., Ban, M., Fulop, A., Bereczki, J., & Hauber, M. Bimodal habitat use in brood parasitic Common Cuckoos (*Cuculus canorus*) revealed by GPS telemetry. *The Auk*, 136:1–12, 2019.
- Munson, M., Caruana, R., Fink, D., Hochachka, W., Iliff, M., Rosenberg, K., Sheldon, D., Sullivan, B., Wood, C., & Kelling, S. A method for measuring the relative information content of data from different monitoring protocols. *Methods* in Ecology and Evolution, 1:263–273, 2010.

- Newson, S., Woodburn, R., Noble, D., Baillie, S., & Gregory, R. Evaluating the Breeding Bird Survey for producing national population size and density estimates. *Bird Study*, 52:42–54, 2005.
- Paul, K., Quinn, M., Huijser, M., Graham, J., & Broberg, L. An evaluation of a citizen science data collection program for recording wildlife observations along a highway. *Journal of Environmental Management*, 139:180–187, 2014.
- Peach, W., Baillie, S., & Balmer, D. Long-term changes in the abundance of passerines in Britain and Ireland as measured by constant effort mist-netting. *Bird Study*, 45:257–275, 1998.
- Prokop, P. & Rodak, R. Ability of Slovakian pupils to identify birds. Eurasia Journal of Mathematics, Science & Technology Education, 5:127–133, 2009.
- QGIS Development Team. *QGIS Geographic Information System*. Open Source Geospatial Foundation, 2009.
- R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2015.
- Ruttenberg, B., Schofield, P., Akins, J., Acosta, A., Feeley, M., Blondeau, J., Smith, S., & Ault, J. Rapid invasion of Indo-Pacific lionfishes (*Pterios volitans* and *Pterois miles*) in the Florida Keys, USA: Evidence from multiple pre- and postinvasion data sets. *Bulletin of Marine Science*, 88:1051–1059, 2012.
- Sauer, J., Fallon, J., & Johnson, R. Use of North American Breeding Bird Survey Data to Estimate Population Change for Bird Conservation Regions. *The Journal* of Wildlife Management, 67:372–389, 2003.
- Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A. S. L., Stuart, S. N., Temple, H. J., Baillie, J., Boitani, L., Lacher Jr, T. E., Mittermeier, R. A., Smith, A. T., Absolon, D., Aguiar, J. M., Amori, G., Bakkour, N., Baldi, R., Berridge, R. J., Bielby, J., Black, P. A., Blanc, J. J., Brooks, T. M., Burton, J. A., Butynski, T. M., Catullo, G., Garshelis, D. L., Gates, C., Gimenez-dixon, M., Gonzalez, S., Gonzalez-Maya, J. F., Good, T. C., Hammerson, G., Hammond, P. S., Happold, D., Happold, M., Hare, J., Harris, R. B., Hawkins, C. E., Haywood, M., Heaney, L. R., Hedges, S., Helgen, K. M., Hilton-taylor, C., Hussain, S. A., Ishii, N., Jefferson, T. A., Jenkins, R. K. B., Johnston, C. H., Keith, M., Kingdon, J., Knox,

D. H., Kovacs, K. M., Langhammer, P., Leus, K., Lewison, R., Lichtenstein, G., Lowry, L. F., Macavoy, Z., Medellín, R. A., Medici, P., Mills, G., Moehlman, P. D., Molur, S., Mora, A., Nowell, K., Oates, J. F., Olech, W., Oliver, W. R. L., Oprea, M., Patterson, B. D., Perrin, W. F., Polidoro, B. A., Pollock, C., Powel, A., Protas, Y., Racey, P., Ragle, J., Ramani, P., Rathbun, G., Reeves, R. R., Reilly, S. B., Reynolds III, J. E., Rondinini, C., Rosell-ambal, R. G., Rulli, M., Rylands, A. B., Savini, S., Schank, C. J., Sechrest, W., Self-sullivan, C., Shoemaker, A., Sillero-zubiri, C., Silva, N. D., Smith, D. E., Taylor, B. L., Timmins, R., Tirira, D. G., Tognelli, M. F., Tsytsulina, K., Veiga, L. M., Vié, J.-C., Williamson, E. A., Wyatt, S. A., Xie, Y., & Young, B. E. The status of the world's land and marine mammals: Diversity, threat and knowledge. *Science*, 322: 225–230, 2008.

- Schmeller, D., Henry, P., Julliard, R., Gruber, B., Clobert, J., Dziock, F., Lengyel, S., Nowicki, P., Deri, E., Budrys, E., Kull, T., Tali, K., Bauch, B., Settele, J., van Swaay, C., Kobler, A., Babij, V., Papastergiadou, E., & Henle, K. Advantages of volunteer-based biodiversity monitoring in Europe. *Conservation Biology*, 23: 307–316, 2008.
- Silvertown, J. A new dawn for citizen science. *Trends in Ecology & Evolution*, 24: 467–471, 2009.
- Sitters, H.P. *Tetrad Atlas of the Breeding Birds of Devon*. Devon Birdwatching and Preservation Society, 1988.
- Snall, T., Kindvall, O., Nilsson, J., & Part, T. Evaluating citizen-based presence data for bird monitoring. *Biological Conservation*, 144:804–810, 2011.
- Soroye, P., Ahmed, N., & Kerr, J. Opportunistic citizen science data transform understanding of species distributions, phenology and diversity gradients for glocal change research. *Global Change Biology*, 24:5281–5291, 2018.
- Tyre, A., Tenhumberg, B., Field, S., Niejalke, D., Parris, K., & Possingham, H. Improving precision and reducing bias in biological surveys: estimating falsenegative error rates. *Ecological Applications*, 13:1790–1801, 2003.
- van der Wal, R., Anderson, H., Robinson, A., Sharma, N., Mellish, C., Roberts, S., Darvill, B., & Siddharthan, A. Mapping species distributions: A comparison of skilled naturalist and lay citizen science recording. *Ambio*, 44:S584–S600, 2015.

- Vogl, W., Taborsky, B., Teuschl, Y., Taborsky, M., & Honza, M. Habitat and space use of European Cuckoo females during the egg laying period. *Behaviour*, 141: 881–898, 2004.
- Wich, S., Fredriksson, G., Usher, G., Peters, H., Priatna, D., Basalamah, F., Susanto, W., & Kuhl, H. Hunting of Sumatran orang-utans and its importance in determining distribution and density. *Biological Conservation*, 146:163–169, 2012.
- Williams, H., Willemoes, M., Klaassen, R., Strandberg, R., & Thorup, K. Common Cuckoo home ranges are larger in the breeding season than in the non-breeding season and in regions of sparse forest cover. *Journal of Ornithology*, 157:461–469, 2016.

# Chapter 7

## **General Discussion**



"I think nature's imagination is so much greater than man's, she's never going to let us relax" - Richard P. Feynman

#### 7.1 Overview

This chapter provides an overview of the main objectives of the thesis, discusses how each objective was met, and highlights the main findings. It then summarises the contribution of new knowledge delivered by the work presented in this thesis, and the wider implications of the findings. Lastly, it discusses the limitations of the work, and provides directions for further study.

#### 7.2 Delivery of thesis objectives

The overarching aims of this thesis were to build an increased understanding of the breeding ecology of ground-nesting birds in Dartmoor National Park, and to assess the use of citizen science for deriving information about species distributions. These aims are met through the following objectives:

- i) To assess avian biodiversity on a site of conservation interest.
- ii) To measure baseline breeding parameters, and interannual variation therein, for three ground-nesting bird species.
- iii) To determine timing of breeding of these species.
- iv) To assess potential conflicts between land management and bird breeding, and to suggest changes in current management to alleviate potential impacts.
- v) To understand nest site choice and potential associations with breeding success.
- vi) To test for associations between habitat characteristics and breeding performance.
- vii) To compare opportunistic citizen science data and systematic volunteer surveys for understanding Cuckoo distributions in Devon.

In the sections below, we briefly discuss how this thesis addressed each objective, and summarise key findings.

#### 7.2.1 Assessing avian biodiversity

The first objective of this thesis was to assess avian biodiversity on an upland moorland site of conservation interest. Using nine years of nest record data, Chapter 2

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delivered this objective by assessing the diversity of breeding bird species on a Dartmoor moorland site of conservation management relevance; both the site's landowners and the Dartmoor National Park Authority expressed strong interest in understanding the importance of the site for breeding bird species. Nests of a total of 34 species were recorded, and a comparison with previous studies in similar habitats in the UK and Ireland showed that our Dartmoor study site may support a relatively high diversity of species (Bracken et al., 2008; Dallimer et al., 2010; Newey et al., 2016). The information derived from this work therefore provides land managers with evidence on the bird conservation importance of this site. The information is accessible to land managers for future use; summary data has been provided to the Dartmoor National Park Authority, and the raw nest data is held by Sara Zonneveld and Charles Tyler, as well as having been submitted as nest records to the British Trust for Ornithology.

#### 7.2.2 Baseline breeding parameters and interannual variation

The second aim of this thesis was to measure baseline breeding parameters, and interannual variation therein, for three ground-nesting bird species. In Chapter 2, this objective was addressed by studying clutch size, brood size and nest success over nine years in Meadow Pipit, Stonechat and Whinchat nests. For all three species, breeding parameters were generally in line with those reported in other studies across Europe; the only difference was a slightly lower clutch size in Meadow Pipit compared with other studies (see for example Fuller and Glue (1977); Pavel et al. (2000); Evans et al. (2005)). Clutch sizes were very consistent across years, as was found in previous studies (e.g. Revaz et al. (2008)). Minor interannual variation was seen in brood size in Meadow Pipit and Stonechat, and nest success was highly variable between years in all three species.

#### 7.2.3 Timing of breeding

The third aim of this thesis was to determine timing of breeding of Meadow Pipit, Stonechat and Whinchat. This was investigated in Chapter 3. Across the years of the study, we found that median hatch weeks fell in late April for Stonechat, mid- to late May for Meadow Pipit and early June for Whinchat. Although general overlap in the breeding seasons of the three species was shown, the onsets, peaks and lengths of the breeding seasons differed substantially between the species, which is consistent with UK studies of these species at a broader spatial scale (see for example Joys and Crick (2004)). Interannual variability in the three species was shown to be in line with that of other passerine species (Wright et al., 2009; Hušek et al., 2012).

#### 7.2.4 Conflicts between bird breeding and land management

One of the main findings of this thesis was related to the fourth objective, which was to assess potential conflicts between land management and bird breeding. Using seven years of data on Meadow Pipit, Stonechat and Whinchat breeding, Chapter 3 quantified the percentage of nests which are active during permitted periods of vegetation burning and bracken control. It was found that neither the national burning guideline nor Dartmoor National Park's voluntary burning code fully avoid overlap between vegetation burning and the breeding seasons of Stonechat and Meadow Pipit. A similar conflict was found for Bracken control, where permitted start dates from current agreements were found to have substantial overlap with the breeding activity of all three species. As vegetation burning and mechanical Bracken control will inevitably cause nest destruction and may also threaten recent fledglings (Tome and Denac, 2012), this conflict in timing could represent a substantial impact on the local reproductive performance of these species. The key findings from this study were provided to the Dartmoor National Park Authority for use in decision-making.

#### 7.2.5 Nest site choice

The fifth objective of this thesis was to understand nest site choice and potential associations with breeding success. Using five years of data on Meadow Pipit, Stonechat and Whinchat nest locations, nest site choice was explored in Chapter 4 in the context of topographical components of microclimate (solar coefficient and altitude). It was found that only Whinchat showed potential selection for these factors; they used higher altitudes and lower solar coefficients compared with the full range of available nesting sites on the study site. Whinchat at the study site appeared to show a preference for higher altitudes compared to a recent UK study conducted at a similar latitude (Border et al., 2017). Significant interspecific differences in both altitude and solar coefficient were shown between Meadow Pipit, Stonechat and Whinchat at this study site, despite large overlap between the three species in both these variables. This suggests that these three co-occurring species may differ in their nesting requirements, and that they potentially show some niche-partitioning even at the very local scale investigated in this study. The objective of studying associations of the microclimatic variables with breeding success was also met; the study looked at the relationship between daily nest success rates and altitude and solar coefficient, however in none of the three species such a relationship was found.

#### 7.2.6 Habitat characteristics and breeding performance

The sixth objective of this thesis was to test for associations between habitat characteristics and breeding performance. As upland landscapes are highly influenced by grazing and vegetation management, a thorough understanding of the links between habitat characteristics and breeding performance is essential. This thesis explored these associations at the scale of the foraging habitat around Meadow Pipit nests, using two years of data on vegetation cover, nest success and nestling growth rates (Chapter 5). Nestling growth rates at this study site were found to be in line with those reported in previous studies (Seel and Walton, 1979; van Oosten, 2016). No association was found between breeding performance (nest failure rate or nestling growth rate), and the amount of four main vegetation cover types around the nest site. Although previous work has shown that Meadow Pipit actively select foraging locations with heterogeneity in vegetation height (Vandenberghe et al., 2009), we found no association between breeding performance and habitat diversity (the measure of which included habitat categories of varying heights).

## 7.2.7 Comparing citizen science surveys for mapping Cuckoo occurrences

The final aim of this thesis was to compare opportunistic citizen science data and systematic volunteer surveys for understanding Cuckoo distributions in Devon. A comparison of the Devon Bird Atlas (a standardised distribution survey) and opportunistic collection of Devon Cuckoo observations was made. We find that although the Cuckoo occurrence maps produced through the two methods show substantial similarities regarding for example key hotspots, significant differences in proportion occupancy are found. Similarity between the two methods increased when results were aggregated to a scale more reflective of Cuckoo range size, although significant differences remained. We conclude that opportunistic surveys can be helpful in identifying potential Cuckoo hotspots which may be overlooked by the shorter survey duration in more systematic surveys. There is not currently an agreed "adequate" level of similarity between different methods in the literature (Lewandowski and Specht, 2015; Aceves-Bueno et al., 2017), and in order to better understand the advantages and limitations of the different survey approaches, we recommend that more work is needed to establish the error in both methodologies.

#### 7.3 Contribution to new knowledge and wider implications

#### 7.3.1 Breeding ecology

The nest-recording work which underpinned most of the chapters presented in this thesis is unique in both data depth and temporal scope. Whilst nest-recording is carried out widely by volunteers across the UK, this study is one of very few long-term local nest recording studies providing data on large numbers of nests for Meadow Pipit, Stonechat, Whinchat and other ground-nesting birds. This thesis represents the first in-depth study of the nesting ecology of these species on Dartmoor. Whilst there has been recent research on the breeding ecology of the Whinchat in other UK areas and countries, in particular in the context of threats from agricultural intensification and mowing regimes (Britschgi et al., 2006; Broyer, 2009), Meadow Pipit and Stonechat breeding ecology has been relatively under-researched. This thesis has therefore established better knowledge on the breeding parameters and breeding ecology of these three species through a multi-species approach for understanding timing of breeding, breeding performance and aspects of nest site selection. This is also the first in-depth study in which extensive nest finding effort, targeting all species, was used to quantify the breeding bird diversity on a Dartmoor upland moorland study site.

The quantification of breeding parameters, as has been provided for Meadow Pipit, Stonechat and Whinchat through this study, has provided essential baseline information for monitoring purposes. Without such data, future studies cannot effectively evaluate the effects of environmental changes (e.g. climate or habitat change) and management interventions (e.g. predator control). The datasets provided through this study will therefore provide researchers and land managers with the baseline knowledge needed to be able to monitor these species into the future. Based on the fact that clutch size showed little interannual variation at this study, we can also learn that for these three species, brood size and particularly nest success are likely the most informative parameters when looking to quantify any effects of environmental changes and management interventions.

One further key finding from this work was the fact that substantial interannual variability in breeding success (nest daily failure rate) was found in all three species. This emphasises the importance of long-term studies; using a single year, or few years, of data is unlikely to provide a representative indication of the population's breeding success for these species, and cannot be used to monitor changes over time. Other studies have highlighted the need to support long-term studies, given their importance for monitoring change (Lindenmayer and Likens, 2009; Magurran et al., 2010). Lindenmayer and Likens (2009) also highlight that ideally, long-term monitoring should be adaptive, informed by clear questions and planned with statistical analyses in mind.

This study was the first, to our knowledge, to explore the importance of solar irradiance on nest site selection and breeding success in these three species. It was also likely the first to look at local-scale interspecific differences in breeding altitudes between these three species. Whilst this study showed no relationship between breeding success and altitude and solar coefficient, we did find some interspecific differences in these variables. Although no strong evidence for nest selection could be found in Whinchat and Meadow Pipit, the interspecific differences suggest that some niche partitioning may be taking place between these three species. The fact that interspecific differences in solar coefficient and altitude were found, along with the finding that Whinchat appear to select nest sites with a cooler microclimate, suggest that microclimatic conditions at the nest site may be important for these species. This could have implications regarding the types of sites which are suitable for breeding for these species, which is relevant for example in the context of future climatic shifts, or the designation of suitable conservation sites. Studying altitude, solar coefficient or related variables at a slightly broader spatial scale in areas with a broader range of altitudes and solar irradiation levels would be needed to fully understand the importance of these effects (the issue of spatial scales and the need to explore other factors are discussed later in this chapter).

#### 7.3.2 Land management and biodiversity conservation

Although many ecological questions remain unanswered, there are some important conservation and land management implications which can be derived from this thesis. The study illustrated that, as mentioned earlier in this discussion, the diversity of breeding birds appears to be relatively high compared to surveys in similar habitats and study site sizes elsewhere in the UK. The global conservation value of UK uplands was highlighted by Thompson and Macdonald (1995), who for example emphasised that five upland plant communities are virtually confined to the UK, and that the UK uplands support a range of threatened bird species and internationally important populations. The importance of uplands for species diversity was also demonstrated in other countries. For example, a study in Arizona found riparian woodlands had greater species richness when located adjacent to upland grassland habitats (Strong and Bock, 1990). The study site in this thesis supports this argument of the importance of upland habitats, with the site supporting a wide range of bird species, including numerous species of conservation concern. Our work provides a quantified narrative on the importance of the Dartmoor uplands for bird conservation, providing the evidence and leverage necessary for policy and financial support for protection of this site and similar areas.

The birds found nesting on the study site ranged from species which nest in low open grass, to species nesting in higher scrub, tussocks in boggy areas, and woodland edges. Furthermore, we showed that whilst species breed across a broad topographic and microclimatic range, species show some interspecific differences in these factors. Together, this niche diversity highlights the fact that any conservation action needs to consider the entire breeding bird community's requirements. Therefore, to safeguard avian biodiversity, we recommend that the uplands should be managed in a way which strives to provide a broad mix of vegetation types across topographically diverse areas (i.e. a range of altitudes, slopes and aspects).

The data on breeding birds and their nesting habitats has been shared with the Dartmoor National Park Authority and Dartmoor's commoners, with annual numbers of nest records and a summary of the season's findings having been prepared for these stakeholders upon completion of each breeding season. The work is thus already contributing to awareness-raising with land managers on bird diversity and avian conservation. This has led to tangible local conservation action, such as the avoidance of wildlife hotspots during land burning on the study site in later years of the study. Following from this, the knowledge of the breeding parameters of clutch size, brood size and breeding success, which were comprehensively quantified for Meadow Pipit, Stonechat and Whinchat in this thesis, can in the future be used alongside surveys of population size to evaluate the effectiveness of any conservation interventions, such as habitat management or predator control.

This study was the first to study timing of breeding on Dartmoor for these three species, and to our knowledge the first in the UK to quantify the extent of overlap between bracken control, burning and the timing of breeding of Meadow Pipit, Stonechat and Whinchat. The most tangible conservation implication of this thesis is the pressing need to consider revised timings for traditional upland management practices, such as land burning and bracken control, to avoid a potential conflict with the conservation of declining upland birds. Based on the timing of nesting activity established in this study, we would recommend that in order to minimise conflict with breeding Stonechat and Meadow Pipit, burning is carried out no later than 15 March. Informal conversations with land managers and commoners on Dartmoor suggest that such a deadline is realistic; it is thought that in most years suitable weather and soil conditions (as needed to carry out burning) should occur within this revised burning window. However, it needs to be noted that there is some disagreement on this within the hill farming community, with some concern that an earlier burning deadline may prevent burning from taking place on preferred dates due to a lack of suitable conditions. Careful communication of the value of earlier burning for breeding bird protection, and perhaps an analysis of the availability of suitable conditions within a revised burning timeframe, may be beneficial in order to evidence the importance and feasibility of a revised burning deadline. We acknowledge that due to the ecology of bracken, mechanical control measures are often only effective during part of the bracken growth cycle, and therefore full avoidance of the breeding season when carrying out control measures may not be feasible (see Chapter 3). In the case of the established timing overlap between breeding and bracken control, we therefore recommend that bracken control is avoided until the end of July to avoid the peak of the bird breeding season, and in August is avoided in known breeding hotspots. As discussed in Chapter 3, shifting the timing of vegetation management has already been proven successful in increasing breeding success in Whinchat and other ground-nesting birds (Grüebler et al., 2012; Perkins et al., 2013).

The information on timing of breeding is not only relevant for the vegetation management practices of burning control, or on Dartmoor alone. There has been wide interest in these findings as evidence of this topic is scarce, and the information from this study is already being used as a case study to support land-management decision-making processes on other Dartmoor sites and beyond. The data on timing overlap has already been requested by, for example, peatland managers who wanted to understand optimal start dates for peatland restoration works on Dartmoor, and Exmoor conservationists looking to understand how moving of Molinia may affect Meadow Pipit and other ground-nesting birds. The timing information from this thesis can be used to calculate overlap in timing in relation to any hypothetical management start and end date, and can therefore be applied to answer a wide range of questions, in addition to the examples already outlined here. Such applications are not restricted to vegetation management; it can be used also to, for example, inform measures to reduce anthropogenic pressures. We propose for instance that dogs-onleads policies are strictly enforced during the key breeding periods presented in this thesis, as disturbance by dog-walkers has been shown to have negative effects on the breeding success of ground-nesting bird species (Langston et al., 2007; Murison et al., 2007).

#### 7.3.3 Citizen science

Using Devon Cuckoos as a case study, we showed that different volunteer-based survey methods can obtain significantly different results regarding the distribution of species, a concern also highlighted by other studies (Munson et al., 2010; van der Wal et al., 2015). In addition, this study also illustrated that the similarity of species occurrence maps resulting from two survey methods is affected by the spatial scale of analysis. For this reason, we recommend that species range size is taken into account, and that any analyses are conducted at a resolution representative of the species' range size. We discuss how systematic surveys by experts or experienced volunteers can increase data quality, but at the same time can be at risk of false absences due their limited survey time (Tyre et al., 2003). Whilst verification of amateur observations is needed, the opportunistic citizen science website, set up for the purposes of this thesis, identified potential new hotspots of Devon Cuckoo which were not recorded by the Devon Bird Atlas. Both survey methods agreed that the uplands are a key hotspot for Cuckoo in Devon, but the additional opportunistic citizen science records in the lowlands, provided through this thesis work, suggest that Cuckoos may still be more widespread in the lowlands and that therefore further research and conservation action outside the uplands may be worthwhile.

#### 7.4 Limitations and further avenues of research

This final section outlines limitations to the research, makes suggestions on improvements to help overcome these limitations, and recommends wider avenues of research which could be explored to build on the knowledge provided by the research in this thesis.

#### 7.4.1 Spatial scale

One main limitation of the research presented in this thesis is that the majority of the research was restricted to one 4km<sup>2</sup> study site. Although the geography and habitats were typical for a Dartmoor site, the area cannot necessarily be considered representative for Dartmoor's upland moorlands as a whole. Indeed, it can be argued that the study site represents only a small selection of the topographical conditions and habitat types found across Dartmoor. This has implications for the generalisability of the findings from this thesis, and needs to be taken into consideration when using the results from this thesis to inform research or land management on other sites. This is particularly important for factors which may vary substantially with latitude and altitude, such as the findings on timing of breeding and topographic conditions. For example, whilst we find evidence for nest site selection for specific topoclimatic conditions in Whinchat, ecological conditions such as weather conditions and predator densities are likely to show strong regional variation, meaning that the drivers of nest site selection are likely to vary across space. The nature and extent of interspecific differences may also vary across geographic areas. Understanding how upland bird species differ in their breeding ecology and nesting requirements is relevant for upland conservation management, for example in aiding conservation decision-making by identifying potential conservation sites which meet the nesting requirements of multiple species. Therefore, if the results of this study are to be built upon and applied at a wider scale, additional work is needed across other sites to establish whether differences between species (such as those shown in this thesis regarding breeding parameters and microclimatic conditions), are consistent across locations.

The overlap between timing of breeding and land management practices may also be very different in other, e.g. higher-latitude, uplands, where breeding may start and finish later, given that latitude and temperature affect bird phenology (Slagsvold, 1976). Additionally, whilst the species recorded breeding on the site are typical for upland breeding bird communities on heather moorland and grassland, avian diversity may vary significantly across uplands, and the species community and breeding diversity presented here should not be considered typical for the whole of Dartmoor. For example, rocky slopes in Dartmoor river valleys are important for species like Ring Ouzel, and the wet upper reaches of the moor support Dunlin and Golden Plover (Beavan and Lock, 2016). Furthermore, the valley woodlands and farmland fringes support further, entirely different, species communities. Therefore, additional findings from other study areas will be needed if general information on avian breeding diversity, and other information on breeding ecology, is required for the entirety of Dartmoor National Park, or UK upland moorlands more generally. On the other hand, it also needs to be acknowledged that due to restrictions in time, access and resources, ecological field studies are commonly carried out at the spatial extent presented here. For example, several of the most highly cited ornithological field studies on breeding success from the last decade were carried out on a study site  $15 \mathrm{km}^2$  or less in size (results from 2009-2019 based on a Web of Science search for the term "breeding success" in the paper title, see for example Lewis et al. (2009); Part et al. (2011); Szotek and Becker (2012)).

Whilst further research may be needed to understand differences between this

Dartmoor site and other upland areas, this thesis has contributed new knowledge to the existing upland bird literature, and represents a valuable baseline for further work on these and similar species and/or habitats.

The importance of not just study site size, but also spatial scale more generally, needs to be acknowledged; the significance and relative importance of ecological factors will vary with both the resolution and extent of a study (Levin, 1992; Willis and Whittaker, 2002). For example, local sub-population numbers and reproductive success may be mostly limited by the presence of predators in the direct vicinity of nests, whereas at the landscape scale weather conditions or the total availability of suitable habitat types may be the main limiting factors (Reynolds et al., 2006). Working across multiple scales is thus necessary for successful wildlife conservation; local knowledge is needed to inform local management decisions, whereas large-scale information is needed to inform long-term conservation strategies across wider areas or entire species' distributions.

#### 7.4.2 True impacts of timing conflicts

As mentioned previously, the overlap between timing of breeding and land management may vary over space, and these regional variations would need to be quantified to establish targeted vegetation management policies. In addition to this, one other considerable limitation of this work needs to be acknowledged. In this study, the potential conflict between bird breeding and vegetation management was assessed by calculating percentages of active nests. However, to accurately quantify true impacts, this needs to be translated into an estimate of the number of impacted nests. The use of an estimate, rather than a true quantification of nest losses, is inevitable as an experimental field study on this topic would be unethical due to the inadvertent nest destruction, leading to the death of eggs and nestlings. To be able to make such an estimate of numbers of impacted nests, further information is needed on i) the bird breeding densities in the area of interest and ii) the dates on which vegetation management took place, along with the exact size of the area which was managed. From this, the total number of impacted nests within a managed area can be calculated. Due to a lack of these data for our Dartmoor study site, the number of impacted nests could not be calculated in this study. We would therefore advise land owners and/or managers to keep detailed records of the exact locations, timings and area sizes of vegetation management sites in order to allow such analyses to be performed on sites of conservation importance. This does not only apply to birds or uplands alone, if suitable data are collected, similar analyses can be carried out for any species likely affected by management interventions, such as amphibians and reptiles.

#### 7.4.3 Habitat

The study on nest habitats and Meadow Pipit growth rates and breeding success was limited in that it considered the entire 100m radius around the nest as foraging habitat. Directly studying the vegetation patches which Meadow Pipit use for foraging trips, and limiting analyses to only those sites, would help better understand the direct links between habitats, foraging ecology and breeding performance. This was not possible due to limitations in field time, but feasible as a future expansion of the work presented in this thesis. However, there is a rich research history of such observational field studies of foraging habitat selection (e.g. Morris et al. (2001); Gilroy et al. (2009)), and methodologies could therefore be easily replicated for Dartmoor's upland birds.

Most importantly, the scale(s) at which vegetation characteristics affect various components of Meadow Pipit breeding needs to be established. In the immediate surroundings of the nest site, understanding the links between nest crypsis and the likelihood of predation would help better understand which vegetation types may maximise breeding success. At the opposite end of the scale, the links between habitat composition and breeding population size need to be established across entire study sites and/or local breeding populations. Along this broad spectrum of ecologically relevant scales, a multitude of methods and resolutions for vegetation classification can be used. Deciding which of these methodologies and avenues of research to explore depends in part on the management decisions which the research may inform.

Due to limitations in field time, only Meadow Pipit were studied here (as there were of key interest to the wider research group due to ongoing research on Cuckoo). However, work on better understanding links between habitat variables and breeding success would be valuable also for other declining ground-nesting upland species.

#### 7.4.4 Biases and limitations of nest-recording data

The majority of this thesis was based on data collected through nest finding and nest monitoring. Some biases and limitations of such nest recording data need to be acknowledged. Firstly, nest recording can suffer from a detection bias, leading to certain species or conspicuous nests being easier to find (Smith et al., 2009). In the case of this study, we worked with highly experienced nest recorders who practically always succeeded in locating the nest cup once a pair was seen in a territory. Notwithstanding this, it is possible that some breeding pairs were not located at all, for example due to their behaviour being more cryptic compared with other birds (e.g. less singing or alarm calling). This could lead to potential biases in the results. For example, some species may go entirely undetected in diversity surveys (Thompson, 2002). Breeding attempts which fail very early in the breeding cycle (e.g. during laying or early in incubation), could be missed altogether by observers, which may lead to an overestimate of nest success.

A second limitation of this work was that some early and late nests may have been missed due to lower nest finding effort in early spring and late summer; nest-finding effort by volunteers was increased from the moment pairs were recorded in territories, and it is therefore possible that early pairs may have been missed during early reconnaissance visits. This may have caused some inaccuracies in the calculated week of onset, and an underestimate in the total length of the breeding season. However, countering this, generally our findings showed strong consistency with national nest record data. Furthermore, the site was visited highly frequently each season, and previous research suggests that repeated nest searches, as carried out in this study, substantially increases detection rate (Smith et al., 2009). We thus feel that additional survey effort is unlikely to significantly change the results obtained in this thesis. Whilst it is possible that additional survey effort (through additional hours or nest recorders) could have resulted in the recording of a few earlier or later nests during some years on the study site, the feasibility and likelihood of potential benefits of expanding survey efforts need to be considered. Nest recording was driven largely by volunteers, and the recording effort at this study site was substantial for an ecological survey of this size: Chapter 1 illustrated that this study monitored a total of 1550 nests, and that monitoring was conducted by 1-4 volunteers per day across an average of 79 days in each breeding season. Other published studies on breeding bird diversity in similar landscapes used only transect walks to estimate numbers of breeding species, and many studies estimating breeding parameters have relied on significantly fewer numbers of nests (see Chapter 2), illustrating the relatively high recording effort of this study.

A further limitation in deriving timing information from nest recording data is the possibility of birds showing laying gaps or incubation delays. Laying gaps and incubation delays have long been known to be relatively common across a range of passerine species (Kluyver et al., 1977; Nilson and Svensson, 1993; Lessells et al., 2002). As our study calculates the length of the breeding season based on recorded hatching dates, any laying gaps or incubation delays would mean that the true onsets of the species' breeding seasons were earlier than those calculated in this study. As nests are most commonly recorded after incubation has already begun, this is a difficult limitation to overcome. Future studies, perhaps using existing nest record data for nests found during the early laying stages, could be used to quantify the extent of laying gaps and incubation delays in the species focused on in this thesis. This would help better understand the frequency of laying and incubation delays, and would therefore help quantify, or control for, the potential error associated with these nest recording data.

A final limitation of the nest recording data which needs to be acknowledged is the fact that in this study, double-broodedness is not accounted for. Both Meadow Pipit and Stonechat are double-brooded (Robinson, 2017), but as individual birds were not marked in the studies presented in this thesis, the assumption had to be made that all nesting attempts were independent. Brood success may differ between first and second broods (Lambrechts et al., 2008), something which is not controlled for in this study. As some nests belonged to the same pair re-nesting later in the season, the inclusion of both first and second broods also adds an element of pseudoreplication into the data. Similarly, pseudoreplication is introduced when pairs are recorded at the study site across multiple years. This limitation can be overcome by individually marking birds (for example using colour rings), and accounting for any double-broodedness or returning pairs in the data analyses, as done in Yasue and Dearden (2008) and Enemar (2009). However, within the wider team conducting this study, it was agreed that disturbance would be kept to a minimum beyond the essential nest visits for nest recording, and thus catching and marking adults was not seen as desirable in this study. In addition, any disturbance associated with adult catching may also introduce additional limitations. Effects of adult trapping on breeding success were seen in some species, and effects of colour-rings on fitness have also been reported (Tinbergen et al., 2013; Uher-Koch et al., 2015).

#### 7.4.5 Measures of success

In this thesis, only selected measures of breeding performance were evaluated, namely clutch size, brood size, daily success rates and nestling growth rate. Whilst no relationship was shown between for example nest microclimate, habitat and nest success and nestling growth rate, other indices of breeding performance could have been considered. Post-fledging survival, in particular, is a vulnerable period in a bird's life cycle, and has been shown to be affected by factors such as habitat and food avail-

ability (Cox et al., 2014; Perrig et al., 2017). This would therefore be worth further investigation in Dartmoor's upland ground-nesting birds, in particular in the context of land burning, bracken control and other vegetation management, in order to understand optimal management practices which can help maximise post-fledging survival.

However, only considering nest success and post-fledging survival is not sufficient. To ensure any conservation action is meaningful, the ultimate aim needs to be the maintenance or increase of population numbers. Knowledge of changes in breeding success and post-fledging survival is of limited value if they do not link to in population-level effects (Siriwardena et al., 1998; Rönkä et al., 2011). Therefore, further studies on these and other upland birds should move beyond just monitoring local breeding efforts. Breeding densities and other population estimates need to be repeatedly measured, and analyses carried out to understand the links between demography, population changes and conservation interventions.

#### 7.4.6 Drivers of success and nest-site choice

This thesis studies Stonechat, Meadow Pipit and Whinchat breeding in the context of nest microclimate, altitude, foraging habitats and potential overlaps with vegetation management practices. However, a far wider understanding of drivers of nest success is needed to obtain a holistic understanding of the breeding ecology of these species. Many additional, and potentially confounding, factors which could not be investigated in this study, could play a substantial part in determining the breeding success of these and other upland species. A near-infinite range of factors can be selected for study, but we here highlight some that we deem worthwile for further investigation.

Firstly, nest orientation was shown to be important in a wide range of species, including species ecologically similar and/or related to those studied in this thesis (Burton, 2006; Long et al., 2009). Nest orientation therefore would be a logical starting point for further exploring nest site selection effects. Furthermore, weather conditions are known to be very important to the breeding success of birds (see for example Hötker and Segebade (2000); Collister and Wilson (2007)). Weather conditions in the upland can be highly variable, and studying the effects of weather conditions on breeding and survival could therefore be very informative in for example understanding the potential drivers of inter-annual variation in breeding performance. The interplay between the various drivers of nest success also needs to be considered. For example, a recent study showed that rainfall affects the insulatory properties of Meadow Pipit and Whinchat nests, illustrating the benefit of studying microclimatic and weather conditions in parallel (Deeming and Campion, 2018).

However, a better understanding of microclimate and weather conditions may be of limited management relevance, as these are not factors over which land managers have direct control. Therefore, we would recommend that the main focus of further research is around factors over which conservationists and land owners may have some influence, namely habitat, predation, and food availability. The importance of further studies on habitat characteristics across a range of spatial scales was already highlighted earlier in this discussion. Predation is the major cause of nest failure on this Dartmoor study site (pers. obs.), a finding which is consistent with other studies on ground-nesting birds. A study on the relative importance of different predator species was attempted during the fieldwork for this thesis through extensive trials with nest cameras, but unfortunately problems with obtaining good quality footage meant that this work was discontinued, and therefore could not be used in this thesis. Whilst the main predator species of upland birds are known (see e.g. Baines et al. (2008); Fletcher et al. (2010)), more work is needed to understand the relative importance of the different predator species on Dartmoor moorlands. Further research on the interplay between vegetation characteristics and predation risk in declining species, as already investigated in some upland species (see for example Douglas et al. (2014)), may inform vegetation management strategies which look to reduce predation. If a strong link between predation and breeding success or population size is shown, more intensive management options could also be considered. For example, placing deterrent substances such as capsaicin around nest sites has been demonstrated to reduce predation by mammalian predators (Baylis et al., 2012), and predator exclusion through the use of nest cages and fences has been shown to increase hatching success (Smith et al., 2011). Predator control has widely been shown to be effective at increasing avian breeding success and population size, for example in Meadow Pipit, Golden Plover and Curlew, but due to its controversial nature, the implementation of predator control should be implemented only after careful consideration of the benefits and limitations, and when evidence for effectiveness is substantial (Fletcher et al., 2010; Smith et al., 2010).

A final driver of breeding success which was overlooked in this thesis, but warrants significant further attention, is food availability for upland birds. Meadow Pipit, Stonechat and Whinchat, along with many other upland species, are insectivorous birds (Cummins and O'Halloran, 2002; Buchanan et al., 2006; Douglas et al., 2008). Insect populations have shown disastrous declines across the UK and the globe more widely (Potts et al., 2010; Brooks et al., 2012; Leather, 2018), and links between insect abundance and bird success have already been shown for other species such as Pied Flycatcher (*Ficedula hypoleuca*) and Barn Swallow (*Hirundo rustica*) (Strasevicius et al., 2013; Teglhøy, 2017). Monitoring upland insect peaks and abundances across the season, and studying potential synchrony with timing of breeding, as well as breeding performance, may therefore help explain possible causes of declines in Meadow Pipit, Whinchat and other upland breeders. Vegetation management techniques, such as encouraging the growth of insects' food plants, can be used to boost insect numbers, not only for the benefit of breeding birds, but also wider ecosystem services such as pollination services and biological control (Wäckers and van Rijn, 2012; Evans et al., 2016; Potts et al., 2016).

#### 7.4.7 Wider upland wildlife

The majority of the work presented in this thesis focused on only three species; Meadow Pipit, Stonechat and Whinchat. Although this multi-species approach has helped gain insights into the breeding ecology of three widespread co-occurring upland passerines, other key species regularly found as part of this avian community were inevitably omitted. A more detailed, community-based approach is needed, especially when aiming to make decisions on local land management practices and their timings, as additional co-occurring species may have fundamentally different timings or breeding requirements. Two nationally declining species which are particularly abundant on the study site of this thesis are Skylark (Alauda arvensis) and Linnet (*Linaria cannabina*) (pers. obs.). These species would be an informative starting point for further study, not only because they are locally relatively abundant and nationally declining (Eaton et al., 2015), but also because their nesting habitats on the study site differ from the three species studied in this thesis. On average, Linnets nest in higher scrub than the other three species, whereas Skylark nest on more open ground (Ferguson-Lees et al. (2011), pers. obs). Therefore, understanding the breeding ecology of those two species in more detail would build on the work presented in this thesis by exploring the diversity of ecological resources needed to support a diverse upland avian community on Dartmoor and beyond. Such work would complement existing research on other declining upland species, such as Curlew (Numenius arquata), Ring Ouzel (Turdus torquatus), Northern Lapwing (Vanellus vanellus) and Golden Plover (Pluvialis apricaria) (Amar et al., 2011; Sim et al., 2013; Douglas et al., 2014).

The wider wildlife community should also be considered. Many other impor-

tant species occur within Dartmoor's landscapes, including for example the rare Blue Ground Beetle (*Carabus intricatus*) and Emperor Moth (*Saturnia pavonia*), the protected Common Lizard (Lacerta vivipara) and charismatic Red Deer (Cervus elaphus) (See Mercer (2009) for a detailed overview of Dartmoor's wildlife). As was highlighted in this thesis (Chapter 3), vegetation management practices such as grazing and Bracken removal may benefit some insect and bird species whilst being detrimental to others. This illustrates that having a broader understanding of wildlife hotspots and species diversity at sites of interest is essential in order to identify potential management conflicts. Although the fieldwork in this study was focused on several focal bird species, opportunistic observations by nest recorders has led to a broader understanding of the wildlife importance of the site, for example as a stopover site for migrating Ring Ouzel and for habitats used by Green Hairstreak (*Callophrys rubi*) and Adder (see Appendix)(pers. obs.). This work could be expanded and combined with other local studies, such as existing studies by local naturalists on insect species, recent moorland bird work carried out by the local RSPB (as yet unpublished), and studies in Dartmoor woodlands on e.g. Wood Warbler (Bellamy et al., 2018). Together, these studies are providing a detailed case study on the conservation importance and recommended management of Dartmoor's habitats.

#### 7.4.8 Threats to uplands

Like most of the world's natural habitats, the uplands are under threats from climatic and wider environmental change (Holden et al., 2007; Reed et al., 2009). The species composition of upland communities is showing strong changes, as animal distributions shift due to climate-induced changes (Durance and Ormerod, 2007; Morecroft et al., 2009; Davey et al., 2012). Changes in plant communities are also predicted (see for example Trivedi et al. (2008)). Furthermore, the timing of breeding of many species is showing significant changes (Parmesan, 2006), and evidence suggests that bird species which have not shifted their phenology are declining (Møller et al., 2008). Changing weather conditions due to climate change have already been shown to affect upland breeding bird species; links between changing weather conditions and territory occupancy was shown in Ring Ouzel, suggesting that changing weather conditions may be underpinning (part of) the decline of this species (Beale et al., 2006). Such climate-driven changes are likely already happening on Dartmoor, with species like Dartford Warbler, a species which on Dartmoor is at the northern end of its range, having substantially increased in both population size and range size on Dartmoor (Beavan and Lock, 2016).

In addition to inevitable climatic changes, land-use changes and inappropriate land management represent a range of threats. For example, Wheater and Evans (2009) reviewed studies which together suggest that increases in sheep numbers on UK uplands may have led to changes in both flood risk and water quality. In the uplands of Thailand, agricultural intensification was linked to increased reliance on pesticides, and adverse health effects on farmers (Riwthong et al., 2015). Inappropriate mowing, burning and grazing can seriously disrupt the delicate balance of the upland ecosystems. A review on the effects of overgrazing and burning highlighted that overgrazing can lead to a loss of heather and an increase in grazingtolerant species such as *Molinia*, and that (excessive or inappropriate) burning can significantly change plant species composition and destroy important sphagnum-rich habitats (Shaw et al., 1996). On the other hand, burning can be a useful tool to maintain diversity in vegetation structure, and undergrazing could lead to unwanted succession and takeover of trees and shrubs (Shaw et al., 1996; Vandvik et al., 2005). Successful wildlife conservation in the uplands will therefore be largely dependent on appropriate, well-balanced future habitat management in this largely man-made landscape.

At the spatial extent of the study size in this thesis, a particularly worthwhile effort would be to explore the links between habitats created by different land burning or grazing regimes, and the breeding numbers and success of key bird species. Such an experimental approach could help inform an appropriate balance of vegetation management strategies for bird conservation. Other upland vegetation management techniques which may pose a threat also need further investigation. The use of aerial spraying for Bracken control (see Chapter 3) and other purposes needs to be monitored, and the effects of any chemicals on non-target plants and insects investigated, along with testing for any bioaccumulation effects into the wider food chain (see for example Myers et al. (2016)).

Threats to the world's upland landscapes and wildlife are not limited to only changes to climate and vegetation. Other concerns include the impacts of management for grouse shooting, with widely published evidence on not only impacts on vegetation and carbon storage through burning, but also illegal raptor killing (Thirgood and Redpath, 2008; Douglas et al., 2015). Furthermore, air pollution has had a range of negative impacts, and whilst some effects of historical pollution have now been resolved, effects on for example lichen and plant species composition are still present (McGovern et al., 2011; Pescott et al., 2015). The installation of wind turbines has also been shown to have negative impacts, affecting breeding densities of multiple bird species (Pearce-Higgins et al., 2009).

A further threat which is particularly pressing is increased anthropogenic disturbance of the upland landscape. Uplands are popular areas for outdoor recreation, and with populations growing, visitor pressures upon the uplands will increase. A local report, co-authored by the author of this thesis, showed that housing developments and population growth around the boundaries of Dartmoor will lead to significant increases in footfall on Dartmoor over the coming decades, thereby increasing pressures on local landscapes and wildlife (Day et al., 2018). With populations growing worldwide, such changes will be happening in other upland areas also, in particular in those near human population centres. Previous research has shown that effects from anthropogenic pressures on uplands can be wide-ranging. Climbing activity on cliffs was shown to reduce breeding success in Peregrine Falcon (*Falco peregrinus*), and human disturbance reduced bird species richness in oak woodlands (Brambilla et al., 2004; Botsch et al., 2017). The information presented in this thesis can help monitor potentially anthropogenic disturbance effects on bird breeding success and species diversity on Dartmoor. However, potential threats are not limited to birds alone, so wider research and monitoring effort will be required in order to protect the upland landscape; recent studies demonstrated anthropogenic effects in uplands on the nutritional intake in Red Deer, and the spread of Japanse Knotweed (Fallopia japonica) (Jayakody et al., 2011; Rouifed et al., 2014).

With continuing threats to species inevitable under global environmental change, monitoring of species diversity, breeding success and species hotspots is essential in order to effectively monitor changes and evaluate the effectiveness of any interventions. Long-term data recording is essential in achieving this, and volunteer driven data collection can help efficiently collect the volume of natural history data required for conservation research purposes. Whilst this thesis contributed to this monitoring and research effort on a local scale on a Dartmoor upland, the same principles apply much more widely. The main challenges facing Dartmoor's uplands are mostly the same as those faced by the rest of the UK and our planet; climate change effects need to be curbed, and a balance needs to be found between human residential landscapes, food production, other ecosystem services and nature conservation.

## References

- Aceves-Bueno, E., Adeleye, A., Feraud, M., Huang, Y., Tao, M., Yang, Y., & Anderson, S. The Accuracy of Citizen Science Data: A Quantitative Review. *The Bulletin of the Ecological Society of America*, 98:278–290, 2017.
- Amar, A., Grant, M., Buchanan, G.and Sim, I., Wilson, J., Pearce-Higgins, J., & Redpath, S. Exploring the relationships between wader declines and current land-use in the British uplands. *Bird Study*, 58:13–26, 2011.
- Baines, D., Redpath, S., Richardson, M., & Thirgood, S. The direct and indirect effects of predation by Hen Harrier *Circus cyanus* on trends in breeding birds on a Scottish grouse moor. *Ibis*, 150:27–36, 2008.
- Baylis, S., Cassey, P., & Hauber, M. Capsaicin as a deterrent against introduced mammalian nest predators. *The Wilson Journal of Ornithology*, 124:518–524, 2012.
- Beale, C. M., Burfield, I. J., Sim, I. M. W., Rebecca, G. W., Pearce-Higgins, J. W., & Grant, M. C. Climate change may account for the decline in British ring ouzels *Turdus torquatus. Journal of Animal Ecology*, 75:826–835, 2006.
- Beavan, S. & Lock, M. Devon Birds Atlas 2007-2013. Devon Birds, 2016.
- Bellamy, P., Burgess, M., Mallord, J., Cristinacce, A., Orsman, C., Davis, T., Grice, P., & Charman, E. Nest predation and the influence of habitat structure on nest predation of Wood Warbler *Phylloscopus sibilatrix*, a ground-nesting forest passerine. *Journal of Ornithology*, 159:493–506, 2018.
- Border, J. A., Henderson, I. G., Redhead, J. W., & Hartley, I. R. Habitat selection by breeding Whinchats *Saxicola rubetra* at territory and landscape scales. *Ibis*, 159(1):139–151, 2017.
- Botsch, Y., Tablado, Z., & Jenni, L. Experimental evidence of human recreational disturbance effects on bird-territory establishment. *Proceedings of the Royal Society B*, 284:20170846, 2017.
- Bracken, F., McMahon, B., & Whelan, J. Breeding bird populations of Irish peatlands. *Bird Study*, 55:169–178, 2008.

- Brambilla, M., Rubolini, D., & Guidali, F. Rock climbing and Raven Corvus corax occurrence depress breeding success of cliff-nesting Peregrines Falco peregrinus. Ardeola, 51:425–430, 2004.
- Britschgi, A., Spaar, R., & Arlettaz, R. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. *Biological Conservation*, 130:193–205, 2006.
- Brooks, D., Bater, J., Clark, S., Monteith, D., Andrews, C., Corbett, S., Beaumont, D., & Chapman, J. Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *Journal of Applied Ecology*, 49:1009–1019, 2012.
- Broyer, J. Whinchat Saxicola rubetra reproductive success according to hay cutting schedule and meadow passerine density in alluvial and upland meadows in France. Journal for Nature Conservation, 17:160–167, 2009.
- Buchanan, G., Grant, M., Sanderson, R., & Pearce-Higgins, J. The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management. *Ibis*, 148:625–628, 2006.
- Burton, N. H. K. Nest orientation and hatching success in the Tree Pipit Anthus trivialis. Journal of Avian Biology, 37:312–317, 2006.
- Collister, D. M. & Wilson, S. Contributions of weather and predation to reduced breeding success in a threatened northern Loggerhead Shrike population. Avian Conservation and Ecology, 2(2):11, 2007.
- Cox, W., Thompson, F., Cox, A., & Faaborg, J. Factors affecting post-fledging survival in passerine birds and the value of post-fledging studies to conservation. *Journal of Wildlife Management*, 78:183–193, 2014.
- Cummins, S. & O'Halloran, J. An assessment of the diet of nestling Stonechats Saxicola torquata using compositional analysis. Bird Study, 49:139–145, 2002.
- Dallimer, M., Marini, L., Skinner, A., Hanley, N., Armsworth, P., & Gaston, K. Agricultural land-use in the surrounding landscape affects moorland bird diversity. Agriculture, Ecosystems and Environment, 139:578–583, 2010.

- Davey, C., Chamberlain, D.E. Newson, S., D.G., N., & Johnston, A. Rise of the generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography*, 21:568–578, 2012.
- Day, B., Harwood, A., Tyler, C., & Zonneveld, S. Population futures and Dartmoor National Park. Implications of development around the outskirts of Dartmoor for recreational use and management of access. *Report to Dartmoor National Park Authority*, 2018.
- Deeming, D. & Campion, E. Simulated rainfall reduces the insulative properties of bird nests. Acta Ornithologica, 53:91–97, 2018.
- Douglas, D., Bellamy, P., Stephen, L., Pearce-Higgins, J., Wilson, J., & Grant, M. Upland land use predicts population decline in a globally near-threatened wader. *Journal of Applied Ecology*, 51:194–203, 2014.
- Douglas, D. J., Evans, D. M., & Redpath, S. M. Selection of foraging habitat and nestling diet by Meadow Pipits Anthus pratensis breeding on intensively grazed moorland. Bird Study, 55:290–296, 2008.
- Douglas, D. J. T., Buchanan, G. M., Thompson, P., Amar, A., Fielding, D. A., Redpath, S. M., & Wilson, J. D. Vegetation burning for game management in the UK uplands is increasing and overlaps spatially with soil carbon and protected areas. *Biological Conservation*, 191:243–250, 2015.
- Durance, I. & Ormerod, S. Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology*, 13:942–957, 2007.
- Eaton, M., Aebischer, N., Brown, A., Hearn, R., Lock, L., Musgrove, A., Noble, D., Stroud, D., & Gregory, R. Birds of conservation concern 4: The population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds*, 108:708–746, 2015.
- Enemar, A. First, second and replacement broods in the breeding biology of a Treecreeper Certhia familiaris population. Ornis Svecica, 19:97–114, 2009.
- Evans, D. M., Redpath, S. M., & Evans, S. A. Seasonal patterns in the productivity of Meadow Pipits in the uplands of Scotland. *Journal of Field Ornithology*, 76(3): 245–251, 2005.

- Evans, T., Mahoney, M., Cashatt, E., De Snoo, G., & Musters, C. Enhancement of linear agricultural areas to provide invertebrates as potential food for breeding birds. *Land*, 5:26, 2016.
- Ferguson-Lees, J., Castell, R., & Leech, D. A field guide to monitoring nests. BTO, Thetford, 2011.
- Fletcher, K., Aebischer, N. J., Baines, D., Foster, R., & Hoodless, A. N. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecology*, 47:263–272, 2010.
- Fuller, R. J. & Glue, D. E. The breeding biology of the Stonechat and Whinchat. Bird Study, 24(4):215–228, 1977.
- Gilroy, J., Anderson, G., Grice, P., Vickery, J., Watts, P., & Sutherland, W. Foraging habitat selection, diet and nestling condition in Yellow Wagtails *Motacilla flava* breeding on arable farmland. *Bird Study*, 56:221–232, 2009.
- Grüebler, M. U., Schuler, H., Horch, P., & Spaar, R. The effectiveness of conservation measures to enhance nest survival in a meadow bird suffering from anthropogenic nest loss. *Biological Conservation*, 146:197–203, 2012.
- Holden, J., Shotbolt, L., Bonn, A., Burt, T. P., Chapman, P. J., Dougill, A. J., Fraser, E. D., Hubacek, K., Irvine, B., Kirkby, M. J., Reed, M. S., Prell, C., Stagl, S., Stringer, L. C., Turner, A., & Worrall, F. Environmental change in moorland landscapes. *Earth-Science Reviews*, 82:75–100, 2007.
- Hötker, H. & Segebade, A. Effects of predation and weather on the breeding success of Avocets *Recurvirostra avosetta*. *Bird Study*, 47(1):91–101, 2000.
- Hušek, J., Weidinger, K., Adamík, P., & Slagsvold, T. Impact of nesting mortality on avian breeding phenology: A case study on the Red-Backed Shrike (*Lanius collurio*). *Plos One*, 7(8):e43944, 2012.
- Jayakody, S., Sibbald, A., Mayes, R., Hooper, R., Gordon, I., & Lambin, X. Effects of human disturbance on the diet composition of wild red deer *Cervus elaphus*. *European Journal of Wildlife Research*, 57:939–948, 2011.
- Joys, A. C. & Crick, H. Q. P. Breeding periods for selected bird species in England. BTO Research Report No. 352, 2004.

- Kluyver, H., van Balen, J., & Cave, A. The occurrence of time-saving mechanisms in the breeding biology of the Great Tit *Parus major*. *Evolutionary Ecology*, pages 153–169, 1977.
- Lambrechts, M., Rieux, A., Galan, M., Cartan-Son, M., Perret, P., & Blondel, J. Double-brooded Great Tits *Parus major* in mediterranean oak habitats: Do first broods always perform better than second broods. *Russian Journal of Ecology*, 38:516–522, 2008.
- Langston, R., Liley, D., Murison, G., Woodfield, E., & Clarke, R. What effects do walkers and dogs have on the distribution and productivity of breeding European Nightjar *Caprimulgus europaeus*. *Ibis*, 149:27–36, 2007.
- Leather, S. "Ecological Armageddon" more evidence for the drastic decline in insect numbers. Annals of Applied Biology, 1-3:1–3, 2018.
- Lessells, C., Dingemanse, N., & Both, C. Egg weights, egg component weights, and laying gaps in Great Tit (*Parus major*) in relation to ambient temperature. *The Auk*, 119:1091–1103, 2002.
- Levin, S. The problem of pattern and scale in ecology. *Ecology*, 73:1943–1967, 1992.
- Lewandowski, E. & Specht, H. Influence of volunteer and project characteristics on data quality of biological surveys. *Conservation Biology*, 29:713–723, 2015.
- Lewis, S., Elston, D., DAunt, F., Cheney, B., & Thompson, P. Effects of extrinsic and intrinsic factors on breeding success in a long lived seabird. *Oikos*, 118: 521–528, 2009.
- Lindenmayer, D. & Likens, G. Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends in Ecology & Evolution*, 24:482–486, 2009.
- Long, A., Jensen, W., & With, K. Orientation of Grasshopper Sparrow and Eastern Meadowlark nests in relation to wind direction. *The Condor*, 111:395–399, 2009.
- Magurran, A., Baillie, S., Buckland, S., Dick, J., Elston, D., Scott, E., Smith, R., Somerfield, P., & Watt, A. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology & Evolution*, 25:574–582, 2010.
- McGovern, S., Evans, C., Dennis, P., Walmsley, C., & McDonald, M. Identifying drivers of species compositional change in a semi-natural upland grassland over a 40-year period. *Journal of Vegetation Science*, 22:346–356, 2011.

- Møller, A., Rubolini, D., & Lehikoinen, E. Populations of migratory bird species that did not show a phenological response to climate change are declining. *PNAS*, 105:16195–16200, 2008.
- Morecroft, M., Bealey, C., Beaumont, D., Benham, S., Brooks, D., Burt, T., Critchley, C., Dick, J., Littlewood, N., Monteith, D., Scott, W., Smith, R., Walmsley, C., & Watson, H. The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation*, 142:2814–2832, 2009.
- Morris, A., Whittingham, M., Bradbury, R., Wilson, J., Kyrkos, A., Buckingham, D., & Evans, A. Foraging habitat selection by yellowhammers (*Emberiza citrinella*) nesting in agriculturally contrasting regions in lowland England. *Biological Conservation*, 101:197–210, 2001.
- Munson, M., Caruana, R., Fink, D., Hochachka, W., Iliff, M., Rosenberg, K., Sheldon, D., Sullivan, B., Wood, C., & Kelling, S. A method for measuring the relative information content of data from different monitoring protocols. *Methods* in Ecology and Evolution, 1:263–273, 2010.
- Murison, G., Bullock, J. M., Underhill-Day, J., Langston, R., Brown, A. F., & Sutherland, W. J. Habitat type determines the effects of disturbance on the breeding productivity of the Dartford Warbler Sylvia undata. Ibis, 149(Suppl. 1): 16–26, 2007.
- Myers, J. P., Antoniou, M. N., Blumberg, B., Carroll, L., Colborn, T., Everett, L. G., Hansen, M., Landrigan, P. J., Lanphear, B. P., Mesnage, R., Vandenberg, L. N., Vom Saal, F. S., Welshons, W. V., & Benbrook, C. M. Concerns over use of glyphosate-based herbicides and risks associated with exposures: A consensus statement. *Environmental Health*, 15:1–13, 2016.
- Newey, S., Mustin, K., Bryce, R., Fielding, D., Redpath, S., Bunnefeld, N., Bronwen, D., & Irvine, R. Impact of management on avian communities in the Scottish highlands. *PLoS ONE*, 115:e0155473, 2016.
- Nilson, J. & Svensson, E. The frequency and timing of laying gaps. Ornis Scandinavica, 24:122–126, 1993.

- Parmesan, C. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics, 37(1):637–669, 2006.
- Part, T., Arlt, D., Doligez, B., Low, M., & Qvarnstrom, A. Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year. *Journal of Animal Ecology*, 80:1227–1235, 2011.
- Pavel, A., Buresï, S., Weidinger, K., & Kovarï, P. Distraction displays in Meadow Pipit (Anthus pratensis) females in central and Northern Europe. Ethology, 106: 1007–1019, 2000.
- Pearce-Higgins, J. W., Stephen, L., Langston, R. H. W., Bainbridge, I. P., & Bullman, R. The distribution of breeding birds around upland wind farms. *Journal* of Applied Ecology, 46(6):1323–1331, 2009.
- Perkins, A., Maggs, H., Wilson, J., & Watson, A. Delayed mowing increases corn bunting *Emberiza calandra* nest success in an agri-environment scheme trial. Agriculture, Ecosystems & Environment, 181:80–89, 2013.
- Perrig, M., Gruebler, M., Keil, H., & Naef-Daenzer, B. Post-fledging survival of Little Owls Athene noctua in relation to nestling food supply. *Ibis*, 159:532–540, 2017.
- Pescott, O., Simkin, J., August, T., Randle, Z., Dore, A., & Botham, M. Air pollution and its effects on lichens, bryophytes, and lichen-feeding Lepidoptera: review and evidence from biological records. *Biological Journal of the Linnean Society*, 115:611–635, 2015.
- Potts, S., Biesmeijer, J., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25:345–353, 2010.
- Potts, S., Imperatriz-Fonseca, V., Ngo, H., Aizen, M., Biesmeijer, J., Breeze, T., Dicks, L., Garibaldi, L., Hill, R., Settele, J., & Vanbergen, A. Safeguarding pollinators and their values to human well-being. *Nature*, 540:220–229, 2016.
- Reed, M. S., Bonn, A., Slee, W., Beharry-Borg, N., Birch, J., Brown, I., Burt,
  T. P., Chapman, D., Chapman, P. J., Clay, G. D., Cornell, S. J., Fraser,
  E. D., Glass, J. H., Holden, J., Hodgson, J. A., Hubacek, K., Irvine, B., Jin,
  N., Kirkby, M. J., Kunin, W. E., Moore, O., Moseley, D., Prell, C., Price,
  M. F., Quinn, C. H., Redpath, S., Reid, C., Stagl, S., Stringer, L. C., Termansen,

M., Thorp, S., Towers, W., & Worrall, F. The future of the uplands. *Land Use Policy*, 26:S204–S216, 2009.

- Revaz, E., Schaub, M., & Arlettaz, R. Foraging ecology and reproductive biology of the Stonechat *Saxicola torquata*: Comparison between a revitalized, intensively cultivated and a historical, traditionally cultivated agro-ecosystem. *Journal of Ornithology*, 149:301–312, 2008.
- Reynolds, R., Wiens, J., & Salafsky, S. A review and evaluation of factors limiting Northern Goshawk populations. *Studies in Avian Biology*, 31:260–273, 2006.
- Riwthong, S., Schreinemachers, P., Grovermann, C., & Berger, T. Land use intensification, commercialization and changes in pest management of smallholder upland agriculture in Thailand. *Environmental Science & Policy*, 45:11–19, 2015.
- Robinson, R. A. BirdFacts: Profiles of birds occurring in Britain & Ireland. BTO Research Report 407, 2017.
- Rönkä, M., Saari, L., Hario, M., Hänninen, J., & Lehikoinen, E. Breeding success and breeding population trends of waterfowl: implications for monitoring. *Wildlife Biology*, 17:225–239, 2011.
- Rouifed, S., Piola, F., & Spiegelberger, T. Invasion by *Fallopia* spp. in a French upland region is related to anthropogenic disturbances/. *Basic and Applied Ecology*, 15:435–443, 2014.
- Seel, D. C. & Walton, K. C. Numbers of Meadow Pipits Anthus pratensis on mountain farm grassland in North Wales in the breeding season. *Ibis*, 121:147– 164, 1979.
- Shaw, S., Wheeler, B., Kirby, P., Phillipson, P., & R., E. Literature review of the historical effects of burning and grazing of blanket bog and upland wet heath. . *English Nature Research Report no. 172*, 1996.
- Sim, I., Ludwig, S., Grant, M., Loughrey, J., Rebecca, G., & Redpath, S. Seasonal variation in foraging conditions for Ring Ouzels *Turdus torquatus* in upland habitats and their effects on juvenile habitat selection. *Ibis*, 155:42–54, 2013.
- Siriwardena, G., Baillie, S., & Wilson, J. Variation in the survival rates of some British passerines with respect to their population trends on farmland. *Bird Study*, 45:276–292, 1998.

- Slagsvold, T. Annual and geographical variation in the timing of breeding of the Great Tit Parus major and the Pied Flycatcher Ficedula hypoleuca in relation to environmental phenology and spring temperature. Ornis Scandinavica, 7:127–145, 1976.
- Smith, P., Bart, J., Lanctot, R., McCaffery, B., & Brown, S. Probability of detection of nests and implications for survey design. *The Condor*, 111:414–423, 2009.
- Smith, R., Pullin, A., Stewart, G., & Sutherland, W. Effectiveness of predator removal for enhancing bird populations. *Conservation Biology*, 24:820–829, 2010.
- Smith, R., Pullin, A., Stewart, G., & Sutherland, W. Is nest predator exclusion an effective strategy for enhancing bird populations? *Biological Conservation*, 144: 1–10, 2011.
- Strasevicius, D., Jonsson, M., Nyholm, N., & Malmqvist, B. Reduced breeding success of Pied Flycatchers *Ficedula hypoleuca* along regulated rivers . *Ibis*, 155: 348–356, 2013.
- Strong, T. & Bock, C. Bird species distribution patterns in riparian habitats in southeastern Arizona. *The Condor*, 92:866, 1990.
- Szotek, K. & Becker, P. Terns in trouble: demographic consequences of low breeding success and recruitment on a common tern population in the German Wadden Sea. Journal of Ornithology, 153:313–326, 2012.
- Teglhøy, P. A comparative study of insect abundance and reproductive success of barn swallows *Hirundo rustica* in two urban habitats. *Journal of Avian Biology*, 48:846–853, 2017.
- Thirgood, S. & Redpath, S. Hen harriers and red grouse: science, politics and human–wildlife conflict. *Journal of Applied Ecology*, 45:1550–1554, 2008.
- Thompson, D. B. A. & Macdonald, A. J. Upland heather moorland in Great Britain: A review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation*, 71:163–178, 1995.
- Thompson, W. Towards reliable bird surveys: Accounting for individuals present but not detected. *The Auk*, 119:18–25, 2002.
- Tinbergen, J., Tinbergen, J., & Ubels, R. Is fitness affected by ring colour? Ardea, 101:152–163, 2013.

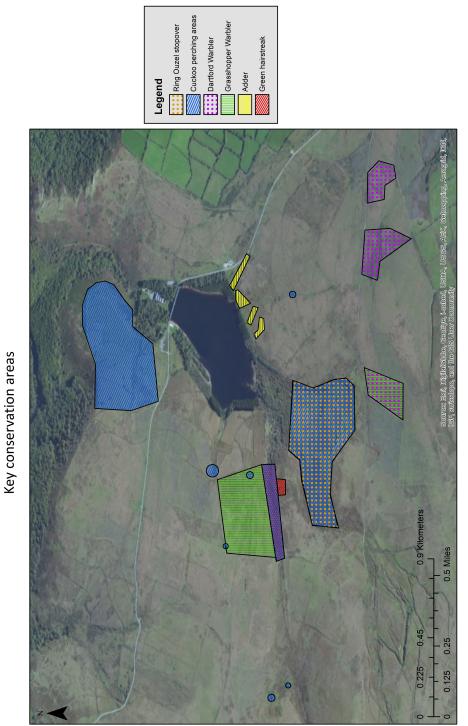
- Tome, D. & Denac, D. Survival and development of predator avoidance in the postfledging period of the whinchat (*Saxicola rubetra*): consequences for conservation measures. *Journal of Ornithology*, 153:131–138, 2012.
- Trivedi, M., Morecroft, M., Berry, P., & Dawson, T. Potential effects of climate change on plant communities in three montane nature reserves in Scotland, UK. *Biological Conservation*, 141:1665–1675, 2008.
- Tyre, A., Tenhumberg, B., Field, S., Niejalke, D., Parris, K., & Possingham, H. Improving precision and reducing bias in biological surveys: estimating falsenegative error rates. *Ecological Applications*, 13:1790–1801, 2003.
- Uher-Koch, B., Schmutz, J., & Wright, K. Nest visits and capture events affect breeding success of Yellow-billed and Pacific loons. *The Condor*, 117:121–129, 2015.
- van der Wal, R., Anderson, H., Robinson, A., Sharma, N., Mellish, C., Roberts, S., Darvill, B., & Siddharthan, A. Mapping species distributions: A comparison of skilled naturalist and lay citizen science recording. *Ambio*, 44:S584–S600, 2015.
- van Oosten, H. H. Comparative breeding biology of three insectivorous songbirds in Dutch dune grasslands. Ardea, 104(3):199–2012, 2016.
- Vandenberghe, C., Prior, G., Littlewood, N. A., Brooker, R., & Pakeman, R. Influence of livestock grazing on Meadow Pipit foraging behaviour in upland grassland. *Basic and Applied Ecology*, 10:662–670, 2009.
- Vandvik, V., Heegaard, E., Måren, I., & Aarrestad, P. Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. *Journal of Applied Ecology*, 42:139–149, 2005.
- Wäckers, F. & van Rijn, P. Biodiversity and insect pests: Key issues for sustainable management. John Wiley & Sons, Ltd., 2012.
- Wheater, H. & Evans, E. Land use, water management and future flood risk. Land Use Policy, 26S:S251–S264, 2009.
- Willis, K. & Whittaker, R. Species diversity scale matters. Science, 295:1245–1248, 2002.
- Wright, L. J., Hoblyn, R. A., Green, R. E., Bowden, C. G. R., Mallord, J. W., Sutherland, W. J., & Dolman, P. M. Importance of climatic and environmental change

in the demography of a multi-brooded passerine, the woodlark *Lullula arborea*. Journal of Animal Ecology, 78(6):1191–1202, 2009.

Yasue, M. & Dearden, P. Replacement nesting and double-brooding in Malaysian Plovers *Charadrius peronii*: Effects of season and food availability. *Ardea*, 96: 59–72, 2008.

# Appendices

## Study site wildlife hotspots



Holne Moor study site - wildlife hotspots

#### List of Presentations and Outreach Activities

- 2019 **Devon Birds seminar** Plymouth (invited speaker) Title: A 10-year study on Dartmoor ground-nesting birds
- 2018 Kent Ornithological Society Canterbury (invited speaker) Title: Dartmoor's ground-nesting birds
- 2017 British Trust for Ornithology annual conference Swanwick (invited speaker)
   Title: Dartmoor's ground-nesting birds
- 2017 Woodland Festival Lectures Dartmoor National Park (invited speaker) Title: Dartmoor's ground-nesting birds
- 2016 Cambridge Conservation Initiative Cuckoo Day (invited speaker) Title: Cuckoos & the upland bird community of Dartmoor
- 2016 **BBC Springwatch** Short feature on the ground-nesting bird study and nest recording
- 2016 Advanced Methods and Techniques for Environmental Research -University of Exeter Biosciences seminar series Title: Citizen Science in ecological & environmental research - examples & tips
- 2016 Ecology & Environment Seminar Series University of Exeter Biosciences

Title: Ground-nesting birds on Dartmoor

- 2016 British Ornithology Union blog Title: The hatching of a long-term nest study
- 2015 Dartmoor Upland Bird Nest Group website

Creation of the website for the Dartmoor Upland Bird Nest Group - covering the fieldwork and research on the study site

2015 European Ornithology Union Poster Presentation - Badajoz conference Title: Breeding success and nest site selection in Meadow Pipits, Stonechats and Whinchats 2015 European Ornithology Union - Badajoz conference (invited speaker) Title: The use of Twitter in the Devon Cuckoo citizen science project. Talk and discussion in a session on the role of social media in ornithology

#### 2014 Devon Cuckoos Citizen Science Initiative

An interactive map on which Cuckoo sightings can be logged and viewed. 3000+ records recorded between 2014-2017. Hosted on the Devon Birds website and promoted on social media and in local media

#### 2014 British Ornithology Union blog

Title: Devon Cuckoos and Citizen Science

### List of Awarded Funding

#### 2016 BTO Research Grant

To purchase catching and ringing equipment for a Whinchat demography project on our Dartmoor study site  $(\pounds 474)$ 

#### 2016 Online Crowdfunding campaign

To fund the continuation of the Dartmoor ground-nesting bird field study  $(\pounds 3728 \text{ from } 88 \text{ donors})$ 

#### 2016 Opticron sponsorship

Five pairs of binoculars for the study site nest recording volunteers

2015 Devon Birds project grant (co-written with Professor C.R. Tyler)

To fund the continuation of the Dartmoor ground-nesting bird field study  $(\pounds 1926)$ 

### 2015 **Charity Grant** (funded as private donation by member of the public) To fund the continuation of the Dartmoor ground-nesting bird field study (£1685)

#### 2014 NERC Course Grant

To attend a Plant Taxonomy, Identification and Field Skills course at Kew Gardens (£900)

## Examples of media coverage of Cuckoo citizen science project

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# Bibliography

- Aceves-Bueno, E., Adeleye, A., Feraud, M., Huang, Y., Tao, M., Yang, Y., & Anderson, S. The Accuracy of Citizen Science Data: A Quantitative Review. *The Bulletin of the Ecological Society of America*, 98:278–290, 2017.
- Alday, J. G., Cox, E. S., Pakeman, R. J., Harris, M. P. K., Leduc, M. G., & Marrs, R. H. Overcoming resistance and resilience of an invaded community is necessary for effective restoration: A multi-site bracken control study. *Journal of Applied Ecology*, 50:156–167, 2012.
- Alderman, R., Gales, R., Hobday, A., & Candy, S. Post-fledging survival and dispersal of shy albatross from three breeding colonies in Tasmania. *Marine Ecology Progress Series*, 405:271–285, 2010.
- Allred, B. W., Fuhlendorf, S. D., Engle, D. M., & Elmore, R. D. Ungulate preference for burned patches reveals strength of fire-grazing interaction. *Ecology and Evolution*, 1(2):132–144, 2011.
- Amar, A., Grant, M., Buchanan, G.and Sim, I., Wilson, J., Pearce-Higgins, J., & Redpath, S. Exploring the relationships between wader declines and current land-use in the British uplands. *Bird Study*, 58:13–26, 2011.
- Ancona, S., Sanchez-Colon, S., Rodriguex, C., & Drummond, H. El Nino in the Warm Tropics: local sea temperature predicts breeding parameters and growth of blue-footed boobies. *Journal of Animal Ecology*, 80:799–808, 2011.
- Andrabi, S. & Maxwell, W. A review on reproductive biotechnologies for conservation of endangered mammalian species. *Animal Reproduction Science*, 99:223–243, 2007.

- Annett, R., Habibi, H. R., & Hontela, A. Impact of glyphosate and glyphosatebased herbicides on the freshwater environment. *Journal of Applied Toxicology*, 34:458–479, 2014.
- Antonov, A., Stokke, B., Vikan, J., Fossøy, F., Ranke, P., Røskaft, E., Moksnes, A., Møller, A., & Shykoff, J. Egg phenotype differentiation in sympatric cuckoo *Cuculus canorus* gentes. *Journal of Evolutionary Biology*, 23:1170–1182, 2010.
- Ardia, D., Perez, J., & Clotfelter, E. Experimental cooling during incubation leads to reduced innate immunity and body condition in nestling tree swallows. *Proceedings* of the Royal Society B - Biological Sciences, 277:1881–1888, 2010.
- Arroyo, B. & Razin, M. Effect of human activities on bearded vulture behaviour and breeding success in the French Pyrenees. *Biological Conservation*, 128:276–284, 2006.
- Ashcroft, M., Gollan, J., Warton, D., & Ramp, D. A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology*, 18:1866–1879, 2012.
- Askew, D., Evans, S., Matthews, R., & Swanton, P. MAGIC: a geoportal for the English countryside. Computers, Environment and Urban Systems, 29:71–85, 2005.
- Assandri, G., Giacomazzo, M., Brambilla, M., Griggio, M., & Pedrini, P. Nest density, nest-site selection, and breeding success of birds in vineyards: Management implications for conservation in a highly intensive farming system. *Biological Conservation*, 205:23–33, 2017.
- Ausden, M. Habitat management for conservation: A handbook of techniques. Oxford University Press, 2007.
- Baasch, D., Farrell, P., Farnsworth, J., & Smith, C. Nest-site selection by Interior Least Terns and Piping Plovers at managed, off-channel sites along the Central Platte River in Nebraska, USA. *Journal of Field Ornithology*, 88:236–249, 2017.
- Baden, A. A description of nesting behaviors, including factors impacting nest site selection, in black-and-white ruffed lemurs (*Varecia variegata*). Ecology and Evolution, 9:1010–1028, 2019.
- Bai, S. H. & Ogbourne, S. M. Glyphosate: environmental contamination, toxicity and potential risks to human health via food contamination. *Environmental Science and Pollution Research*, 23(19):18988–19001, 2016.

- Baines, D., Redpath, S., Richardson, M., & Thirgood, S. The direct and indirect effects of predation by Hen Harrier *Circus cyanus* on trends in breeding birds on a Scottish grouse moor. *Ibis*, 150:27–36, 2008.
- Balmer, D., Gillings, S., Caffrey, B., Swann, R., Downie, I., & Fuller, R. Bird Atlas 2007-2011: The breeding and wintering birds of Britain and Ireland. *BTO*, *Thetford*, 2013.
- Barea, L. Nest-site selection by the Painted Honeyeater (*Grantiella picta*), a mistletoe specialist. *Emu - Austral Ornithology*, 108:213–220, 2008.
- Bargmann, T., Hatteland, B., & Grytnes, J. Effects of prescribed burning on carabid beetle diversity in coastal anthropogenic heathlands. *Biodiversity and Conservation*, 24:2565–2581, 2015.
- Baroni-Urbani, C. & Buser, M. Similarity of binary data. Systematic Biology, 25: 251–259, 1976.
- Barton, K. MuMIn: Multi-Model Inference, 2016. R package version 1.15.6.
- Baylis, S., Cassey, P., & Hauber, M. Capsaicin as a deterrent against introduced mammalian nest predators. *The Wilson Journal of Ornithology*, 124:518–524, 2012.
- Beale, C. M., Burfield, I. J., Sim, I. M. W., Rebecca, G. W., Pearce-Higgins, J. W., & Grant, M. C. Climate change may account for the decline in British ring ouzels *Turdus torquatus. Journal of Animal Ecology*, 75:826–835, 2006.
- Beavan, S. & Lock, M. Devon Birds Atlas 2007-2013. Devon Birds, 2016.
- Bellamy, P., Burgess, M., Mallord, J., Cristinacce, A., Orsman, C., Davis, T., Grice, P., & Charman, E. Nest predation and the influence of habitat structure on nest predation of Wood Warbler *Phylloscopus sibilatrix*, a ground-nesting forest passerine. *Journal of Ornithology*, 159:493–506, 2018.
- Belmaker, J., Zarnetske, P., Tuanmu, M., Zonneveld, S., Record, S., Strecker, A., & Beaudrot, L. Empirical evidence for the scale dependence of biotic interactions. *Global Ecology and Biogeography*, 24:750–761, 2015.
- Bennie, J., Huntley, B., Wiltshire, A., Hill, M. O., & Baxter, R. Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling*, 216(1):47–59, 2008.

- Bergman, E., Bishop, C., Freddy, D., White, G., & Doherty Jr, P. Habitat management influences overwinter survival of mule deer fawns in colorado. *The Journal* of Wildlife Management, 78:448–455, 2014.
- Bergmanis, U., Amerika, K., Vali, U., & Treinys, R. Nest site selection and turnover patterns in support of conservation decisions: Case study of the lesser spotted eagle in the core area of its global population. *Forest Ecology and Management*, 448:67–75, 2019.
- Berry, P. M., Dawson, T. P., Harrison, P. A., & Pearson, R. G. Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography*, 11(6):453–462, 2002.
- Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J., & Kunin, W. E. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313(5785):351–354, 2006.
- Binder, R., Riley, S., Holbrook, C., Hansen, M., Bergstedt, R., Bronte, C., He, J., & Krueger, C. Spawning site fidelity of wild and hatchery lake trout (*Salvelinus namaycush*) in northern Lake Huron. *Canadian Journal of Fisheries and Aquatic Sciences*, 73:18–34, 2016.
- BirdLife International. Anthus pratensis. (amended version published in 2016). The IUCN Red List of Threatened Species, (Accessed July 2017 from http://www.birdlife.org), 2016.
- Blomqvist, D. & Johansson, O. C. Trade-offs in nest-site selection in coastal populations of Lapwings Vanellus vanellus. Ibis, 137:550–558, 1995.
- Bolnick, D., Shim, K., & Brock, C. Female stickleback prefer shallow males: Sexual selection on nest microhabitat. *Evolution*, 69:1643–1653, 2015.
- Bonn, A., Allott, T., Hubacek, K., & Stewart, J., editors. *Drivers of environmental change in uplands*. Routledge, 2009.
- Border, J. A., Henderson, I. G., Redhead, J. W., & Hartley, I. R. Habitat selection by breeding Whinchats *Saxicola rubetra* at territory and landscape scales. *Ibis*, 159(1):139–151, 2017.
- Both, C. & te Marvelde, L. Climate change and timing of avian breeding and migration throughout europe. *Climate Research*, 35:93–105, 2007.

- Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V., Jarvinen, A., Metcalfe, N. B., Nyholm, N. E. I., Potti, J., Ravussin, P.-A., Sanz, J. J., Silverin, B., Slater, F. M., Sokolov, L. V., Torok, J., Winkel, W., Wright, J., Zang, H., & Visser, M. E. Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society B: Biological Sciences*, 271:1657–1662, 2004.
- Both, C., Dingemanse, N., Drent, P., & Tinbergen, J. Pairs of extreme avian personalities have highest reproductive success. *Journal of Animal Ecology*, 74:667–674, 2005.
- Botsch, Y., Tablado, Z., & Jenni, L. Experimental evidence of human recreational disturbance effects on bird-territory establishment. *Proceedings of the Royal Society B*, 284:20170846, 2017.
- Boulton, R., Richard, Y., & Armstrong, D. Influence of food availability, predator density and forest fragmentation on nest survival of New Zealand robins. *Biological Conservation*, 141:580–589, 2008.
- Boyle, W. A. Can variation in risk of nest predation explain altitudinal migration in tropical birds? *Oecologia*, 155:397–403, 2008.
- Bracken, F., McMahon, B., & Whelan, J. Breeding bird populations of Irish peatlands. *Bird Study*, 55:169–178, 2008.
- Brambilla, M. & Rubolini, D. Intra-seasonal changes in distribution and habitat associations of a multi-brooded bird species: implications for conservation planning. *Animal Conservation*, 12:71–77, 2009.
- Brambilla, M., Rubolini, D., & Guidali, F. Rock climbing and Raven Corvus corax occurrence depress breeding success of cliff-nesting Peregrines Falco peregrinus. Ardeola, 51:425–430, 2004.
- Branchini, S., Meschini, M., Covi, C., Piccinetti, C., Zaccanti, F., & Goffredo, S. Participating in a citizen science monitoring program: Implications for environmental education. *PLOS ONE*, 10:e0131812, 2015.
- BRIG. UK Biodiversity Action Plan; priority habitat descriptions. Upland Heathland. 2008a.
- BRIG. UK Biodiversity Action Plan; priority habitat descriptions. Upland Flushes, Fens and Swamps. 2008b.

- Britschgi, A., Spaar, R., & Arlettaz, R. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. *Biological Conservation*, 130:193–205, 2006.
- Britton, A. J. & Fisher, J. M. Interactive effects of nitrogen deposition, fire and grazing on diversity and composition of low-alpine prostrate *Calluna vulgaris* heathland. *Journal of Applied Ecology*, 44:125–135, 2007.
- Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. Synergies among extinction drivers under global change. *Trends in Ecology and Evolution*, 23(8):453–460, 2008.
- Brooke, M. D. L. & Davies, N. B. Recent changes in host usage by Cuckoos Cuculus canorus in Britain. Journal of Animal Ecology, 56(3):873–883, 1987.
- Brooks, D., Bater, J., Clark, S., Monteith, D., Andrews, C., Corbett, S., Beaumont, D., & Chapman, J. Large carabid beetle declines in a United Kingdom monitoring network increases evidence for a widespread loss in insect biodiversity. *Journal of Applied Ecology*, 49:1009–1019, 2012.
- Brown, A. F. & Stillman, R. A. Bird-habitat associations in the Eastern highlands of Scotland. *Journal of Applied Ecology*, 30:31–42, 1993.
- Broyer, J. Whinchat Saxicola rubetra reproductive success according to hay cutting schedule and meadow passerine density in alluvial and upland meadows in France. Journal for Nature Conservation, 17:160–167, 2009.
- Broyer, J., Curtet, L., & Boissenin, M. Does breeding success lead meadow passerines to select late mown fields? *Journal of Ornithology*, 153:817–823, 2012.
- Bubova, T., Vrabec, V., Kulma, M., & Nowicki, P. Land management impacts on european butterflies of conservation concern: a review. *Journal of Insect Conser*vation, 19:805–821, 2015.
- Buchanan, G., Grant, M., Sanderson, R., & Pearce-Higgins, J. The contribution of invertebrate taxa to moorland bird diets and the potential implications of land-use management. *Ibis*, 148:625–628, 2006.
- Buchanan, G., Pearce-Higgings, J., Douglas, D., & Grant, M. Quantifying the importance of multi-scale management and environmental variables on moorland bird abundance. *Ibis*, 159:744–756, 2017.

- Bunce, R., Wood, C., & Smart, S. The ecology of British up-land landscapes. I. Composition of landscapes, vegetation and species. *Journal of Landscape Ecology*, 11:120–139, 2018a.
- Bunce, R., Wood, C., & Smart, S. The ecology of British up-land landscapes. II. The influence of policy on the current character of the uplands and the potential for change. *Journal of Landscape Ecology*, 11:140–154, 2018b.
- Burge, M. N. & Kirkwood, R. C. The control of Bracken. Critical Reviews in Biotechnology, 12(4):299–333, 1992.
- Burke, D. M. & Nol, E. Influence of food abundance nest site habitat and forest fragmentation on breeding Ovenbirds. *The Auk*, 115(1):96–104, 1998.
- Burton, N. H. K. Nest orientation and hatching success in the Tree Pipit Anthus trivialis. Journal of Avian Biology, 37:312–317, 2006.
- Burton, N. H. K. Intraspecific latitudinal variation in nest orientation among ground-nesting passerines: A study using published data. *The Condor*, 109:441– 446, 2007.
- Butchart, S., Stattersfield, A., & Collar, N. How many bird extinctions have we prevented? *Oryx*, 40:266–278, 2006.
- Byers, C. & Eason, P. Conspecifics and their posture influence site choice and oviposition in the Damselfly *Argia moesta*. *Ethology*, 115:721–730, 2009.
- Calladine, J. & Bray, J. The importance of altitude and aspect for breeding Whinchats *Saxicola rubetra* in the uplands: Limitations of the uplands as a refuge for a declining, formerly widespread species? *Bird Study*, 59:43–51, 2012.
- Carey, C. The impacts of climate change on the annual cycles of birds. *Philosophical transactions of the Royal Society B: Biological Sciences*, 364:3321–3330, 2009a.
- Carey, C. The impacts of climate change on the annual cycles of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364:3321–3330, 2009b.
- Carney, K. M. & Sydeman, W. J. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds*, 22(1):68–79, 1999.
- Carroll, J. M., Davis, C. A., Elmore, R. D., & Fuhlendorf, S. D. A ground nesting galliform's response to thermal heterogeneity: implications for ground dwelling birds. *PLoS ONE*, 10(11), 2015.

- Catchpole, C. & Phillips, J. Territory quality and reproductive success in the Dartford warbler Sylvia undata in Droset, England. Biological Conservation, 61:209– 215, 1992.
- Chalfoun, A. D. & Martin, T. E. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *Journal of Applied Ecology*, 44: 983–992, 2007.
- Chamberlain, D. E., Negro, M., Caprio, E., & Rolando, A. Assessing the sensitivity of alpine birds to potential future changes in habitat and climate to inform management strategies. *Biological Conservation*, 167:127–135, 2013.
- Chance, E. The Cuckoo's secret. Sidgwick and Jackson, London, 1922.
- Chapman, D., Termansen, M., Quinn, C., Jin, N., Bonn, A., Cornell, S., Fraser, E., Hubacek, K., Kunin, W., & Reed, M. Modelling the coupled dynamics of moorland management and upland vegetation. *Journal of Applied Ecology*, 46: 278–288, 2009.
- Charmantier, A., McCleery, R., Cole, L., Perrins, C., Kruuk, L., & Sheldon, B. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, 320:800–803, 2008.
- Chastel, O., Weimerskirch, H., & Jouventin, P. High annual variability in reproductive success and survival of an Antarctic seabird, the Snow Petrel *Pagodroma nivea* - A 27-year study. *Oecologia*, 94(2):278–285, 1993.
- Chesterton, C. Environmental impacts of land management. *Natural England Re*search Report NERR030, 2009.
- Clark, R. G. & Shutler, D. Avian habitat selection: Pattern from process in nest-site use by ducks? *Ecology*, 80(1):272–287, 1999.
- Collister, D. M. & Wilson, S. Contributions of weather and predation to reduced breeding success in a threatened northern Loggerhead Shrike population. Avian Conservation and Ecology, 2(2):11, 2007.
- Colombelli-Negrel, D. & Kleindorfer, S. Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). Ecological Research, 24:921–928, 2009.

- Combrink, L., Combrink, H., Botha, A., & Downs, C. Habitat structure and diversity influence the nesting success of an endangered large cavity-nesting bird, the Southern Ground-hornbill. *Koedoe*, 59:1–8, 2017.
- Conrad, K. F., Warren, M. S., Fox, R., Parsons, M. S., & Woiwod, I. P. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biological Conservation*, 132:279–291, 2006.
- Conway, G. J. & Fuller, R. J. Multi-scale relationships between vegetation pattern and breeding birds in the upland margins (ffridd) of North Wales. BTO Research Report No. 566, 2010.
- Costello, E., Lauber, C., Hamady, M., Fierer, N., Gordon, J., & Knights, R. Bacterial Community Variation in Human Body Habitats Across Space and Time. *Science*, 326:1694–1697, 2009.
- Côté, I. M. & Sutherland, W. J. The effectiveness of removing predators on bird populations. *Conservation Biology*, 11(2):395–405, 1997.
- Cothran, R. The importance of reproductive interference in ecology and evolution: from organisms to communities. *Population Ecology*, 57:339–341, 2015.
- Coulson, J. C. Mortality and egg production of the Meadow Pipit with special reference to altitude. *Bird Study*, 3(2):119–132, 1956.
- Cox, W., Thompson, F., Cox, A., & Faaborg, J. Factors affecting post-fledging survival in passerine birds and the value of post-fledging studies to conservation. *Journal of Wildlife Management*, 78:183–193, 2014.
- Crall, A., Newman, G., Stohlgren, T., Holfelder, K., Graham, J., & Waller, D. Assessing citizen science data quality: and invasive species case study. *Conservation Letters*, 4:433–442, 2011.
- Cramp, S. & Perrins, C. The birds of the Western Palearctic. Oxford University Press, 1994.
- Crick, H. Q., Baillie, S. R., & Leech, D. I. The UK Nest Record Scheme: Its value for science and conservation. *Bird Study*, 50(3):254–270, 2003.
- Crick, H. Q. P. & Sparks, T. H. Climate change related to egg-laying trends. Nature, 399:423–423, 1999.

- Crick, H. Q. P., Dudley, C., Evans, A. D., & Smith, K. W. Causes of nest failure among buntings in the UK. *Bird Study*, 41(2):88–94, 1994.
- Crow, P. & Moffat, A. The management of the archaeological resource in uk wooded landscapes: An environmental perspective. *Conservation and Management of Archaeological Sites*, 7:103–116, 2005.
- Cummins, S. & O'Halloran, J. An assessment of the diet of nestling Stonechats Saxicola torquata using compositional analysis. Bird Study, 49:139–145, 2002.
- Curtis, C. J., Battarbee, R. W., Monteith, D. T., & Shilland, E. M. The future of upland water ecosystems of the UK in the 21st century: A synthesis. *Ecological Indicators*, 37:412–430, 2014.
- D'Alba, L., Monaghan, P., & Nager, R. G. Thermal benefits of nest shelter for incubating female Eiders. *Journal of Thermal Biology*, 34:93–99, 2009.
- Dallimer, M., Marini, L., Skinner, A., Hanley, N., Armsworth, P., & Gaston, K. Agricultural land-use in the surrounding landscape affects moorland bird diversity. Agriculture, Ecosystems and Environment, 139:578–583, 2010.
- Dartmoor Biodiversity Steering Group. Dartmoor Species Action Plan for Bats. 2007.
- Dartmoor National Park Authority. State of the Park Report, 2008.
- Dartmoor National Park Authority. Dartmoor National Park Swaling Code of Conduct. http://www.dartmoor.gov.uk/lookingafter/laf-landmanagement/lafswaling/swaling-code-of-conduct, 2011a.
- Dartmoor National Park Authority. Birds of the open moor, 2011b.
- Dartmoor National Park Authority. Dartmoor National Park Management Plan 2014-2019., 2014.
- Davey, C., Chamberlain, D.E. Newson, S., D.G., N., & Johnston, A. Rise of the generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography*, 21:568–578, 2012.
- Davies, N. Cuckoos, cowbirds and other cheats. T & A D Poyser, 2016.
- Davies, N. B. & de L. Brooke, M. An experimental study of co-evolution between the Cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *Journal* of Animal Ecology, 58(1):207–224, 1989.

- Davies, S. & Deviche, P. At the crossroads of physiology and ecology: Food supply and the timing of avian reproduction. *Hormones and Behavior*, 66(1):41–55, 2014.
- Davies, Z., Wilson, R., Brereton, T., & Thomas, C. The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. *Biological Conservation*, 124:189–198, 2005.
- Davis, S. K. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *The Condor*, 107(3):605–616, 2005.
- Dawson, R. D., Lawrie, C. C., & O'Brien, E. L. The importance of microclimate variation in determining size, growth and survival of avian offspring: Experimental evidence from a cavity nesting passerine. *Oecologia*, 144:499–507, 2005.
- Day, B., Harwood, A., Tyler, C., & Zonneveld, S. Population futures and Dartmoor National Park. Implications of development around the outskirts of Dartmoor for recreational use and management of access. *Report to Dartmoor National Park Authority*, 2018.
- de L. Brooke, M. & Davies, N. gg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature*, 335:630–632, 1988.
- De Vere, R. A., Warren, Y., Nicholas, A., Mackenzie, M. E., & Higham, J. P. Nest site ecology of the cross river gorilla at the Kagwene Gorilla Sanctuary, Cameroon, with special reference to anthropogenic influence. *American Journal* of Primatology, 73(3):253–261, 2011.
- Deeming, D. & Campion, E. Simulated rainfall reduces the insulative properties of bird nests. Acta Ornithologica, 53:91–97, 2018.
- DEFRA. The Heather and Grass Burning Code 2007, Best Practice Guide 7: Burning in the uplands of south-west England, 2007a.
- DEFRA. The Heather and Grass Burning Code (2007 version), 2007b.
- Delgado, J. D., Morales, G., Arroyo, N. L., Arévalo, J. R., & Fernández-Palacios, J. M. Logging and topography effects on artificial nest predation by rats in laurel forests. *Applied Ecology and Environmental Research*, 11(1):53–65, 2013.
- Delibes-Mateos, M., Ferreras, P., & Villafuerte, R. European rabbit population trends and associated factors: A review of the situation in the Iberian Peninsula. *Mammal Review*, 39(2):124–140, 2009.

- Denerley, C., Redpath, S., van der Wal, R., Newson, S., Chapman, J., & Wilson, J. Breeding ground correlates of the distribution and decline of the Common Cuckoo *Cuculus canorus* at two spatial scales. *Ibis*, 161:346–358, 2019.
- Dennis, P., Skartveit, J., McCracken, D. I., Pakeman, R. J., Beaton, K., Kunaver, A., & Evans, D. M. The effects of livestock grazing on foliar arthropods associated with bird diet in upland grasslands of Scotland. *Journal of Applied Ecology*, 45: 279–287, 2008.
- Dickinson, J., Zuckerberg, B., & Bonter, D. Citizen Science as an Ecological Research Tool: Challenges and Benefits. Annual Review of Ecology, Evolution and Systematics, 41:149–172, 2010.
- Dickinson, J., Shirk, J., Bonter, D., Bonney, R., Crain, R., Martin, J., Phillips, T., & Purcell, K. The current state of citizen science as a tool for ecological research and public engagement. *Frontiers in Ecology and the Environment*, 10:291–297, 2012.
- Diefenbach, D., Brauning, D., & Mattice, J. Variability in grassland bird counts related to observer differences and species detection rates. *The Auk*, 120:1168– 1179, 2003.
- Dillen, L., Jordaens, K., De Bruyn, L., & Backeljau, T. Fecundity in the hermaphroditic land snail Succinea putris (Pulmonata: Succineidae): does body size matter? *Journal of Molluscan Studies*, 76:376–383, 2010.
- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. Defaunation in the Anthropocene. *Science*, 345(6195):401–406, 2014.
- Douglas, D., Bellamy, P., Stephen, L., Pearce-Higgins, J., Wilson, J., & Grant, M. Upland land use predicts population decline in a globally near-threatened wader. *Journal of Applied Ecology*, 51:194–203, 2014.
- Douglas, D. J., Evans, D. M., & Redpath, S. M. Selection of foraging habitat and nestling diet by Meadow Pipits Anthus pratensis breeding on intensively grazed moorland. Bird Study, 55:290–296, 2008.
- Douglas, D. J. T. & Pearce-Higgins, J. W. Relative importance of prey abundance and habitat structure as drivers of shorebird breeding success and abundance. *Animal Conservation*, 17(6):535–543, 2014.

- Douglas, D. J. T., Buchanan, G. M., Thompson, P., Amar, A., Fielding, D. A., Redpath, S. M., & Wilson, J. D. Vegetation burning for game management in the UK uplands is increasing and overlaps spatially with soil carbon and protected areas. *Biological Conservation*, 191:243–250, 2015.
- Douglas, D. J. T., Beresford, A., Selvidge, J., Garnett, S., Buchanan, G. M., Gullett, P., & Grant, M. C. Changes in upland bird abundances show associations with moorland management. *Bird Study*, 64(2):242–254, 2017.
- Dunn, J. C., Gruar, D., Stoate, C., Szczur, J., & Peach, W. J. Can hedgerow management mitigate the impacts of predation on songbird nest survival? *Journal* of Environmental Management, 184:535–544, 2016.
- Durance, I. & Ormerod, S. Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology*, 13:942–957, 2007.
- Eaton, M., Aebischer, N., Brown, A., Hearn, R., Lock, L., Musgrove, A., Noble, D., Stroud, D., & Gregory, R. Birds of conservation concern 4: The population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds*, 108:708–746, 2015.
- Enemar, A. First, second and replacement broods in the breeding biology of a Treecreeper *Certhia familiaris* population . *Ornis Svecica*, 19:97–114, 2009.
- Engelbrecht, B., Comita, L., Condit, R., Kursar, T., Tyree, M., Turner, B., & Hubbell, S. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, 447:80, 2007.
- English Nature & Dartmoor National Park Authority. The nature of Dartmoor. A biodiversity profile. 2001.
- Environment Act 1995. https://www.legislation.gov.uk/ukpga/1995/25/section/1/enacted - Accessed November 2018.
- Erwin, W. J. & Stasiak, R. H. Vertebrate mortality during the burning of a reestablished prairie in Nebraska. *The American Midland Naturalist*, 101(1):247–249, 1979.
- Evans, D. M., Redpath, S. M., & Evans, S. A. Seasonal patterns in the productivity of Meadow Pipits in the uplands of Scotland. *Journal of Field Ornithology*, 76(3): 245–251, 2005a.

- Evans, D. M., Redpath, S. M., Evans, S. A., Elston, D. A., & Dennis, P. Livestock grazing affects the egg size of an insectivorous passerine. *Biology Letters*, 1:322– 325, 2005b.
- Evans, T., Mahoney, M., Cashatt, E., De Snoo, G., & Musters, C. Enhancement of linear agricultural areas to provide invertebrates as potential food for breeding birds. *Land*, 5:26, 2016.
- Ferguson-Lees, J., Castell, R., & Leech, D. A field guide to monitoring nests. BTO, Thetford, 2011.
- Ferraccioli et al. LiDAR based Digital Terrain Model (DTM) data for South West England. NERC Environmental Information Data Centre, 2014.
- Ferreira, C., Touza, J., Rouco, C., Diaz-Ruiz, F., Fernandez-de Simon, J., Rios-Saldana, C., Ferreras, P., Villafuerte, R., & Delibes-Mateos, M. Habitat management as a generalized tool to boost european rabbit *Oryctolagus cuniculus* populations in the iberian peninsula: a cost-effectiveness analysis. *Mammal Review*, 44:30–43, 2014.
- Fischer, J., Debski, I., Taylor, G. A., & Wittmer, H. Nest site selection of South Georgia Diving petrels Pelecanoider georgicus on Codfish Island, New Zealand: Implications for conservation management. *Bird Conservation International*, 28: 216–227, 2017.
- Fisher, R., Wellicome, T., Bayne, E., Poulin, R., Todd, L., & Ford, A. Extreme precipitation reduces reproductive output of an endangered raptor. *Journal of Applied Ecology*, 52:1500–1508, 2015.
- Flaspohler, D. J., Temple, S. A., & Rosenfield, R. N. Relationship between nest success and concealment in two ground-nesting passerines. *Journal of Field Ornithology*, 71(4):736–747, 2000.
- Flemming, S., Nol, E., Kennedy, L., & Smith, P. Hyperabundant herbivores limit habitat availability and influence nest site selection of Arctic-breeding birds. *Jour*nal of Applied Ecology, 56:976–987, 2019.
- Fletcher, K., Aebischer, N. J., Baines, D., Foster, R., & Hoodless, A. N. Changes in breeding success and abundance of ground-nesting moorland birds in relation to the experimental deployment of legal predator control. *Journal of Applied Ecology*, 47:263–272, 2010.

- Fletcher, L., Forrest, B., Atalah, J., & Bell.J.J. Reproductive seasonallity of the invasive ascidian *Didemnum vexillum* in New Zealand and implications for shellfish aquaculture. *Aquaculture environment interactions*, 3:197–211, 2013.
- Flinks, H., Helm, B., & Rothery, P. Plasticity of moult and breeding schedules in migratory European Stonechats Saxicola rubicola. Ibis, 150:687–697, 2008.
- Forrester, J. A., Leopold, D. J., & Hafner, S. D. Maintaining critical habitat in a heavily managed landscape: Effects of power line corridor management on Karner blue butterfly (*Lycaeides melissa samuelis*) habitat. *Restoration Ecology*, 13(3): 488–498, 2005.
- Forstmeier, W. & Weiss, I. Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos*, 104:487–499, 2004.
- Fox, R. The decline of moths in Great Britain: A review of possible causes. Insect Conservation and Diversity, 6:5–19, 2013.
- Fox, R., Brereton, T., Asher, J., August, T., Botham, M. S., Bourn, N., Cruickshanks, K., Bulman, C., Ellis, S., Harrower, C., Middlebrook, I., Noble, D., Powney, G., Randle, Z., Warren, M., & Roy, D. B. The State of the UK's Butterflies 2015. *Butterfly Conservation and the Centre for Ecology & Hydrology*, 2015.
- Friedman, W. & Floyd, S. Perspective: The origin of flowering plants and their reproductive biology - A tale of two phylogenies. *Evolution*, 55:217–231, 2001.
- Fuller, R. J. & Glue, D. E. The breeding biology of the Stonechat and Whinchat. Bird Study, 24(4):215–228, 1977.
- Galbraith, H., Murray, S., Duncan, K., Smith, R., Whitfield, D., & Thompson, D. Diet and habitat use of the Dotterel *Charadrius morinellus* in Scotland. *Ibis*, 135: 148–155, 1993.
- Gelman, A. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine, 27:2865–2873, 2008.
- Gibbs, H. L., Sorenson, M. D., Marchetti, K., de L. Brooke, M., Davies, N. B., & Nakamura, H. Genetic evidence for female host-specific races of the Common Cuckoo. *Nature*, 407:183–186, 2000.

- Gill, V., Hatch, S., & Lanctot, R. Sensitivity of breeding parameters to food supply in Black-legged Kittiwakes *Rissa tridactyla*. *Ibis*, 144:268–283, 2002.
- Gillings, S., Balmer, D. E., & Fuller, R. J. Directionality of recent bird distribution shifts and climate change in Great Britain. *Global Change Biology*, 21(6):2155– 2168, 2015.
- Gilroy, J., Anderson, G., Grice, P., Vickery, J., Watts, P., & Sutherland, W. Foraging habitat selection, diet and nestling condition in Yellow Wagtails *Motacilla flava* breeding on arable farmland. *Bird Study*, 56:221–232, 2009.
- Gjerdrum, C., Elphic, C. S., & Rubega, M. Nest site selection and nesting success in saltmarsh breeding Sparrows: The importance of nest habitat, timing, and study site differences. *The Condor*, 107(4):849–862, 2005.
- Gloutney, M. L. & Clark, R. G. Nest-site selection by Mallards and Blue-Winged Teal in relation to microclimate. *The Auk*, 114(3):381–395, 1997.
- Glue, D. & Morgan, R. Cuckoo Hosts in British Habitats. Bird Study, 19(4):187–192, 1972.
- González, L. M., Margalida, A., Sánchez, R., & Oria, J. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (Aquila adalberti). Biological Conservation, 129:477–486, 2006.
- Goodenough, A. E. & Hart, A. G. Correlates of vulnerability to climate-induced distribution changes in European avifauna: Habitat, migration and endemism. *Climatic Change*, 118(3-4):659–669, 2013.
- Goodwin, C. E. D., Hodgson, D. J., Al-Fulaij, N., Bailey, S., Langton, S., & Mcdonald, R. A. Voluntary recording scheme reveals ongoing decline in the United Kingdom Hazel Dormouse *Muscardinus avellanarius* population. *Mammal Review*, 47(3):183–197, 2017.
- Grand-Clement, E., Anderson, K., Smith, D., Luscombe, D., Gatis, N., Ross, M., & Brazier, R. Evaluating ecosystem goods and services after restoration of marginal upland peatlands in South-West England. *Journal of Applied Ecology*, 50:324–334, 2013.
- Grant, D., Cohen, J., Stantial, M., & Linhart, R. Substrate-level nest site selection of sympatric Piping Plovers (*Charadrius melodus*) and American Oystercatchers (*Haematopus palliatus*) in New Jersey, USA. Waterbirds, 42:272–281, 2019.

- Greig-Smith, P. Weight differences, brood reduction, and sibling competition among nestling Stonechats Saxicola torquata (Aves: Turdidae). Journal of Zoology, 205 (3):453–465, 1985.
- Griffiths, R. A. & Pavajeau, L. Captive breeding, reintroduction, and the conservation of amphibians. *Conservation Biology*, 22(4):852–861, 2008.
- Grisham, B., Godar, A., Boal, C., & Haukos, D. Interactive effects between nest microclimate and nest vegetation structure confirm microclimate thresholds for Lesser Prairie-Chicken nest survival. *The Condor*, 118:728–746, 2016.
- Grüebler, M. U., Schuler, H., Horch, P., & Spaar, R. The effectiveness of conservation measures to enhance nest survival in a meadow bird suffering from anthropogenic nest loss. *Biological Conservation*, 146:197–203, 2012.
- Guerry, A., Polasky, S., Lubchenco, J., Chaplin-Kramer, R., Daily, G., Griffin,
  R., Ruckelshaus, M., Bateman, I., Duraiappah, A., Elmqvist, R., Feldman,
  M., Folke, C., Hoekstra, J., Kareiva, P., Keeler, B., Li, S., McKenzie, E., Ouyang,
  Z., Reyers, B., Ricketts, T., Rockstrom, J., Tallis, H., & Vira, B. Natural capital
  and ecosystem services informing decisions: From promise to practice. *PNAS*,
  112:7348–7355, 2015.
- Guillera, G. & Lahoz-Monfort, J. Designing studies to detect differences in species occupancy: power analysis under imperfect detection. *Methods in Ecology and Evolution*, 3:860–869, 2012.
- Gurr, G., Wratten, S., Landis, D., & You, M. Habitat management to suppress pest populations: Progress and prospects. Annual Review of Entomology, 62:91–109, 2017.
- Hagemeijer, E. & Blair, M. The EBCC Atlas of European Breeding Birds: their distribution and abundance. 1997.
- Haines-Young, R. & Potschin, M. Upland ecosystem services. Report to Natural England. Coordination contract. NE Project Code: PTY02/10/002.27. CEM Report No 10., 2009.
- Halupka, K. Nest-site selection and nest predation in Meadow Pipits. Folia Zoologica, 47(1):29–37, 1998a.
- Halupka, K. Nest predation in Meadow Pipits Anthus pratensis nesting in natural conditions. Ornis Fennica, 75:139–143, 1998b.

- Hamby, K., Bellamy, D., Chiu, J., Lee, J., Walton, V., Wiman, N., York, R., & Biondi, A. Biotic and abiotic factors impacting development, behavior, phenology, and reproductive biology of *Drosophila suzukii*. Journal of Pest Science, 89:605– 619, 2016.
- Hanane, S. Multi-scale turtle dove nest habitat selection in a Mediterranean agroforestry landscape: implications for the conservation of a vulnerable species. *European Journal of Wildlife Research*, 64:1–9, 2018.
- Harris, S. J., Massimino, S., Newson, S. E., Eaton, M. A., Marchant, J. H., Balmer, D. E., Noble, D. G., Gillings, S., Procter, D., & Pearce-Higgins, J. W. The Breeding Bird Survey 2015. BTO Research Report 687, British Trust for Ornithology, Thetford, 2016.
- Hayhow, D., Conway, G., Eaton, M., Grice, P., Hall, C., Holt, C., Kuepfer, A., Noble, D., Oppel, S., Risely, K., Stringer, C., Stroud, D., Wilkinson, N., & Wotton, S. The state of the UK's birds 2014. *RSPB*, *BTO*, *WWT*, *JNCC*, *NE*, *NIEA*, *NRW* and SNH, Sandy, Bedfordshire., 2014.
- Hayhow, D., Bond, A., Douse, A., Eaton, M., Frost, T., Grice, P., Hall, C., Harrist, S., Havery, S., Hearn, R., Noble, D., Oppel, S., Williams, J., Win, I., & Wotton, S. The state of the UK's birds 2016. *RSPB, BTO, WWT, DAERA, JNCC, NE, NRW and SNH, Sandy, Bedfordshire.*, 2016a.
- Hayhow, D. B., Burns, F., Eaton, M. A., Al Fulaij, N., August, T. A., Babey, L., Bacon, L., Bingham, C., Boswell, J., Boughey, K. L., Brereton, T., Brookman, E., Brooks, D. R., Bullock, D. J., Burke, O., Collis, M., Corbet, L., Cornish, N., De Massimi, S., Densham, J., Dunn, E., Elliott, S., Gent, T., Godber, J., Hamilton, S., Havery, S., Hawkins, S., Henney, J., Holmes, K., Hutchinson, N., Isaac, N. J. B., Johns, D., Macadam, C. R., Mathews, F., Nicolet, P., Noble, D. G., Outhwaite, C. L., Powney, G. D., Richardson, P., Roy, D. B., Sims, D., Smart, S., Stevenson, K., Stroud, R. A., Walker, K. J., Webb, J. R., Webb, T. J., Wynde, R., & Gregory, R. D. The state of Nature 2016. The State of Nature partnership, 2016b.
- Hazler, K. R. Mayfield Logistic Regression: A practical approach for analysis of nest survival. *The Auk*, 121(3):707–716, 2004.
- Hedgren, S. Effects of fledging weight and time of fledging on survival of Guillemot Uria aalge chicks. Ornis Scandinavica, 12(1):51–54, 1981.

- Helm, B., Fiedler, W., & Callion, J. Movements of European stonechats Saxicola torquata according to ringing recoveries. Ardea, 94(1):33–44, 2006.
- Henderson, I. G., Fuller, R. J., Conway, G. J., & Gough, S. J. Evidence for declines in populations of grassland-associated birds in marginal upland areas of Britain. *Bird Study*, 51:12–19, 2004.
- Hewson, C. M., Thorup, K., Pearce-Higgins, J. W., & Atkinson, P. W. Population decline is linked to migration route in the Common Cuckoo. *Nature Communications*, 7:12296, 2016.
- Hinsley, S., Hill, R., Bellamy, P. E., Harrison, N., Speakman, J., Wilson, A., & Ferns, P. Effect of structural and functional habitat gaps on breeding woodland birds: working harder for less. *Landscape Ecology*, 23:615–626, 2008.
- HM Government. A Green Future: Our 25 year plan to improve the environment., 2018.
- Hof, C., Araújo, M. B., Jetz, W., & Rahbek, C. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, 480:516–521, 2011.
- Hofierka, J. & Šúri, M. The solar radiation model for Open Source GIS: implementation and applications. Proceedings of the Open source GIS-GRASS users conference, 2002.
- Hogan, B., Grigione, M., Marconi, M., Thomas, R., & Sarno, R. Asymmetric antagonism between Piping Plovers (*Charadrius melodus*) and American Oystercatchers (*Haematopus palliatus*), New York, USA. Waterbirds, 41:443–448, 2018.
- Holden, J., Shotbolt, L., Bonn, A., Burt, T. P., Chapman, P. J., Dougill, A. J., Fraser, E. D., Hubacek, K., Irvine, B., Kirkby, M. J., Reed, M. S., Prell, C., Stagl, S., Stringer, L. C., Turner, A., & Worrall, F. Environmental change in moorland landscapes. *Earth-Science Reviews*, 82:75–100, 2007.
- Hoover, J. P. & Brittingham, M. C. Nest-site selection and nesting success of Wood Thrushes. Wilson Bulletin, 110(3):375–383, 1998.
- Hötker, H. & Segebade, A. Effects of predation and weather on the breeding success of Avocets *Recurvirostra avosetta*. *Bird Study*, 47(1):91–101, 2000.

- Hovick, T. J., Elmore, R., Fuhlendorf, S. D., & Dahlgren, D. K. Weather constrains the influence of fire and grazing on nesting Greater Prairie-Chickens. *Rangeland Ecology and Management*, 68(2):186–193, 2015.
- Hughes, T. P. & Tanner, J. E. Recruitment failure, life histories, and long-term decline of caribbean corals. *Ecology*, 81(8):2250–2263, 2000.
- Huin, N. & Sparks, T. Spring arrival patterns of the Cuckoo Cuculus canorus, Nightingale Luscinia megarhynchos and Spotted Flycatcher Musciapa striata in Britain. *Bird Study*, 47:22–31, 2000.
- Humphrey, J. W. Benefits to biodiversity from developing old-growth conditions in British upland spruce plantations: A review and recommendations. *Forestry*, 78 (1):33–53, 2005.
- Hušek, J., Weidinger, K., Adamík, P., & Slagsvold, T. Impact of nesting mortality on avian breeding phenology: A case study on the Red-Backed Shrike (*Lanius collurio*). *Plos One*, 7(8):e43944, 2012.
- Illera, J. C., von Wehrden, H., & Wehner, J. Nest site selection and the effects of land use in a multi-scale approach on the distribution of a passerine in an island arid environment. *Journal of Arid Environments*, 74:1408–1412, 2010.
- Ims, R., Henden, J., Stromeng, M. A., Thingness, A., Garmo, M., & Jepsen, J. Arctic greening and bird nest predation risk across tundra ecotones. *Nature Climate Change*, pages 1–6, 2019.
- Indykiewicz, P. Egg losses caused by cold snap in the Black-Headed Gull Chroicocephalus ridibundus L. Polish Journal of Ecology, 63:460–466, 2015.
- Jaccard, P. Étude comparative de la distribution florale dans une portion des Alpes et des Jura. Bulletin de la Societe Vaudoise des Sciences Naturelles, 37:547–579, 1901.
- Jackson, M., Gergel, S., & Martin, K. Citizen science and field survey observations provide comparable results for mapping Vancouver Island White-tailed Ptarmigan (*Lagopus leucura saxatilis*) distributions. *Biological Conservation*, 181:162–172, 2015.
- Jayakody, S., Sibbald, A., Mayes, R., Hooper, R., Gordon, I., & Lambin, X. Effects of human disturbance on the diet composition of wild red deer *Cervus elaphus*. *European Journal of Wildlife Research*, 57:939–948, 2011.

- Jefferson, R. G. The conservation management of upland hay meadows in Britain: a review. *Grass and Forage Science*, 60:322–331, 2005.
- Jeffs, C., Davies, M., Carter, I., Gregson, J., Sainsbury, A., & Lister, J. Reintroducing the Cirl Bunting to Cornwall. *British Birds*, 109:374–388, 2016.
- Jenner, E. Observations on the natural history of the cuckoo. *Philosophical Trans*actions of the Royal Society B, 78:219–237, 1788.
- JNCC. UK priority species pages version 2. (*http://jncc.defra.gov.uk/page-5169* Accessed August 2017).
- JNCC. Special Areas of Conservation (SAC). (http://jncc.defra.gov.uk/ Protected-Sites/SACselection/ - Accessed September 2017), 2017.
- Johnson, D. Estimating nest success: The Mayfield method and an alternative. The Auk, 96:651–661, 1979.
- Johnson, M. D. Measuring habitat quality: A review. *The Condor*, 109:489–504, 2007.
- Jongsomjit, D., Jones, S., Gardali, T., Geupel, G., & Gouse, P. A guide to nestling development and aging in altricial passerines. U.S. Department of Interior, Fish and Wildlife Service, Biological Technical Publication, FWS/BTP-R6008-2007, 2007.
- Joys, A. C. & Crick, H. Q. P. Breeding periods for selected bird species in England. BTO Research Report No. 352, 2004.
- Kalinski, A., Wawrzyniak, J., Banbura, M., Skwarska, J., Zielinski, P., & Banbura, J. Haemoglobin concentration and body condition of nestling Great Tits *Parus major*: a comparison of first and second broods in two contrasting seasons. *Ibis*, 151:667–676, 2009.
- Keating, K. A., Gogan, P. J. P., Vore, J. M., & Irby, L. R. A simple solar radiation index for wildlife habitat studies. *Journal of Wildlife Management*, 71(4):1344– 1348, 2007.
- Keyser, A. J., Hill, G. E., & Soehren, E. C. Effects of forest fragment size, nest density and proximity to edge on the risk of predation to ground-nesting passerine birds. *Conservation Biology*, 12(5):986–994, 1998.

- Klomp, H. The determination of clutch size in birds: A review. Ardea, 58(1-2): 1–121, 1970.
- Kluyver, H., van Balen, J., & Cave, A. The occurrence of time-saving mechanisms in the breeding biology of the Great Tit *Parus major*. *Evolutionary Ecology*, pages 153–169, 1977.
- Kosmala, M., Wiggins, A., Swanson, A., & Simmons, B. Assessing data quality in citizen science. Frontiers in Ecology and the Environment, 14:551–560, 2016.
- Krist, M. Egg size and offspring quality: a meta-analysis in birds. *Biological Reviews*, 86:692–716, 2011.
- Kruse, A. D. & Piehl, J. L. The impact of prescribed burning on ground-nesting birds. Proceedings of the Ninth North American Prairie Conference, pages 153– 156, 1984.
- Lack, D. Habitat selection in birds. With special reference of the effects of afforestation on the Breckland avifauna. *British Ecological Society*, 2(2):239–262, 1933.
- Lack, D. The significance of clutch-size. *Ibis*, 89(2):302–352, 1946.
- Laidlaw, R. A., Smart, J., Smart, M. A., & Gill, J. A. Scenarios of habitat management options to reduce predator impacts on nesting waders. *Journal of Applied Ecology*, 54:1219–1229, 2017.
- Lambert, M., Quy, R., Smith, R., & Cowan, D. The effect of habitat management on home-range size and survival of rural norway rat populations. *Journal of Applied Ecology*, 45:1753–1761, 2008.
- Lambrechts, M., Rieux, A., Galan, M., Cartan-Son, M., Perret, P., & Blondel, J. Double-brooded Great Tits *Parus major* in mediterranean oak habitats: Do first broods always perform better than second broods. *Russian Journal of Ecology*, 38:516–522, 2008.
- Langston, R., Liley, D., Murison, G., Woodfield, E., & Clarke, R. What effects do walkers and dogs have on the distribution and productivity of breeding European Nightjar *Caprimulgus europaeus*. *Ibis*, 149:27–36, 2007.
- Larivière, S. & Messier, F. Effect of density and nearest neighbours on simulated waterfowl nests: Can predators recognize high-density nesting patches? Oikos, 83(1):12–20, 1998.

- Leather, S. "Ecological Armageddon" more evidence for the drastic decline in insect numbers. Annals of Applied Biology, 1-3:1–3, 2018.
- Lee, A. & Barnard, P. How well do bird atlas reporting rates reflect bird densities? Correlates of detection from the Fynbos biome, South Africa, with applications for population estimation. Ostrich, 88:9–17, 2017.
- Lenoir, J., Gegout, J., Marquet, P., de Ruffray, P., & Brisse, H. A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320: 1768–1771, 2008.
- Lessells, C., Dingemanse, N., & Both, C. Egg weights, egg component weights, and laying gaps in Great Tit (*Parus major*) in relation to ambient temperature. *The Auk*, 119:1091–1103, 2002.
- Levin, S. The problem of pattern and scale in ecology. *Ecology*, 73:1943–1967, 1992.
- Lewandowski, E. & Specht, H. Influence of volunteer and project characteristics on data quality of biological surveys. *Conservation Biology*, 29:713–723, 2015.
- Lewis, S., Elston, D., DAunt, F., Cheney, B., & Thompson, P. Effects of extrinsic and intrinsic factors on breeding success in a long lived seabird. *Oikos*, 118: 521–528, 2009.
- Liebezeit, J. R. & George, T. L. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed ponderosa pine forest. *The Condor*, 104:507–517, 2002.
- Lindenmayer, D. & Likens, G. Adaptive monitoring: a new paradigm for long-term research and monitoring. *Trends in Ecology & Evolution*, 24:482–486, 2009.
- Lockyer, Z., Coates, P., Casazza, M., Espinosa, S., & Delehanty, D. Nest-site selection and reproductive success of Greater Sage-Grouse in a fire-affected habitat of Northwestern Nevada. *Journal of Wildlife Management*, 79:785–797, 2015.
- Long, A., Jensen, W., & With, K. Orientation of Grasshopper Sparrow and Eastern Meadowlark nests in relation to wind direction. *The Condor*, 111:395–399, 2009.
- López-López, P., García-Ripollés, C., Aguilar, J. M., García-López, F., & Verdejo, J. Modelling breeding habitat preferences of Bonelli's eagle (*Hieraaetus fasciatus*) in relation to topography, disturbance, climate and land use at different spatial scales. *Journal of Ornithology*, 147:97–106, 2006.

- Lorenz, T., Vierling, K., Johnson, T., & Fischer, P. The role of wood hardness in limiting nest site selection in avian cavity excavators. *Ecological Applications*, 25: 1016–1033, 2015.
- Macdonald, E. C., Camfield, A. F., Martin, M., Wilson, S., & Martin, K. Nest-site selection and consequences for nest survival among three sympatric songbirds in an alpine environment. *Journal of Ornithology*, 157:393–405, 2016.
- Maclean, I. M. D., Suggitt, A. J., Wilson, R. J., Duffy, J. P., & Bennie, J. J. Finescale climate change: Modelling spatial variation in biologically meaningful rates of warming. *Global Change Biology*, 23(1):256–268, 2017.
- Madders, M. & Whitfield, D. P. Upland raptors and the assessment of wind farm impacts. *Ibis*, 148:43–56, 2006.
- Mägi, M., Mänd, R., Tamm, H., Sisask, E., Kilgas, P., & Tilgar, V. Low reproductive success of great tits in the preferred habitat: A role of food availability. *Ecoscience*, 16(2):145–157, 2009.
- Magrath, R. D. Nestling weight and juvenile survival in the Blackbird, *Turdus* merula. Journal of Animal Ecology, 60(1):335–351, 1991.
- Magurran, A., Baillie, S., Buckland, S., Dick, J., Elston, D., Scott, E., Smith, R., Somerfield, P., & Watt, A. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology & Evolution*, 25:574–582, 2010.
- Mainwaring, M. C., Hartley, I. R., Bearhop, S., Brulez, K., du Feu, C. R., Murphy, G., Plummer, K. E., Webber, S. L., James Reynolds, S., & Deeming, D. C. Latitudinal variation in Blue Tit and Great Tit nest characteristics indicates environmental adjustment. *Journal of Biogeography*, 39:1669–1677, 2012.
- Mair, L. & Ruete, A. Explaining Spatial Variation in the Recording Effort of Citizen Science Data across Multiple Taxa. PLOS ONE, 11:e0147796, 2016.
- Mallord, J. W., Smith, K. W., Bellamy, P. E., Charman, E. C., & Gregory, R. D. Are changes in breeding habitat responsible for recent population changes of longdistance migrant birds? *Bird Study*, 63(2):250–261, 2016.
- Marboutin, E., Bray, Y., Peroux, R., Mauvy, B., & Lartiges, A. Population dynamics in European hare: breeding parameters and sustainable harvest rates. *Journal of Applied Ecology*, 40:580–591, 2003.

- Marcia Barbosa, A., Estrada, A., Marquez, A., Purvis, A., & Orme, C. Atlas versus range maps: robustness of chorological relationships to distribution data types in European mammals. *Journal of Biogeography*, 39:1391–1400, 2012.
- Maren, I. E., Vandvik, V., & Ekelund, K. Restoration of bracken-invaded Calluna vulgaris heathlands: Effects on vegetation dynamics and non-target species. Biological Conservation, 141:1032–1042, 2008.
- Martin, T. E. Abiotic vs . biotic influences on habitat selection of coexisting species: Climate change impacts? *Ecology*, 82(1):175–188, 2001.
- Mayfield, H. F. Suggestions for calculating nest success. The Wilson Bulletin, 87 (4):456–466, 1975.
- Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. Habitat selection at multiple scales. *Ecoscience*, 16(2):238–247, 2009.
- McCaffrey, R. Using citizen science in urban bird studies. Urban Habitats, 3:70–86, 2005.
- McGill, B. J. Matters of scale. *Science*, 328:575–576, 2010.
- McGovern, S., Evans, C., Dennis, P., Walmsley, C., & McDonald, M. Identifying drivers of species compositional change in a semi-natural upland grassland over a 40-year period. *Journal of Vegetation Science*, 22:346–356, 2011.
- McKinley, D., Miller-Rushing, A., Ballard, H., Bonney, R., Brown, H., Cook-Patton, S., Evans, D., French, R., Parrish, J., Phillips, T., Ryan, S., Shanley, L., Shirk, J., Stepenuck, K., Weltzin, J., Wiggins, A., Boyle, O., Briggs, R.D.and Chapin III, S., Hewitt, D., Preuss, P., & Soukup, M. Citizen science can improve conservation science, natural resource management, and environmental protection. *Biological Conservation*, 208:15–28, 2017.
- Medina-Roldán, E., Paz-Ferreiro, J., & Bardgett, R. D. Grazing exclusion affects soil and plant communities, but has no impact on soil carbon storage in an upland grassland. Agriculture, Ecosystems and Environment, 149:118–123, 2012.
- Mercer, I. Dartmoor. 2009.
- Merenlender, A., Crall, A., Drill, S., Prysby, M., & Ballard, H. Evaluating environmental education, citizen science, and stewardship through naturalist programs. *Conservation Biology*, 30:1255–1265, 2016.

- Mikula, P., Hromada, M., Albrecht, T., & Tryjanowski, P. Nest site selection and breeding success in three *Turdus* thrush species coexisting in an urban environment. *Acta Ornithologica*, 49:83–92, 2014.
- Milligan, G., Cox, E., Alday, J., Santana, V., McAllistar, H., Pakeman, R., Le Duc, M., & Marrs, R. The effectiveness of old and new strategies for the long-term control of *Pteridium aquilinum*, an 8-year test. Weed Research, 56:247–257, 2016.
- Ministry of Defence. DTE South West public information leaflet. (www.gov.uk/guidance/defence-infrastructure-organisation-and-the-defencetraining-estate - Accessed September 2017), 2017.
- Misenhelter, M. & Rotenberry, J. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology*, 81:2892–2901, 2000.
- Mol, J. H. Reproductive seasonality and nest-site differentiation in three closely related armoured catfishes (Siluriformes: Callichthyidae). *Environmental Biology* of Fishes, 45:363–381, 1996.
- Møller, A., Rubolini, D., & Lehikoinen, E. Populations of migratory bird species that did not show a phenological response to climate change are declining. *PNAS*, 105:16195–16200, 2008.
- Møller, A., Antonov, A., Stokke, B., Føssoy, F., Moksnes, A., Røskaft, E., & Takasu,
  F. Isolation by time and habitat and coexistence of distinct host races of the common cuckoo. *Journal of Evolutionary Biology*, 24:676–684, 2011.
- Morales Fernaz, J., Schifferli, L., & Gruebler, M. Ageing nestling barn swallows *Hirundo rustica*: an illustrated guide and cautionary comments. *Ringing & Mi*gration, 27:65–75, 2012.
- Morecroft, M., Bealey, C., Beaumont, D., Benham, S., Brooks, D., Burt, T., Critchley, C., Dick, J., Littlewood, N., Monteith, D., Scott, W., Smith, R., Walmsley, C., & Watson, H. The UK Environmental Change Network: Emerging trends in the composition of plant and animal communities and the physical environment. *Biological Conservation*, 142:2814–2832, 2009.
- Morris, A., Whittingham, M., Bradbury, R., Wilson, J., Kyrkos, A., Buckingham, D., & Evans, A. Foraging habitat selection by yellowhammers (*Emberiza citrinella*) nesting in agriculturally contrasting regions in lowland England. *Biological Conservation*, 101:197–210, 2001.

- Moskat, C., Ban, M., Fulop, A., Bereczki, J., & Hauber, M. Bimodal habitat use in brood parasitic Common Cuckoos (*Cuculus canorus*) revealed by GPS telemetry. *The Auk*, 136:1–12, 2019.
- Müller, M., Spaar, R., Schifferli, L., & Jenni, L. Effects of changes in farming of subalpine meadows on a grassland bird, the Whinchat (*Saxicola rubetra*). Journal of Ornithology, 146:14–23, 2005.
- Muñoz, A. R., Altamirano, M., Takasu, F., Nakamura, H., & Briskie, J. V. Nest light environment and the potential risk of Common Cuckoo (*Cuculus canorus*) parasitism. *The Auk*, 124(2):619–627, 2007.
- Munson, M., Caruana, R., Fink, D., Hochachka, W., Iliff, M., Rosenberg, K., Sheldon, D., Sullivan, B., Wood, C., & Kelling, S. A method for measuring the relative information content of data from different monitoring protocols. *Methods* in Ecology and Evolution, 1:263–273, 2010.
- Murison, G., Bullock, J. M., Underhill-Day, J., Langston, R., Brown, A. F., & Sutherland, W. J. Habitat type determines the effects of disturbance on the breeding productivity of the Dartford Warbler Sylvia undata. Ibis, 149(Suppl. 1): 16–26, 2007.
- Myers, J. P., Antoniou, M. N., Blumberg, B., Carroll, L., Colborn, T., Everett, L. G., Hansen, M., Landrigan, P. J., Lanphear, B. P., Mesnage, R., Vandenberg, L. N., Vom Saal, F. S., Welshons, W. V., & Benbrook, C. M. Concerns over use of glyphosate-based herbicides and risks associated with exposures: A consensus statement. *Environmental Health*, 15:1–13, 2016.
- Naef-Daenzer, B., Widmer, F., & Nuber, M. Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging data. *Journal of Animal Ecology*, 70:730–738, 2001.
- Natural England. Bracken management: Ecological, archaeological and landscape issues and priorities (TIN047), 2008a.
- Natural England. Bracken management and control (TIN048), 2008b.
- Natural England. Agri-environment schemes in England 2009 (NE194), 2009.
- Natural England. Higher Level Stewardship: Environmental Stewardship Handbook (NE350). 2013.

Natural England. SB5: Mechanical Bracken Control. https://www.gov.uk/ countryside-stewardship-grants/mechanical-bracken-control-sb5 - Accessed April 2017, 2015.

Natural England. Countryside Stewardship Higher Tier Manual, 2016.

- Natural England. Designated Sites View. http://jncc.defra.gov.uk/ Protected-Sites/SACselection/ - Accessed September2017. 2017.
- Newbold, T., Hudson, L. N., Arnell, A. P., Contu, S., De Palma, A., Ferrier, S., Hill,
  S. L. L., Hoskins, A. J., Lysenko, I., Phillips, H. R. P., Burton, V. J., Chng, C.
  W. T., Emerson, S., Gao, D., Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz,
  K., Simmons, B. I., Whitmee, S., Zhang, H., Scharlemann, J. P. W., & Purvis,
  A. Has land use pushed terrestrial biodiversity beyond the planetary boundary?
  a global assessment. *Science*, 353(6296):288–291, 2016.
- Newey, S., Mustin, K., Bryce, R., Fielding, D., Redpath, S., Bunnefeld, N., Bronwen, D., & Irvine, R. Impact of management on avian communities in the Scottish highlands. *PLoS ONE*, 115:e0155473, 2016.
- Newson, S., Woodburn, R., Noble, D., Baillie, S., & Gregory, R. Evaluating the Breeding Bird Survey for producing national population size and density estimates. *Bird Study*, 52:42–54, 2005.
- Newson, S. E., Evans, K. L., Noble, D. G., Greenwood, J. J. D., & Gaston, K. J. Use of distance sampling to improve estimates of national population sizes for common and widespread breeding birds in the UK. *Journal of Applied Ecology*, 45:1330–1338, 2008.
- Newton, I. Experiments on the limitations of bird breeding densities: a review. *Ibis*, 136:397–411, 1994.
- Nilson, J. & Svensson, E. The frequency and timing of laying gaps. Ornis Scandinavica, 24:122–126, 1993.
- Nisbet, I. C. T. Courtship feeding, egg size and breeding success in Common Terns. Nature, 241:141–142, 1973.
- Norment, C. & Green, K. Breeding ecology of Richard's Pipit (Anthus novaeseelandiae) in the Snowy Mountains. Emu - Austral Ornithology, 104:327–336, 2004.

- Norris, K. J. Female choice and the quality of parental care in the Great Tit Parus major. Behavioral Ecology and Sociobiology, 27:275–281, 1990.
- Nunes, D., Magalhaes, A., Weber, A., Gomes, R., Normando, F., Santiago, K., Rizzo, E., & Bazzoli, N. Influence of a large dam and importance of an undammed tributary on the reproductive ecology of the threatened fish matrinxa Brycon orthotaenia Gunther, 1864 (Characiformes: Bryconidae) in southeastern Brazil. *Neotropical Ichthyology*, 13:317–324, 2015.
- Nur, N. The consequences of brood size for breeding Blue Tits II. Nestling weight, offspring survival and optimal brood size. *Journal of Animal Ecology*, 53:479–517, 1984.
- O'Brien, M., Green, R. E., & Wilson, J. D. Partial recovery of the population of Corncrakes *Crex crex* in Britain, 1993-2004. *Bird Study*, 53:213–224, 2006.
- O'Connor, J., Dudaniec, R., & Kleindorfer, S. Parasite infestation and predation in Darwin's small ground finch: contrasting two elevational habitats between islands. *Journal of Tropical Ecology*, 26:285–292, 2010.
- O'Donnell, C. F. J. & Hoare, J. M. Quantifying the benefits of long-term integrated pest control for forest bird populations in a New Zealand temperate rainforest. *New Zealand Journal of Ecology*, 36(2):131–140, 2012.
- Olah, G., Vigo, G., Heinsohn, R., & Brightsmith, D. Nest site selection and efficacy of artificial nests for breeding success of Scarlet Macaws Ara macao macao in lowland Peru. Journal for Nature Conservation, 22:176–185, 2014.
- ONS. 2011 Census: Characteristics of National Parks., 2011.
- Oppliger, A., Richner, H., & Christe, P. Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the Great Tit (*Parus major*). *Behavioral Ecology*, 5(2):130–134, 1993.
- O'Rourke, E., Charbonneau, M., & Poinsot, Y. High nature value mountain farming systems in Europe: Case studies from the Atlantic Pyrenees, France and the Kerry Uplands, Ireland. *Journal of Rural Studies*, 46:47–59, 2016.
- Orr, H., Wilby, R., McKenzie Hedger, M., & Brown, I. Climate change in the uplands: A UK perspective on safeguarding regulatory ecosystem services. *Climate Research*, 37:77–98, 2008.

- Owen, T. & Pierce, A. Hatching success and nest site characteristics of Black Skimmer (*Rynchops niger*) on the Isles Dernieres Barrier Island Refuge, Louisiana. *Waterbirds*, 36:342–347, 2013.
- Pakanen, V., Luukkonen, A., & Koivula, K. Nest predation and trampling as management risks in grazed coastal meadows. *Biodiversity and Conservation*, 20: 2057–2073, 2011.
- Pakeman, R., Le Duc, M., & Marrs, R. A review of current bracken control and associated vegetation strategies in great britain. Web Ecology, 3:6–11, 2001.
- Parmesan, C. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics, 37(1):637–669, 2006.
- Parr, R. The decline to extinction of a population of Golden Plover in north-east Scotland. Ornis Scandinavica, 23(2):152–158, 1992.
- Part, T. & Wretenberg, J. Do artificial nests reveal relative nest predation risk for real nests? *Journal of Avian Biology*, 33:39–46, 2002.
- Part, T., Arlt, D., Doligez, B., Low, M., & Qvarnstrom, A. Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year. *Journal of Animal Ecology*, 80:1227–1235, 2011.
- Pasinelli, G. Nest site selection in middle and great spotted woodpeckers *Dendro-copos medius & D. major*: implications for forest management and conservation. *Biodiversity & Conservation*, 16:1283–1298, 2007.
- Paul, K., Quinn, M., Huijser, M., Graham, J., & Broberg, L. An evaluation of a citizen science data collection program for recording wildlife observations along a highway. *Journal of Environmental Management*, 139:180–187, 2014.
- Pavel, A., Buresï, S., Weidinger, K., & Kovarï, P. Distraction displays in Meadow Pipit (Anthus pratensis) females in central and Northern Europe. Ethology, 106: 1007–1019, 2000.
- Peach, W., Baillie, S., & Balmer, D. Long-term changes in the abundance of passerines in Britain and Ireland as measured by constant effort mist-netting. *Bird Study*, 45:257–275, 1998.
- Pearce-Higgins, J. W. Using diet to assess the sensitivity of northern and upland birds to climate change. *Climate Research*, 24:119–130, 2010.

- Pearce-Higgins, J. W. & Grant, M. C. Relationships between bird abundance and the composition and structure of moorland vegetation. *Bird Study*, 53:112–125, 2006.
- Pearce-Higgins, J. W., Stephen, L., Langston, R. H. W., Bainbridge, I. P., & Bullman, R. The distribution of breeding birds around upland wind farms. *Journal* of Applied Ecology, 46(6):1323–1331, 2009.
- Pearce-Higgins, J. W., Dennis, P., Whittingham, M. J., & Yalden, D. W. Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Global Change Biology*, 16(1):12–23, 2010.
- Peck, K., Franke, A., Lecomte, N., & Bety, J. Nesting habitat selection and distribution of an avian top predator in the Canadian Arctic. Arctic Science, 4:499–512, 2018.
- Pedroli, J.-C. Breeding success of the Meadow Pipit Anthus pratensis in the Swiss Jura. Ornis Scandinavica, 9(2):168–171, 1978.
- Perkins, A., Maggs, H., Wilson, J., & Watson, A. Delayed mowing increases corn bunting *Emberiza calandra* nest success in an agri-environment scheme trial. Agriculture, Ecosystems & Environment, 181:80–89, 2013.
- Perlut, N. & Strong, A. Grassland birds and rotational-grazing in the northeast: Breeding ecology, survival and management opportunities. *The Journal of Wildlife Management*, 75:715–720, 2011.
- Perrig, M., Gruebler, M., Keil, H., & Naef-Daenzer, B. Post-fledging survival of Little Owls Athene noctua in relation to nestling food supply. *Ibis*, 159:532–540, 2017.
- Pescott, O., Simkin, J., August, T., Randle, Z., Dore, A., & Botham, M. Air pollution and its effects on lichens, bryophytes, and lichen-feeding Lepidoptera: review and evidence from biological records. *Biological Journal of the Linnean Society*, 115:611–635, 2015.
- Pineiro, A., Barja, I., Silvan, G., & Illera, J. Effect of tourist pressure and reproduction on physiological stress response in wildcats: management implications for species conservation. Wildlife Research, 39:532–539, 2012.
- Podkowa, P. & Surmacki, A. The importance of illumination in nest site choice and nest characteristics of cavity nesting birds. *Scientific Reports*, 7:1329, 2017.

- Potts, S. & Willmer, P. Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. *Ecological Entomology*, 22: 319–328, 1997.
- Potts, S., Biesmeijer, J., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25:345–353, 2010.
- Potts, S., Imperatriz-Fonseca, V., Ngo, H., Aizen, M., Biesmeijer, J., Breeze, T., Dicks, L., Garibaldi, L., Hill, R., Settele, J., & Vanbergen, A. Safeguarding pollinators and their values to human well-being. *Nature*, 540:220–229, 2016.
- Powell, A. & Busby, W. Effects of grassland management on breeding birds at the western edge of the tallgrass prairie ecosystem in kansas. *Natural Areas Journal*, 33:130–138, 2013.
- Powell, L., Hodgman, T., Glanz, W. E., Osenton, J., & Fisher, C. Nest-site selection and nest survival of the Rusty Blackbird: Does timber managament adjacent to wetlands create ecological traps? *The Condor*, 112:800–809, 2010.
- Prokop, P. & Rodak, R. Ability of Slovakian pupils to identify birds. Eurasia Journal of Mathematics, Science & Technology Education, 5:127–133, 2009.
- QGIS Development Team. *QGIS Geographic Information System*. Open Source Geospatial Foundation, 2009.
- R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, 2015.
- Ramchunder, S., Brown, L., & Holden, J. Environmental effects of drainage, drainblocking and prescribed vegetation burning in UK upland peatlands. *Progress in Physical Geography*, 33(1):49–79, 2009.
- Ratcliffe, D. A. & Thompson, D. B. A. The British uplands: their ecological character and international significance. In: Ecological change in the uplands. Blackwell Scientific Publications, Oxford, 1988.
- Reed, M. S., Bonn, A., Slee, W., Beharry-Borg, N., Birch, J., Brown, I., Burt,
  T. P., Chapman, D., Chapman, P. J., Clay, G. D., Cornell, S. J., Fraser,
  E. D., Glass, J. H., Holden, J., Hodgson, J. A., Hubacek, K., Irvine, B., Jin,
  N., Kirkby, M. J., Kunin, W. E., Moore, O., Moseley, D., Prell, C., Price,

M. F., Quinn, C. H., Redpath, S., Reid, C., Stagl, S., Stringer, L. C., Termansen,
M., Thorp, S., Towers, W., & Worrall, F. The future of the uplands. *Land Use Policy*, 26:S204–S216, 2009.

- Refsnider, J. & Janzen, F. Putting eggs in one basket: Ecological and evolutionary hypotheses for variation in oviposition-site choice. Annual Review of Ecology, Evolution and Systematics, 41:39–57, 2010.
- Regulation (EC) No 1107/2009. http://eur-lex.europa.eu/legalcontent/EN/TXT/?uri=celex%3A32009R1107, 2009.
- Regulation (EU) No 1045/2011. https://eur-lex.europa.eu/legalcontent/EN/TXT/?uri=CELEX%3A32011R1045, 2011.
- Remeš, V. Birds and rodents destroy different nests: A study of Blackcap Sylvia atricapilla using the removal of nest concealment. Ibis, 147:213–216, 2005.
- Revaz, E., Schaub, M., & Arlettaz, R. Foraging ecology and reproductive biology of the Stonechat *Saxicola torquata*: Comparison between a revitalized, intensively cultivated and a historical, traditionally cultivated agro-ecosystem. *Journal of Ornithology*, 149:301–312, 2008.
- Reynolds, R., Wiens, J., & Salafsky, S. A review and evaluation of factors limiting Northern Goshawk populations. *Studies in Avian Biology*, 31:260–273, 2006.
- Rhodes, B., O'Donnel, C., & Jamieson, I. Microclimate of natural cavity nests and its implications for a threatened secondary cavity-nesting passerine of New Zealand, the South Island Saddleback. *The Condor*, 111:462–469, 2009.
- Riwthong, S., Schreinemachers, P., Grovermann, C., & Berger, T. Land use intensification, commercialization and changes in pest management of smallholder upland agriculture in Thailand. *Environmental Science & Policy*, 45:11–19, 2015.
- Robertson, B. Nest-site selection in a post-fire landscape: Do parents make tradeoffs between microclimate and predation risk? *The Auk*, 500-510:500–510, 2009.
- Robertson, G., Newborn, D., M., R., & D., B. Does rotational burning increase red grouse abundance and breeding success on moors in northern england? Wildlife Biology, page SP1, 2017.
- Robinson, R., Julliard, R., & Saracco, J. Constant effort: Studying avian population processes using standardised ringing. *Ringing & Migration*, 24:199–204, 2011.

- Robinson, R. A. BirdFacts: Profiles of birds occurring in Britain & Ireland. BTO Research Report 407, 2017.
- Rönkä, M., Saari, L., Hario, M., Hänninen, J., & Lehikoinen, E. Breeding success and breeding population trends of waterfowl: implications for monitoring. *Wildlife Biology*, 17:225–239, 2011.
- Rose, L. N. Breeding ecology of British pipits and their Cuckoo parasite. *Bird Study*, 29(1):27–40, 1982.
- Rotenberry, J. T. & Wiens, J. A. Reproductive biology of shrubsteppe passerine birds: Geographical and temporal variation. *The Condor*, 91(1):1–14, 1989.
- Rouifed, S., Piola, F., & Spiegelberger, T. Invasion by *Fallopia* spp. in a French upland region is related to anthropogenic disturbances/. *Basic and Applied Ecology*, 15:435–443, 2014.
- Royal Society for the Protection of Birds. The uplands: Time to change. https://www.rspb.org.uk/Images/uplands\_tcm9-166286.pdf - Accessed September 2017. 2017a.
- Royal Society for the Protection of Birds. East Dartmoor Moorland Breeding Bird Survey 2016. 2017b.
- Ruttenberg, B., Schofield, P., Akins, J., Acosta, A., Feeley, M., Blondeau, J., Smith, S., & Ault, J. Rapid invasion of Indo-Pacific lionfishes (*Pterios volitans* and *Pterois miles*) in the Florida Keys, USA: Evidence from multiple pre- and postinvasion data sets. *Bulletin of Marine Science*, 88:1051–1059, 2012.
- Saab, V., Russell, R., & Dudley, J. Nest-site selection by cavity-nesting birds in relation to postfire salvage logging. *Forest Ecology and Management*, 257:151– 159, 2009.
- Sæther, B., Ringsby, T. H., & Røskaft, E. Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos*, 77:217–226, 1996.
- Saino, N., Romano, M., Ferrari, R. P., Martinelli, R., & Møller, A. P. Stressed mothers lay eggs with high corticosterone levels which produce low-quality offspring. *Journal of Experimental Zoology*, 303A:998–1006, 2005.

- Sanz, J. J. Effects of geographic location and habitat on breeding parameters of Great Tits. *The Auk*, 115(4):1034–1051, 1998.
- Sasvári, L. & Hegyi, Z. Effects of breeding experience on nest-site choice and the reproductive performance of Tawny Owls (*Strix aluco*). Journal of Raptor Research, 39(1):26–35, 2005.
- Sasvari, L. & Hegyi, Z. Predation risk of Tawny Owl Strix aluco nests in relation to altitude, breeding experience, breeding density and weather conditions. Ardea, 99:227–232, 2011.
- Sauer, J., Fallon, J., & Johnson, R. Use of North American Breeding Bird Survey Data to Estimate Population Change for Bird Conservation Regions. *The Journal* of Wildlife Management, 67:372–389, 2003.
- Schielzeth, H. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution, 1:103–113, 2010.
- Schill, K. & Yahner, R. Nest-Site Selection and Nest Survival of Early Successional Birds in Central Pennsylvania. . The Wilson Journal of Ornithology, 121:476–484, 2009.
- Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A. S. L., Stuart, S. N., Temple, H. J., Baillie, J., Boitani, L., Lacher Jr, T. E., Mittermeier, R. A., Smith, A. T., Absolon, D., Aguiar, J. M., Amori, G., Bakkour, N., Baldi, R., Berridge, R. J., Bielby, J., Black, P. A., Blanc, J. J., Brooks, T. M., Burton, J. A., Butynski, T. M., Catullo, G., Garshelis, D. L., Gates, C., Gimenez-dixon, M., Gonzalez, S., Gonzalez-Maya, J. F., Good, T. C., Hammerson, G., Hammond, P. S., Happold, D., Happold, M., Hare, J., Harris, R. B., Hawkins, C. E., Haywood, M., Heaney, L. R., Hedges, S., Helgen, K. M., Hilton-taylor, C., Hussain, S. A., Ishii, N., Jefferson, T. A., Jenkins, R. K. B., Johnston, C. H., Keith, M., Kingdon, J., Knox, D. H., Kovacs, K. M., Langhammer, P., Leus, K., Lewison, R., Lichtenstein, G., Lowry, L. F., Macavoy, Z., Medellín, R. A., Medici, P., Mills, G., Moehlman, P. D., Molur, S., Mora, A., Nowell, K., Oates, J. F., Olech, W., Oliver, W. R. L., Oprea, M., Patterson, B. D., Perrin, W. F., Polidoro, B. A., Pollock, C., Powel, A., Protas, Y., Racey, P., Ragle, J., Ramani, P., Rathbun, G., Reeves, R. R., Reilly, S. B., Reynolds III, J. E., Rondinini, C., Rosell-ambal, R. G., Rulli,

M., Rylands, A. B., Savini, S., Schank, C. J., Sechrest, W., Self-sullivan, C., Shoemaker, A., Sillero-zubiri, C., Silva, N. D., Smith, D. E., Taylor, B. L., Timmins, R., Tirira, D. G., Tognelli, M. F., Tsytsulina, K., Veiga, L. M., Vié, J.-C., Williamson, E. A., Wyatt, S. A., Xie, Y., & Young, B. E. The status of the world's land and marine mammals: Diversity, threat and knowledge. *Science*, 322: 225–230, 2008.

- Schmeller, D., Henry, P., Julliard, R., Gruber, B., Clobert, J., Dziock, F., Lengyel, S., Nowicki, P., Deri, E., Budrys, E., Kull, T., Tali, K., Bauch, B., Settele, J., van Swaay, C., Kobler, A., Babij, V., Papastergiadou, E., & Henle, K. Advantages of volunteer-based biodiversity monitoring in Europe. *Conservation Biology*, 23: 307–316, 2008.
- Schmidt, K. A. Nest predation and population declines in Illinois songbirds: A case for mesopredator effects. *Conservation Biology*, 17(4):1141–1150, 2003.
- Scotland's Environmental and Rural Services. Bracken control, a guide to best practice, 2008.
- Seaton, R., Minot, E., & Holland, J. Nest-site selection of New Zealand Falcons (*Falco novaeseelandiae*) in plantation forests and the implications of this to forestry management. *Emu-Austral Ornithology*, 110:316–323, 2010.
- Sedgwick, J. A. & Knopf, F. L. Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains. *Journal of Wildlife Management*, 54(1):112–124, 1990.
- Seel, D. C. & Walton, K. C. Numbers of Meadow Pipits Anthus pratensis on mountain farm grassland in North Wales in the breeding season. *Ibis*, 121:147– 164, 1979.
- Sekercioĝlu, C. H., Primack, R. B., & Wormworth, J. The effects of climate change on tropical birds. *Biological Conservation*, 148:1–18, 2012.
- Sen, B., Tavares, J., & Bilgin, C. Nest site selection patterns of a local Egyptian Vulture Neophron percoopterus population in Turkey. Bird Conservation International, 27:568–581, 2017.
- Shaw, S., Wheeler, B., Kirby, P., Phillipson, P., & R., E. Literature review of the historical effects of burning and grazing of blanket bog and upland wet heath. . *English Nature Research Report no. 172*, 1996.

- Shine, R. & Brown, G. Adapting to the unpredictable: reproductive biology of vertebrates in the Australian wet-dry tropics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363:363–373, 2008.
- Shitikov, D. A., Vaytina, T. M., Gagieva, V. A., & Fedchuk, D. V. Breeding success affects site fidelity in a Whinchat *Saxicola rubetra* population in abandoned fields. *Bird Study*, 62:96–105, 2015.
- Silvertown, J. A new dawn for citizen science. *Trends in Ecology & Evolution*, 24: 467–471, 2009.
- Sim, I., Ludwig, S., Grant, M., Loughrey, J., Rebecca, G., & Redpath, S. Seasonal variation in foraging conditions for Ring Ouzels *Turdus torquatus* in upland habitats and their effects on juvenile habitat selection. *Ibis*, 155:42–54, 2013a.
- Sim, I. M. W., Gregory, R. D., Hancock, M. H., & Brown, A. F. Recent changes in the abundance of British upland breeding birds. *Bird Study*, 52:261–275, 2005.
- Sim, I. M. W., Ludwig, S. C., Grant, M. C., Loughrey, J. L., Rebecca, G. W., & Reid, J. M. Postfledging survival, movements, and dispersal of Ring Ouzels (*Turdus torquatus*). *The Auk*, 130(1):69–77, 2013b.
- Simmons, I. G. The mid-Holocene ecological history of the moorlands of England and Wales and its relevance for conservation. *Environmental Conservation*, 17(1): 61–69, 1990.
- Siriwardena, G., Baillie, S., & Wilson, J. Variation in the survival rates of some British passerines with respect to their population trends on farmland. *Bird Study*, 45:276–292, 1998.
- Sitters, H.P. Tetrad Atlas of the Breeding Birds of Devon. Devon Birdwatching and Preservation Society, 1988.
- Skiftesvik, A., Durif, C., Bjelland, R., & Browman, H. Distribution and habitat preferences of five species of wrasse (Family Labridae) in a Norwegian fjord. *ICES Journal of Marine Science*, 72:890–899, 2015.
- Slagsvold, T. Annual and geographical variation in the timing of breeding of the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca* in relation to environmental phenology and spring temperature. *Ornis Scandinavica*, 7:127–145, 1976.

- Smith, P., Bart, J., Lanctot, R., McCaffery, B., & Brown, S. Probability of detection of nests and implications for survey design. *The Condor*, 111:414–423, 2009.
- Smith, R., Pullin, A., Stewart, G., & Sutherland, W. Effectiveness of predator removal for enhancing bird populations. *Conservation Biology*, 24:820–829, 2010.
- Smith, R., Pullin, A., Stewart, G., & Sutherland, W. Is nest predator exclusion an effective strategy for enhancing bird populations? *Biological Conservation*, 144: 1–10, 2011.
- Snall, T., Kindvall, O., Nilsson, J., & Part, T. Evaluating citizen-based presence data for bird monitoring. *Biological Conservation*, 144:804–810, 2011.
- Soroye, P., Ahmed, N., & Kerr, J. Opportunistic citizen science data transform understanding of species distributions, phenology and diversity gradients for glocal change research. *Global Change Biology*, 24:5281–5291, 2018.
- Stewart, G., Cox, E., Le Duc, M., Pakeman, R., Pullin, A., & Marrs, R. Control of *Pteridium aquilinum*: Meta-analysis of a multi-site study in the UK. Annals of Botany, 101:957–970, 2008.
- Stillman, R. A. Population sizes and habitat associations of upland breeding birds in the South Pennines, England. *Biological Conservation*, 69:307–314, 1994.
- Strasevicius, D., Jonsson, M., Nyholm, N., & Malmqvist, B. Reduced breeding success of Pied Flycatchers *Ficedula hypoleuca* along regulated rivers . *Ibis*, 155: 348–356, 2013.
- Strebel, G., Jacot, A., Horch, P., & Spaar, R. Effects of grassland intensification on Whinchats Saxicola rubetra and implications for conservation in upland habitats. *Ibis*, 157:250–259, 2015.
- Strong, T. & Bock, C. Bird species distribution patterns in riparian habitats in southeastern Arizona. *The Condor*, 92:866, 1990.
- Suarez, S., Balbontin, J., & Ferrer, M. Nesting habitat selection by booted eagles *Hieraaetus pennatus* and implications for management. *Journal of Applied Ecology*, 37:215–223, 2000.
- Sugden, L. G. & Beyersbergen, G. W. Effect of density and concealment on American Crow predation of simulated duck nests. *The Journal of Wildlife Management*, 50(1):9–14, 1986.

- Suggitt, A., Wilson, R., August, T., Beale, C., Bennie, J., Dordolo, A., Fox, R., Hopkins, J. J., Isaac, N. J. B., Jorieux, P., MacGregor, N., Marcetteau, J., Massimini, D., Morecroft, M., Pearce-Higgins, J., Walker, K., & Maclean, I. Climate change refugia for the flora and fauna of England. *Natural England Commissioned Reports, Number 162*, 2014.
- Sullivan, T. & Sullivan, D. Fertilisation, cattle grazing and voles: collapse of meadow vole populations in young forests? Wildlife Research, 41:367–378, 2014.
- Sumasgutner, P., Schulze, C., Krenn, H., & Gamauf, A. Conservation related conflicts in nest-site selection of the Eurasian Kestrel (Falco tinnunculus) and the distribution of its avian prey. *Landscape and Urban Planning*, 127:94–103, 2014.
- Swaisgood, R., Nordstrom, L., Schuets, J., Boylan, J., Fournier, J., & Shemai, B. A management experiment evaluating nest-site selection by beach-nesting birds. *The Journal of Wildlife Management*, 82:192–201, 2018.
- Szotek, K. & Becker, P. Terns in trouble: demographic consequences of low breeding success and recruitment on a common tern population in the German Wadden Sea. Journal of Ornithology, 153:313–326, 2012.
- Teglhøy, P. A comparative study of insect abundance and reproductive success of barn swallows *Hirundo rustica* in two urban habitats. *Journal of Avian Biology*, 48:846–853, 2017.
- Tharme, A., Green, R., Baines, D., Bainbridge, I., & O'Brien, M. The effect of management for red grouse shooting on the population density of breeding birds on heather-dominated moorland. *Journal of Applied Ecology*, 38:439–457, 2001.
- Thirgood, S. & Redpath, S. Hen harriers and red grouse: science, politics and human-wildlife conflict. *Journal of Applied Ecology*, 45:1550–1554, 2008.
- Thompson, D. B. A. & Macdonald, A. J. Upland heather moorland in Great Britain: A review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation*, 71:163–178, 1995.
- Thompson, F. R. Factors affecting nest predation on forest songbirds in North America. *Ibis*, 149(Suppl. 2):98–109, 2007.
- Thompson, P., Douglas, D., Hoccom, D., Knott, J., Roos, S., & Wilson, J. Environmental impacts of high-output driven shooting of red grouse *Lagopus lagopus scotica*. *Ibis*, 158:446–452, 2016.

- Thompson, W. Towards reliable bird surveys: Accounting for individuals present but not detected. *The Auk*, 119:18–25, 2002.
- Thomson, D. L., Baillie, S. R., & Peach, W. J. A method for studying post-fledging survival rates using data from ringing recoveries. *Bird Study*, 46:S104–S111, 1999.
- Tinbergen, J., Tinbergen, J., & Ubels, R. Is fitness affected by ring colour? Ardea, 101:152–163, 2013.
- Tome, D. & Denac, D. Survival and development of predator avoidance in the postfledging period of the whinchat (*Saxicola rubetra*): consequences for conservation measures. *Journal of Ornithology*, 153:131–138, 2012.
- Tripp, S., Phelps, Q., Colombo, Q., Garvey, J., Burr, B., Herzog, D., & Hrabik, R. Maturation and reproduction of Shovelnose Sturgeon in the middle Mississippi river. North American Journal of Fisheries Management, 29:730–738, 2009.
- Trivedi, M., Morecroft, M., Berry, P., & Dawson, T. Potential effects of climate change on plant communities in three montane nature reserves in Scotland, UK. *Biological Conservation*, 141:1665–1675, 2008.
- Tyre, A., Tenhumberg, B., Field, S., Niejalke, D., Parris, K., & Possingham, H. Improving precision and reducing bias in biological surveys: estimating falsenegative error rates. *Ecological Applications*, 13:1790–1801, 2003.
- Uher-Koch, B., Schmutz, J., & Wright, K. Nest visits and capture events affect breeding success of Yellow-billed and Pacific loons. *The Condor*, 117:121–129, 2015.
- UK Biodiversity Group. Tranche 2 action plans: terrestrial and freshwater species and habitats. 1999.
- Valdes, K., Hunter, E., & Nibbelink, N. Salt marsh elevation is a strong determinant of nest-site selection by Clapper Rails in Georgia. *Journal of Field Ornithology*, 87:65–73, 2016.
- van der Wal, R., Anderson, H., Robinson, A., Sharma, N., Mellish, C., Roberts, S., Darvill, B., & Siddharthan, A. Mapping species distributions: A comparison of skilled naturalist and lay citizen science recording. *Ambio*, 44:S584–S600, 2015.
- van Klink, R., Mandema, F. S., Bakker, J. P., & Tinbergen, J. M. Foraging site choice and diet selection of Meadow Pipits Anthus pratensis breeding on grazed salt marshes. *Bird Study*, 61(1):101–110, 2014.

- van Oosten, H. H. Comparative breeding biology of three insectivorous songbirds in Dutch dune grasslands. Ardea, 104(3):199–2012, 2016.
- Vandenberghe, C., Prior, G., Littlewood, N. A., Brooker, R., & Pakeman, R. Influence of livestock grazing on Meadow Pipit foraging behaviour in upland grassland. *Basic and Applied Ecology*, 10:662–670, 2009.
- Vandvik, V., Heegaard, E., Måren, I., & Aarrestad, P. Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. *Journal of Applied Ecology*, 42:139–149, 2005.
- Vickery, J. A., Tallowin, J. R., Feber, R. E., Asteraki, E. J., Atkinson, P. W., Fuller, R. J., & Brown, V. K. The management of lowland neutral grassland in Britain: effects of agricultural practice on birds and their food resources. *Journal of Applied Ecology*, 38:647–664, 2001.
- Vickery, J. A., Bradbury, R. B., Henderson, I. G., Eaton, M. A., & Grice, P. V. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. *Biological Conservation*, 119:19–39, 2004.
- Visser, M. E., Caro, S. P., van Oers, K., Schaper, S. V., & Helm, B. Phenology, seasonal timing and circannual rhythms: Towards a unified framework. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365:3113–3127, 2010.
- Vogl, W., Taborsky, B., Teuschl, Y., Taborsky, M., & Honza, M. Habitat and space use of European Cuckoo females during the egg laying period. *Behaviour*, 141: 881–898, 2004.
- Wachob, D. A microclimate analysis of nest-site selection by Mountain Chickadees. Journal of Field Ornithology, 67(4):525–533, 1996.
- Wäckers, F. & van Rijn, P. Biodiversity and insect pests: Key issues for sustainable management. John Wiley & Sons, Ltd., 2012.
- Wagner, K. & Seymour, R. Nesting climate and behaviour of Cape Barren geese (*Cereopsis novaehollandiae* Latham). Australian Journal of Zoology, 49(2):155– 170, 2001.
- Watson, H., Bolton, M., & Monaghan, P. Out of sight but not out of harm's way: Human disturbance reduces reproductive success of a cavity-nesting seabird. *Biological Conservation*, 174:127–133, 2014.

- Webb, C. & Kelly, D. The reproductive biology of New Zealand flora. Trends in Ecology & Evolution, 8:442–447, 1993.
- Webb, N. R. The traditional management of European heathlands. Journal of Applied Ecology, 35:987–990, 1998.
- Weidinger, K. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. *Journal of Animal Ecology*, 71:424–437, 2002.
- Westmoreland, D. & Best, L. B. The effect of disturbance on Mourning Dove nesting success. The Auk, 102(4):774–780, 1985.
- Wheater, H. & Evans, E. Land use, water management and future flood risk. Land Use Policy, 26S:S251–S264, 2009.
- Whittingham, M. J., Percival, S. M., & Brown, A. F. Nest-site selection by Golden Plover: Why do shorebirds avoid nesting on slopes? *Journal of Avian Biology*, 33:184–190, 2002.
- Wich, S., Fredriksson, G., Usher, G., Peters, H., Priatna, D., Basalamah, F., Susanto, W., & Kuhl, H. Hunting of Sumatran orang-utans and its importance in determining distribution and density. *Biological Conservation*, 146:163–169, 2012.
- Wikum, D. A. & Shanholtzer, G. F. Application of the Braun-Blanquet coverabundance scale for vegetation analysis in land development studies. *Environmental Management*, 2(4):323–329, 1978.
- Williams, H., Willemoes, M., Klaassen, R., Strandberg, R., & Thorup, K. Common Cuckoo home ranges are larger in the breeding season than in the non-breeding season and in regions of sparse forest cover. *Journal of Ornithology*, 157:461–469, 2016.
- Williams, T. D. Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. *Biological Reviews*, 68:35–59, 1994.
- Willis, K. & Whittaker, R. Species diversity scale matters. Science, 295:1245–1248, 2002.
- Wilson, J. D., Whittingham, M. J., & Bradbury, R. B. The management of crop structure: A general approach to reversing the impacts of agricultural intensification on birds? *Ibis*, 147:453–463, 2005.

- Wilson, S. & Martin, K. Breeding habitat selection of sympatric White-tailed, Rock and Willow Ptarmigan in the southern Yukon Territory, Canada. *Journal of Ornithology*, 149:629–637, 2008.
- Wink, M., Sauer-Gürth, H., & Gwinner, E. Evolutionary relationships of stonechats and related species inferred from mitochondrial-DNA sequences and genomic fingerprinting. *British Birds*, 95:349–355, 2002.
- Winter, M., Johnson, D., & Shaffer, J. Variability in vegetation effects on density and nesting success of grassland birds. *The Journal of Animal Ecology*, 69(1): 185–197, 2005.
- Wood, K. A., Newth, J. L., Hilton, G. M., Nolet, B. A., & Rees, E. C. Inter-annual variability and long-term trends in breeding success in a declining population of migratory swans. *Journal of Avian Biology*, 47:597–609, 2016.
- Woodward, I., Massimino, D., Hammond, M., Harris, S., Leech, D., Noble, D., Walker, R., Barimore, C., Dadam, D., Eglington, S., Marchant, J., Sullivan, M., Baillie, S., & Robinson, R. BirdTrends 2018: trends in numbers, breeding success and survival for UK breeding birds. *Research report 708. BTO, Thetford*, 2018.
- Wright, L. J., Hoblyn, R. A., Green, R. E., Bowden, C. G. R., Mallord, J. W., Sutherland, W. J., & Dolman, P. M. Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark *Lullula arborea*. *Journal of Animal Ecology*, 78(6):1191–1202, 2009.
- Wyllie, I. The Cuckoo. Batsford, London, 1981.
- Yallop, A. R., Thacker, J. I., Thomas, G., Stephens, M., Clutterbuck, B., Brewer, T., & Sannier, C. A. D. The extent and intensity of management burning in the English uplands. *Journal of Applied Ecology*, 43:1138–1148, 2006.
- Yasue, M. & Dearden, P. Replacement nesting and double-brooding in Malaysian Plovers *Charadrius peronii*: Effects of season and food availability. *Ardea*, 96: 59–72, 2008.
- Zavaleta, E. S., Hobbs, R. J., & Mooney, H. A. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution*, 16(8):454–459, 2001.

Zockler, C., Syroechkovskiy, E., & Atkinson, P. Rapid and continued population decline in the Spoon-billed Sandpiper *Eurynorhynchus pygmeus* indicates imminent extinction unless conservation action is taken. *Bird Conservation International*, 20:95–111, 2010.