Breeding ground correlates of the distribution and decline of the Common Cuckoo

*Cuculus canorus* at two spatial scales

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Many migratory bird species are undergoing population declines as a result of potentially multiple, interacting mechanisms. Understanding the environmental associations of spatial variation in population change can help tease out the likely mechanisms involved. Common Cuckoo *Cuculus canorus* populations have declined by 75% in England, but increased by 29% in Scotland. The declines have mainly occurred in lowland agricultural landscapes, but their mechanisms are unknown. At both the local scale within the county of Devon (SE England) and at the national (UK) scale, we analysed the breeding season distribution of Cuckoos in relation to habitat variation, the abundance of host species and the abundance of moth species whose caterpillars are a key food of adult Cuckoos. At the local scale, we found that Cuckoos were more likely to be detected in areas with more semi-natural habitat, more Meadow Pipit *Anthus pratensis* (but fewer Dunnock *Prunella modularis*) and where, later in the summer, higher numbers of moths were captured whose larvae are Cuckoo prey. Nationally, Cuckoos have become more associated with upland heath characterised by the presence of Meadow Pipit hosts, and with wetland habitats occupied by Eurasian Reed Warbler *Acrocephalus scirpaceus* hosts. The core distribution of Cuckoos has shifted from south to north within the UK. By the end of 2009, the abundance of macro-moth species identified as prey has also declined four times faster than that of species not known to be taken by Cuckoos. The abundance of these moths has shown the sharpest declines in grassland, arable and woodland habitats and has increased in semi-natural habitats (heaths and rough grassland). Our correlative data suggest that Cuckoos are likely to remain a very scarce bird in lowland agricultural landscapes without large scale changes in agricultural practices.
Many long-distance, migratory birds are in long-term decline (Robbins et al. 1989, Sanderson et al. 2006, Vickery et al. 2014, Bairlein 2016). Reversing such population declines is a major nature conservation challenge and involves identifying and addressing the underlying causes (Caughley 1994). This is often not straightforward, as there may be multiple interacting mechanisms operating on breeding or wintering grounds or on migration routes (Vickery et al. 2014). These include the effects of climate change, which are manifested through the impact of changing temperature on physiology (Şekercioğlu et al. 2012), on laying dates in breeding grounds (Ockendon et al. 2013), on the mismatch between timing of food requirements and food availability (Both et al. 2010), and through the effects of rainfall on seasonal resources in wintering grounds (Ockendon et al. 2014). Other mechanisms affecting migratory birds include habitat loss and fragmentation in breeding and non-breeding areas (Vickery et al. 2014), reduced food abundance in breeding areas (Townsend et al. 2016, Bairlein 2016), hunting and predation during migration (Lehikoinen et al. 2011) and possible increases in deleterious effects of competitors, parasites and pathogens (Fuller et al. 2012, Wittmer et al. 2015).

Obligate brood parasite such as the Common Cuckoo *Cuculus canorus* (henceforth, ‘Cuckoo’) face an additional challenge, as the impacts of environmental change on both the brood parasite and its host must be considered. The Cuckoo has declined by 27% across Europe over the period 1980-2015 (www.ebcc.info), but in the UK, the overall decline is more severe, with a 43% decline between 1994 and 2014 (Harris et al. 2016). However, there is spatial variation in these trends. Harris et al. (2016) found that population declines were most severe and long-term in England (75% between 1967 and 2014, and 68% between 1995 and 2014), whereas, by contrast, there has been a recent increase in Scotland (29% between 1995 and 2014). This pattern has also been found in a range of other migratory bird species (Ockendon et al. 2012, Morrison et al. 2013, Morrison et al. 2016). Recent trends are also habitat-specific. In lowland farmland habitats, where the Dunnock *Prunella modularis* is the main host species, rates of decline have exceeded the overall mean, whilst there has been little change since the 1990s in wetland and semi-natural grassland and heathland habitats where Eurasian Reed Warbler *Acrocephalus scirpaceus* and Meadow Pipit *Anthus pratensis*, respectively, are the main host species (Brooke & Davies 1987, Newson et al. 2009, Robinson et al. 2015).

The causes of Cuckoo population declines remains unknown (Thorogood & Davies 2013). Changing conditions on the equatorial African wintering rounds and increasing phenological mismatch with the timing of breeding of host species have been suggested, but there is no strong empirical evidence that either of these mechanisms is playing a significant role (Saino et al. 2009, Douglas et al. 2010, Ockendon et al. 2012). Evidence of a possible driver of decline outside the
breeding grounds derives from recent satellite tagging of 42 adult male Cuckoos breeding in the UK over a four year period, which has revealed two distinct autumn migratory routes to a common equatorial wintering area (Hewson et al. 2016). Birds following a more westerly route (via the Iberian peninsula, and the western side of the Sahara) had a significantly higher mortality probability than birds following a more easterly route (via Corsica, Italy or Greece, and the central Sahara), but only during the phase of migration between leaving the UK and crossing the Sahara, with excess mortality tending to occur in Spain. Notably, birds following this apparently riskier migration route are more likely to have bred in lowland, southern and eastern areas of the UK where long-term population declines have been greatest (Hewson et al. 2016).

In this paper, we compliment these previous studies by analysing correlates of spatial patterns of change in Cuckoo populations on the UK breeding grounds. Cuckoos have declined particularly in the UK’s lowland agricultural landscapes where the impacts of agricultural intensification have caused serious population declines of a wide range of breeding birds (Donald et al. 2001, Newton 2004, Wilson et al. 2009). Moreover, adult Cuckoos prey upon large invertebrates that are known to be highly sensitive to agricultural intensification (Wilson et al. 1999). These include lepidopteran larvae, notably of large, aposematic, hairy species avoided by other birds, or smaller species which can be found aggregated in high numbers (e.g. some Geometridae and Pieridae), as well as some adult beetles (e.g. Scarabaeidae and Chrysomelidae), grasshoppers and odonates (Wyllie 1981, Cramp 1985). This relative dependence on large-bodied invertebrates and, especially, large caterpillars highlights the importance of gaining a greater understanding of the extent to which Cuckoo declines may be associated with changes in the abundance of their prey.

We worked at two scales, local and national, to analyse the distribution of Cuckoos in relation to habitat variation, the abundance of host species and the abundance of moth (Lepidoptera) species, whose caterpillars are a key food of adult Cuckoos (Wyllie 1981, Cramp 1985).

Specifically, we address the following hypotheses and predictions:

H1. At a national scale, Cuckoos’ habitat associations have changed over the period of population decline (1995-2010), with the probability of detecting Cuckoos becoming more positively associated with suitable semi-natural habitats and the hosts which characterise those habitats (Reed Warbler and Meadow Pipit), and less positively (or negatively) associated with intensively managed agricultural habitats and the hosts which most characterise these habitats (Dunnock).

H2. At a local scale, cuckoos are more likely to be associated with semi-natural habitats and the abundance of Meadow Pipits.
H3. Moth species whose caterpillars are known to be preyed upon by Cuckoos have declined nationally over the long-term at a greater rate than those not known to be Cuckoo prey and abundance trends of moth species preyed on by Cuckoos differs between habitat types.

H4. The presence of territorial Cuckoos locally is associated with higher abundance of moth species whose larvae are exploited as prey by adult Cuckoos.

METHODS

Local Scale

Field data collection

We chose the county of Devon as our study area as Cuckoos were recorded in 81% of 2 km tetrads \((n = 1,858)\) in 1977-1985 (Sitters 1988), but this occupancy had declined to 18% by 2007-2013, with distribution increasingly limited to the semi-natural heathland habitats of the Dartmoor and Exmoor National Parks (Fig. 1; Beavan & Lock 2016). We used the Centre for Ecology and Hydrology’s Land Cover Map 2000 (LCM2000) data (Fuller et al. 2002) to select all 1 km squares which had no more than 10% cover of unsuitable habitat (water, bare rock and sediment, saltmarsh, and built habitats) and contained 10-30% woodland cover, recognising that Cuckoos require trees and other vantage points to parasitize hosts (Øien et al. 1996, Roskaft et al. 2002, Fuller et al. 2007). 1x1 km squares were selected to account for the more fragmented nature of habitats in the area. Using these criteria, 223 potential 1 km squares were identified across Devon. These were then ranked by semi-natural habitat cover (Table S1) and divided into five evenly sized groups. Nine sites were then randomly selected from each group to give a total sample of 45 squares. Each site was surveyed to estimate Cuckoo presence and measure host abundance.

Cuckoo surveys took place during daylight hours by one observer (CD) at the centre of each 1x1 km square in May and June 2012. Adult male Cuckoos respond well to playback recordings (Wyllie 1981), so we played an amplified recording of a male Cuckoo song for one minute towards each of the four cardinal points. The recording was audible to an observer over 200 m. After playing the song, the observer waited for 15 minutes for a response. One survey was conducted per square and surveys were not conducted in high winds (Beaufort scale 5 or above) or heavy rain. The main potential Cuckoo hosts in this area, Meadow Pipits and Dunnocks, were also counted once in each square along two parallel 1 km transects, 500m apart, in late April or early May, using standard Breeding Bird Survey (BBS) techniques (Harris et al. 2016).

Moths were sampled once between late June and the end of July, using Ranger traps fitted with 40W actinic bulbs, run from a 12V battery. This timing was designed to coincide with the flight
period of those moths whose larvae are preyed upon by adult Cuckoos on return to the breeding grounds. Four moth traps were placed, one in each of four main available habitat types (semi-
natural grassland, heath, improved grassland and arable) in each square where all these habitats
were present. Where only three habitats were present, then a second trap was placed in the
dominant habitat by area, where two habitats were present then two traps were placed in each, and
in one square where only one habitat was present, all four traps were placed in that habitat. Traps
were always placed >50m away from the nearest habitat edge and 100m from the nearest other
trap (Dodd et al. 2008) to reduce the risk that one trap influenced the catch rate of another. Exactly
as for bird surveys, no trapping took place in heavy rain or strong wind. The total count of all macro-
moths caught and, secondly, the total count of all those species whose caterpillars have been
identified as Cuckoo prey (Table 1) were used as response variables in subsequent analyses. A
temperature logger was attached to each trap to record minimum air temperature (°C) on the
trapping night, and wind speed was recorded (Beaufort scale) when the trap was set at dusk. In
total, moths were trapped in 21 of the 45 squares where it was possible to locate traps according to
the criteria described above and where overnight trapping was secure and permitted by the
landowner.

Data analysis

First, we modelled the probability of Cuckoo detection (1) or non-detection (0) in the 45 study
squares as a function of their habitat composition and host abundances using a Generalized Linear
Model (GLM), and specifying a binomial error distribution. To do this, we added 0.01 to all mean
counts of Dunnocks and Meadow Pipits (to allow zero counts to be transformed) and log_{e}-
transformed these counts (lnD and lnMP) as the two measures of host abundance. The proportion
of the square covered by each of semi-natural grassland (SNG), heathland (HEATH), arable farmland
(ARABLE), and agriculturally improved, sown grasslands (GRASS), as derived from LCM 2000 data
(Table S1) were the four measures of habitat composition. However, all six variables showed
moderate or high collinearity (Pearson’s r for pairwise correlation coefficient > 0.5 for at least one
pairwise correlation for every variable) so we carried out a Principal Components Analysis. The first
two principal components had Eigenvalues >1 (PC1 - Eigenvalue = 3.40, proportion of variance
explained = 0.567; PC2 – Eigenvalue = 1.11, proportion of variance explained = 0.185), so these two
components were taken forward as explanatory variables in a final model in which both were fitted.
The partial correlation coefficients (Table 2) show that PC1 describes a gradient from squares rich in
semi-natural habitats and with higher densities of Meadow Pipits and lower densities of Dunnocks
(high values) to squares rich in agriculturally improved grasslands with lower densities of Meadow
Pipits and higher densities of Dunnocks (low values). PC2 describes a gradient between squares where the agriculturally improved component is dominated by grassland to those where it is dominated by arable crops.

Secondly, we modelled moth abundance as a function of whether or not Cuckoos had been detected in the square during playback surveys in the subset of 21 squares in which moth trapping took place. We again used a GLM, and specified a Poisson error distribution whilst correcting denominator degrees of freedom for overdispersion using DSACE in SAS9.4 (SAS Institute Inc. 2014). Cuckoo detection, or not, during the prior playback session in the square was recorded as a binary categorical variable (CKDET). We also included minimum air temperature recorded on the night of moth trapping (MINAIR) and wind speed (WIND) because we expected that these weather conditions would be confounding effects on the number of moths caught. The best-approximating model was identified by fitting all seven possible models and finding the model which minimised AICc.

**National scale**

*Data preparation*

At a national scale, we used data from the UK Breeding Bird Survey (BBS) and Rothamsted Insect Survey (RIS) light trap network in conjunction with Land Cover Map (LCM) data. The BBS is based on a random sample of 1 x 1 km squares across the UK, within which volunteer observers carry out two breeding season visits (one between early April and mid-May, and one between mid-May and late June) and record birds along two 1 km transects (Harris et al. 2016). Specifically, we extracted BBS data for Cuckoos and the three main host species for two time periods, 1995-1999 (n = 2767) and 2006-2010 (n = 4101), to examine correlates of change in Cuckoo presence and abundance over this 15-year period. Separately for each time period, for each square, the detection (1) or non-detection (0) of at least one adult Cuckoo during the years in which a square was surveyed was used as the response variable in models. The first (April – May) count of each host species was used as an explanatory variable to reduce the risk of young birds affecting counts, and the mean count was calculated, for each time period, over all years in which a square was surveyed. Given that territorial Cuckoos may range over several kilometres (Wyllie 1981), we then measured the habitat composition of each BBS square plus its surrounding buffer of eight squares (i.e. a 3 km square in total) using the LCM 1 km raster data set for both 2000 (target year 1998, Fuller et al. 2002) and 2007 (target year 2007, Morton et al. 2011). These two data sets were the best available matches in time to the two BBS periods. The 1 km raster data set provides a measure of the coverage of each 1 km square by each of 26 (LCM2000) or 23 (LCM2007) land cover categories, but we pooled these
into seven explanatory variables: woodland (WOOD), semi-natural grassland (SNG), heathland
(HEATH), arable farmland (ARABLE), agriculturally improved, sown grasslands (GRASS), ‘fen, marsh
and swamp’ (FMS) and ‘OTHER’ for this study (Table S1), and calculated the proportion of land
covered by each of these land uses for each 3 x 3 km square.

The Rothamsted Insect Survey (RIS) light-trap network was established in 1968 and consists
of a national network of approximately 100 volunteer-operated light traps of standard design with a
200W tungsten bulb, each emptied daily. The RIS light-trap network has generated the largest and
longest-running dataset of terrestrial invertebrate population dynamics anywhere in the world, and
has been used to document national-scale changes in abundance and distribution of UK macro-moth
populations (Conrad et al. 2004, 2006a; Fox et al. 2013).

First, we used annual rates of abundance change for 337 macro-moth species published by
Conrad et al. (2006a) from the RIS database (1868 – 2002) to test whether these differed between
those species known to be taken by Cuckoos as prey (n = 17) and the remainder. We then extracted
the total annual count of each macro-moth species recorded in the Cuckoo diet (Table 1) for every
RIS trap that was operated for more than one year between 1975 and 2009 (n = 274, Fig. 2a). We
chose 1975 as the start year because annual samples of traps were low before this year, but had
increased to 90 by 1975. We summed this count over all these species for each site. We used the
same approach as for the BBS squares to calculate the habitat composition of each 1 km square
containing a light trap (using LCM2007 data) and, because of the small number of traps in semi-
natural habitats, we pooled the three semi-natural habitat categories of HEATH, SNG and FMS into
one (SN). We then determined which habitat type covered the greatest area in the square and
considered that as the habitat allocated to that trap for further analysis. The final sample sizes were:
SN (n = 26), WOOD (n = 49), ARABLE (n = 93), and GRASS (n = 106).

Cuckoo detection probability as a function of host abundance and habitat composition
As in the local scale analysis, we used SAS 9.4 (SAS Institute Inc. 2014), and we first modelled the
probability of Cuckoo detection in BBS squares as a function of their habitat composition and host
abundance using a GLM, and specifying a binomial error distribution. We modelled these
relationships separately for 1995-1999 and 2006-2010. Loge of the number of years surveyed
(InYEARS) was fitted as a nuisance variable in all models to control for variation in survey effort
between squares. We added 0.01 to all mean counts of Dunnocks and Meadow Pipits and loge-
transformed these counts (lnD and lnMP). We expressed squares with (1) and without (0) Reed
Warblers as a two-level, categorical effect (RW) given the rarity of BBS squares in which this species
was recorded (n = 70 in 1995-1999 and n = 148 in 2006-2010). Habitat areas (except ‘OTHER’ to
avoid the unit sum constraint) were converted into proportions. The longitude and latitude (LONG, LAT - degrees) and elevation (ELEV - metres above sea level) of the square were also calculated. All twelve of these variables were considered initially as explanatory variables for modelling, but HEATH, LAT, ELEV, lnD and lnMP showed moderately high collinearity (Pearson’s r for pairwise correlation coefficient of approximately 0.5 for all pairs in this group), so we subjected this group of five variables to a Principal Components Analysis. Only the first principal component had an Eigenvalue >1 (Eigenvalue = 3.00 and 2.89; proportion of variation explained = 0.600 and 0.576 for 1995-1999 and 2006-2010, respectively), and so this component (PC1) was taken forward as a covariate in further modelling together with other seven explanatory variables. The partial correlation coefficients of the original variables and PC1 were (LAT 0.424 and 0.395; ELEV 0.431 and 0.444, lnMP 0.463 and 0.464, lnD -0.439 and -0.428, HEATH 0.477 and 0.498 for 1995-1999 and 2006-2010 respectively). So, in both time periods, this indicates a gradient from squares at higher elevations and latitudes, rich in heath cover and with more Meadow Pipits and fewer Dunnocks, to lower elevation and latitude squares with less heathland, more Dunnocks and fewer Meadow Pipits. The best-approximating model was identified by fitting all possible main effects models (n = 255) and identifying the model which minimised AICc. If the variable PC1 was not included in the best-approximating model, then all possible combinations of the five original variables comprising PC1 were added to the model to test whether any of these further reduced AICc.

Comparing population trends of moths that are known to be Cuckoo prey and those not known to be Cuckoo prey

To test whether moth species known to be Cuckoo prey show different long-term trends than those not known to be Cuckoo prey, we modelled the (1968 – 2002) annual population change (taken from Conrad et al. 2006a) in Table 1 as a function of these two categories (Cuckoo prey species = 1; non-Cuckoo prey species = 0), using a linear, mixed model (PROC GLMM) with normal errors. Moth family was fitted as a categorical, random effect as a basic correction for phylogenetic non-independence of trends (Sanderson et al. 2016).

Modelling habitat-specific trends of moths known to be Cuckoo prey

For the macro-moth species forming part of the diet of Cuckoos (Table 1), we used a GLM to model moth count in the RIS database as a function of HABITAT (fixed, categorical effect with four levels: SN, WOOD, ARABLE, GRASS), SITE (fixed, categorical effect with 274 levels) and the YEAR x HABITAT interaction term in order to generate year and habitat-specific indices of moth abundance, specifying a Poisson error structure and log link. We corrected for overdispersion using the DSQUEUE
option in SAS 9.4. We then re-fitted the same model, but with YEAR fitted as a covariate in order to test whether annual rate of moth abundance change differed between the four habitat types.

RESULTS

Local scale

Cuckoos were detected in 14 of 45 (31.1%) sites surveyed across Devon. The probability of Cuckoo detection increased strongly with values of PC1 (PC1 = 0.89 ± 0.25, Wald $\chi^2_1 = 12.55$, $P = 0.0004$) but was unrelated to PC2 (PC2 = 0.41 ± 0.47, Wald $\chi^2_1 = 0.77$, $P = 0.38$). This indicates that Cuckoos were more likely to be detected in squares with a high cover of semi-natural habitats, which also tended to have higher numbers of Meadow Pipits and lower numbers of Dunnocks (Fig. 3). Agricultural land cover, along the spectrum from grassland to arable crops (PC2), had no influence on the probability that Cuckoos would be detected.

Total catches of macro-moths fell strongly with increasing wind speed (WIND = -0.407 ± 0.159, Wald $\chi^2_1 = 6.5$, $P = 0.01$), but there was no significant additive effect of either night-time air temperature or whether the square had previously recorded a territorial Cuckoo. Nonetheless, the best-approximating model ($\Delta$AICc = 41.4) contained all three variables. When the data set was restricted to moth species known to be taken as prey by adult Cuckoos, the wind speed effect was no longer significant and there was a significant additive tendency for squares which had previously recorded Cuckoos to have higher catches than squares that did not (mean = 7.1 vs. 3.4 per trap; Wald $\chi^2_1 = 5.1$, $P = 0.024$). Again, the best-approximating model ($\Delta$AICc = 8.7) included all three explanatory variables. There was no collinearity between the two most important explanatory variables; squares which had recorded Cuckoos did not experience different wind strength on moth trapping nights than those that had not recorded Cuckoos (two-sample $t_{16} = 0.86$, $P = 0.4$). In summary, at the local scale in Devon, Cuckoos were more likely to be detected in areas with more semi-natural habitat, more Meadow Pipits (but fewer Dunnocks) and, later in the summer, higher numbers of moths whose larvae are known to be preyed upon by adult Cuckoos are captured at sites at which territorial Cuckoos have previously been recorded.

National scale

During 1995-1999, Cuckoos were encountered in 59.2% of squares over the five years pooled ($n = 2767$ surveyed square-years), but this had fallen to 39.3% by 2006-2010 ($n = 4101$ surveyed square-years). In 1995-1999, the best-approximating model was clear-cut ($\Delta$AICc = 51). Using this model for inference, Cuckoos were more likely to be encountered at lower elevation and at more southerly
and easterly sites (i.e. the lowland south and east of Britain), and likelihood of detection increased with the proportion of all habitats other than the rarest (FMS; Table 3). However, there was no additive effect of the abundance of Dunnocks or Meadow Pipits, and the effect of presence of Reed Warblers was very weak (Table 3). In 2006-2010, the best-approximating model was moderately clear (ΔAICc = 5). Using this model for inference, the same habitat associations existed, but the associations with ARABLE and GRASS habitats had much reduced slopes, and there was now a clear positive association with sites with Reed Warblers and, as reflected by PC1, with northerly, higher elevation sites with more heathland and Meadow Pipits and fewer Dunnocks (Table 3). In summary, over a 10-15 year period, Cuckoos had become detected less often on BBS plots. Moreover, they had become more associated with upland heath characterised by the presence of Meadow Pipit hosts, and with wetland habitats occupied by Reed Warbler hosts, and relatively less associated with lowland sites associated with agricultural land and Dunnocks as the most available host. In addition, the core distribution of Cuckoos had shifted from south to north within the UK.

At the beginning of the period 1975-2009, moths captured in light traps of those species whose larvae are known to be prey of adult Cuckoos were many times (up to approximately 15-fold) more numerous in improved grassland and woodland habitats than in either arable or semi-natural habitats (Fig. 2b). However, significant and consistent declines in abundance in woodland (4.4% per annum, Wald $\chi^2 = 402.4, P < 0.0001$), improved grassland (3.1% per annum, Wald $\chi^2 = 118.1, P < 0.0001$) and arable (3.2% per annum, Wald $\chi^2 = 57.5, P < 0.0001$) habitats, and a similar magnitude of annual abundance increase in semi-natural habitats (4.4% per annum, Wald $\chi^2 = 32.8, P < 0.0001$) mean that moth abundance overall varied only roughly four-fold across these four habitat types by the end of the time period. By the end of the time period in 2009, numbers in semi-natural habitat were consistently higher than those in arable habitats, and similar to those in improved grassland and woodland habitats.

The annual population changes of a much larger sample of macro-moths between 1968 and 2002, as published by Conrad et al. (2006a) differed significantly ($P = 0.009$) between those species known to be preyed upon by Cuckoos (mean annual population change = -3.2% ± 0.9 se, n = 17) and those not known to be taken as Cuckoo prey (-0.7% ± 0.4 se, n = 320; Fig. 2c).

**DISCUSSION**

Our data found support for the hypotheses that Cuckoo habitat associations have changed (H1), with Cuckoos now more likely to be associated with semi-natural habitats and with the presence of...
Meadow Pipits (H2). Similarly, the macro-moth prey have declined at a greater rate than other macro-moth species (H3) and Cuckoo presence is associated with their macro-moth prey (H4).

Both at local (Devon) and national (UK) scales, our results show that a declining Cuckoo population is becoming increasingly associated with upland heath and grassland habitats in which Meadow Pipit is the predominant host species, and less prevalent in lowland, agricultural habitats in which Dunnock is the predominant host species. There is also evidence from our national analyses that remaining lowland populations are now increasingly associated with habitats supporting Reed Warblers; these are likely to range from extensive freshwater wetland systems, often associated with nature reserves, to drainage systems in lowland agricultural landscapes where these are colonised by extensive stands of reed.

The changing abundance and distribution of Cuckoos accords broadly with changing abundance and distribution of macro-moths in the UK (Conrad et al. 2004, 2006a, Fox et al. 2013), especially changes in the species with hairy caterpillars which are preyed upon by adult Cuckoos (Conrad et al. 2002, 2003, 2006b). One of these, the Garden Tiger Arctia caja, has been studied in detail and, like the Cuckoo, shows a long-term distributional shift from the south and east towards the north and west of the UK, which is suggested to reflect the combined influences of climate and land management change (Conrad et al. 2002, 2006b). Specifically, we found that, nationally across all habitats, the abundance of macro-moth species identified as Cuckoo prey by Wyllie (1981) has declined over four times faster (3.2 ± 0.9% annual decline) than that of species not known to be taken by Cuckoos (0.7 ± 0.4% annual decline). Moths preyed upon by Cuckoos have shown steep declines in lowland landscapes dominated by agriculture and woodland, whilst increasing in semi-natural habitats, including heathland, semi-natural grasslands and fen, marsh and swamp habitats.

Locally, in Devon, even a modest moth-trapping data set suggested that, after controlling for weather conditions, sites that had recorded territorial Cuckoos in the preceding breeding season supported larger, later-summer catches of moth species whose larvae are known to be prey for adult Cuckoos than sites that did not record Cuckoos.

These findings provide strong correlative evidence that Cuckoos are becoming increasingly confined to areas of semi-natural habitat such as heathlands, moorlands and wetlands, and that declining populations of key prey species of adult Cuckoos are a strong candidate explanation for this change. Other factors such as environmental impacts on abundance of hosts (Douglas et al. 2010), changing climate or land use on migration routes or in wintering areas (Ockendon et al. 2012, Hewson et al. 2016), and mismatches in timing of breeding with some host species (Saino et al. 2009, Moller et al. 2011, but see Douglas et al. 2010), may also contribute. However, our results do suggest that there are important opportunities to test whether Cuckoo population declines can be
reversed through the management of prey and hosts on the breeding grounds. In particular, our results highlight the need to further test hypotheses related to food resource availability. For a landscape to support breeding Cuckoos, it must have: i) habitat conditions and prey resources sufficient to support the host species; ii) habitat conditions necessary to support sufficient populations of moths (especially in the families Lasiocampidae, Sphingidae, Notodontidae and Erebididae) whose caterpillars are available when Cuckoos return to the breeding grounds in spring, as well as other large invertebrates later in the summer; iii) habitat conditions which accommodate the preferred ‘perch-and-scan’ behaviour of Cuckoos which is used both to detect prey and host nests; and, iv) the availability of all the above habitat conditions at an appropriate spatial scale, considering the Cuckoo home range.

Cuckoos are known to fly several kilometres between areas where hosts are nesting to areas rich in caterpillars, historically in aggregations of many tens of birds (Wyllie 1981, Davis 1996). This suggests that habitat patches that support high caterpillar concentrations are an important component of landscapes in which breeding Cuckoos can persist. In this context, the fact that lepidopteran populations are known to be highly sensitive to the impacts of agricultural intensification (Wilson et al. 1999) suggests that agricultural change over recent decades could have substantially reduced the ability of the lowland agricultural landscape to support Cuckoos.

Important impacts on Lepidoptera include effects of agrochemical use, hedgerow loss and frequent mechanical trimming of those that remain, conversion of grassland to arable cultivation, replacement of semi-natural grassland with sown and heavily grazed or frequently cut ryegrass *Lolium* swards (Wilson et al. 1999, Conrad et al. 2006, Woiwod & Gould 2008, Fox 2013) as well as, potentially, the impact of new generations of pesticides such as neonicotinoids (Pisa et al. 2017). In the summary by Fox et al. (2013) of long-term trends (1968 – 2007) of 337 species of the UK’s larger moths, three of the key prey species of Cuckoos had declined by over 90% during this time (Figure-of-Eight *Diloba caeruleocephala*, -96%; Lackey *Malacosoma neustria*, -93%, Garden Tiger, -92%) but none were recorded as having increased. Recent evidence of positive responses of moth abundance and diversity to interventions designed to reverse the impacts of agricultural intensification, such as organic farming conversion, and agri-environment schemes which provide sensitively managed hedgerows, hedgerow trees and wide, uncultivated and unsprayed field margins (e.g. Wickramsinghe et al. 2004, Fuentes-Montemayor et al. 2011, Merckx & Macdonald 2015), provides further evidence of the causal relationship between agricultural change and moth populations.

Restoring lowland agricultural landscapes capable of supporting breeding Cuckoo populations and their key prey resources is a major challenge. To test the causality of the
relationships found here, and to trial an effective management solution, we suggest that a replicated landscape-scale intervention be designed. This should focus around the coordinated restoration of species-rich grasslands, reduced pesticide use on arable land, hedgerows with less-than-annual trimming and minimal understorey disturbance, and grass field margins not subject to agrochemical application, ideally located close to a remaining centre of Cuckoo population such as Dartmoor. Merckx et al. (2009) have already tested the effect of landscape-scale targeting of agri-environment management designed to benefit macro-moth populations by establishing contiguous blocks of farmland either subjected to concerted, targeted agri-environment interventions or left as controls. Using interventions similar to those we list above, that study demonstrated increases of 38% in species diversity and 60% in abundance of larger moths in the trial landscapes, leading the authors to suggest that larger moths might be suitable as a bio-indicator of landscape quality. Although such an intervention may need to be scaled up further in order to also detect any effect on settlement by territorial Cuckoos, this earlier study shows the potential impact of a landscape-scale trial.

Evaluation of responses in trial and control landscapes should include moth populations, presence and numbers of territorial Cuckoos, and also the abundance and breeding success of Dunnocks, given that it is also possible that agricultural intensification has limited the ability of this species to rear a Cuckoo nesting to fledging. With such a commitment, the restoration of populations of Cuckoos and the moth species upon which they depend could become emblematic of the achievement of Lawton et al.’s (2010) vision for the restoration of an ecological network across England. Without such a commitment, the continuing rapid decline of this iconic species suggests that the Cuckoo, a bird with an exceptionally rich folklore (Cocker & Mabey 2005) may soon disappear completely from lowland agricultural Britain.

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REFERENCES


Table 1. Macro-moths recorded in Cuckoo diet by Wyllie (1981) and Cramp (1985).

<table>
<thead>
<tr>
<th>English name</th>
<th>Scientific name</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td>Poplar Hawkmoth⁵⁶</td>
<td><em>Laothoe populi</em></td>
<td>Sphingidae</td>
</tr>
<tr>
<td>Elephant Hawkmoth⁵⁶</td>
<td><em>Deilephila elpenor</em></td>
<td>Sphingidae</td>
</tr>
<tr>
<td>Buff-tip</td>
<td><em>Phalera bucephala</em></td>
<td>Notodontidae</td>
</tr>
<tr>
<td>Antler Moth</td>
<td><em>Cerapteryx graminis</em></td>
<td>Noctuidae</td>
</tr>
<tr>
<td>Yellow-tail</td>
<td><em>Euproctis similis</em></td>
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<tr>
<td>Lackey</td>
<td><em>Malacosoma neustria</em></td>
<td>Lasiocampidae</td>
</tr>
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<td>Oak Eggar</td>
<td><em>Lasiocampa quercus</em></td>
<td>Lasiocampidae</td>
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<tr>
<td>Drinker</td>
<td><em>Euthrix potatoria</em></td>
<td>Lasiocampidae</td>
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<td>Lappet</td>
<td><em>Gastropacha quercifolia</em></td>
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<td>Small Eggar</td>
<td><em>Eriogaster lanestris</em></td>
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<td>Figure of Eight</td>
<td><em>Diloba caeruleocephala</em></td>
<td>Noctuidae</td>
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<tr>
<td>White Ermine⁵</td>
<td><em>Spilosoma lubricipeda</em></td>
<td>Erebididae</td>
</tr>
<tr>
<td>Buff Ermine⁵</td>
<td><em>Spilosoma luteum</em></td>
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<td>Garden Tiger</td>
<td><em>Arctia caja</em></td>
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<tr>
<td>Cinnabar</td>
<td><em>Tyria jacobaeae</em></td>
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<td>March Moth</td>
<td><em>Alsophila aescularia</em></td>
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<tr>
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<td><em>Operophtera brumata</em></td>
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<td><em>Selenia dentaria</em></td>
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<td><em>Abraxas grossulariata</em></td>
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<tr>
<td>Mottled Umber</td>
<td><em>Erannis defoliaria</em></td>
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<tr>
<td>Dotted Border</td>
<td><em>Agriopis marginaria</em></td>
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<tr>
<td>Six-spot Burnet</td>
<td><em>Zygaena filipendulae</em></td>
<td>Zygaenidae</td>
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</table>

⁵⁶Wyllie (1981) identifies hawkmoths and ermines, respectively, as species groups of Cuckoo prey. Poplar and Elephant Hawkmoths and White and Buff Ermines are identified specifically here as they are the species within each of these groups with sufficient data for analysis in the RIS database.
Table 2. Partial Pearson correlation coefficients for Principal Components Analysis of explanatory variables in modelling of variation in territorial Cuckoo detection across 45 1 km squares in Devon in 2012. See text for explanatory variable definitions.

<table>
<thead>
<tr>
<th>Explanatory variable</th>
<th>PC1 (Eigenvalue 3.40; % of variation explained = 56.7)</th>
<th>PC2 (Eigenvalue = 1.11; % of variation explained = 18.5)</th>
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<td>ARABLE</td>
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<td>lnMP</td>
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<td>0.213</td>
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<tr>
<td>lnD</td>
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Table 3. Final GLMs showing relationship between Cuckoo presence on Breeding Bird Survey plots and their habitat composition and abundance or presence of host species. Rows in bold refer to 1995-1999 and rows in italics refer to 2005-2009.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>SE</th>
<th>Wald $\chi^2_1$</th>
<th>Significance</th>
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<td>1.521</td>
<td>0.197</td>
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</table>
Figure legends

**Figure 1.** Map showing the dramatic change in the distribution of Cuckoos in Devon, south west England from 1977-1985 to 2007-2014. Dots represent different categories of Cuckoo presence (see legend). The shaded area to the south represents an area of uplands called Dartmoor and the shaded area in the north represents Exmoor. Reproduced with permission from Beavan & Lock (2016), Devon Bird Atlas 2007-2013. © Devon Birds.

**Figure 2.** Long-term, annual estimates of abundance of moth species known to be key food sources of adult Cuckoos as recorded by Rothamsted light traps in four broad habitat types in Britain, 1975-2009 (3a). Precision of individual annual estimates is not shown for clarity, but these data show significant linear percentage declines in abundance in woodland, improved grassland and arable habitats, and a significant linear percentage increase in abundance in semi-natural habitats (3b). Macro-moth species known to be prey for adult Cuckoos ($n = 17$) are declining faster than other moth species ($n = 320$). Each category is labelled with its maximum annual percentage population change. Data from Conrad *et al.* (2006a) (3c).

**Figure 3.** Fitted relationship across 45 1x1 km squares between probability of Cuckoo detection during a single song playback survey in May/June and Principal Component 1, in which high values indicate squares with more semi-natural heath and grassland habitat (less agricultural land cover), more Meadow Pipits and fewer Dunnocks. Filled circles indicate squares in which one or more Cuckoos were detected in response to playback and open circles indicate squares in which no Cuckoo was detected.
Figure 1.

(a) 1977-1985

(b) 2007-2013
Figure 2.
Figure 3.

Principal Component 1 (higher values indicate more semi-natural habitat, more Meadow Pipits and fewer Dunnocks)