Understanding the Role of Ecology in Variation of Breeding Phenology and Success in Two Bird Populations

Submitted by

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to the University of Exeter as a thesis for the degree of

Master's by Research in Biological Sciences

May 2023.

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Thesis Abstract

Climate change has a well-established impact on the trait dynamics of wild populations. Trophic mismatches driven by climate shifts have been associated with observations of a negative relationship between phenology and breeding success at the population level, driving directional selection for early breeding. However, phenology and its relationship with breeding success is variable even under population-level selection. Can these two observations be reconciled? This thesis presents two studies investigating the possibility of environmentally-driven variation in selection at fine spatiotemporal scales (e.g., between habitats/territories) in small passerines. I first used additive modelling frameworks to quantify spatial variation and autocorrelation in the breeding ecology of blue and great tits, and then attempt to explain this with environmental covariates. I found limited evidence of spatial variation in phenology and success, despite spatially non-random environmental effects on nestbox occupancy. However, the relationship between phenology and success interacted with environmental covariates. Following this, I used random slopes modelling to test how the strength and shape of selection for early breeding varies at multiple spatiotemporal scales which I then attempt to explain using scale-dependent environmental variation. I found that the phenology-success relationship (and thus selection) varied among territories and breeding seasons, with different environmental effects operating at each scale. My research shows that ecologically-driven variation in selection within populations can persist alongside directional selection for early breeding at the population level. This may explain persistent variation in phenological strategy under mismatch-driven selection pressure. My findings therefore constitute a significant advancement towards formulating predictions of how climate effects could continue to shape breeding ecology in the wild.

Acknowledgements

The following research is only possible through the efforts of a number of individuals other than myself, who have been instrumental in providing me with the guidance necessary to complete this thesis and go on to further academic pursuits. Of course, I must thank Prof Andy Russell first for enabling me to explore this incredibly important dataset and tackle important eco-evolutionary questions for so many years. That we've continued this partnership for this long is a testament to our patience and tenacity. Further I need to thank A/Prof Erik Postma for being a lifeline, especially during the latter stages of this research, in matters quantitative and pastoral. Without Erik, I am not certain I would have reached the end of this long and winding road. Thanks must also be tendered to Dr Alexis Chaine of the CNRS, who has been invaluable in providing context for the particulars of the study system and dataset. Thanks also to the post-docs, students & volunteers responsible for collecting all the data used here, especially Louis Salle, Aisha Bründl and Leah Lejeune. I would also like to extend my gratitude to the PGR support staff for the University of Exeter in Penryn, including (but not limited to) Jo Shepherd, Monique Clark, and Cathryn Baker. In the same vein, I also thank A/Prof Nick Royle. All these individuals have been instrumental in keeping my research on track and deserve no small measure of recognition for the expedience and professionalism with which they have helped me overcome the most challenging periods of my research degree.

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Author’s Declaration

James Harris declares that all data handling and analyses, literature searches, manuscript writing and thesis composition contributing directly to the work submitted here were carried out only by James Harris. Prof Andy Russell, A/Prof Erik Postma and Dr Alexis Chaine provided advice and feedback on drafts of this work throughout the MByRes programme. Though some example pieces of planned thesis sections were composed by the supervisory team as an aid, none of these were directly included as components of the final product presented below. All raw data used were collected and provided by the staff and volunteers at *Centre National de la Recherche Scientifique* (CNRS). Dr Alexis Chaine provided access to the relevant data repositories and further guidance on the particulars of data collection protocols, none of which were carried out by James Harris.

Chapter 1: Thesis Introduction

1.1: A Review of Phenology in Evolutionary Ecology

The eco-evolutionary dynamics of animal life histories are key to understanding trait variation in the wild. Ecological interactions and evolutionary processes governing variation in fecundity, reproductive success (Pincheira-Donoso & Hunt 2017) and timing of reproduction (Brakefield 1984) are key to predicting life history variation. Such projections are becoming increasingly important in the context of climate change, which has been shown to have complex and sometimes deleterious effects on wild populations (Thackeray *et al* 2016, Gutiérrez & Wilson 2021, Smith *et al* 2022). Reproductive phenology is a prolific example of the influence climate change exerts on trait dynamics.

Phenology has been repeatedly observed to be negatively associated with reproductive success, interpreted by some as directional selection for early breeding (Perrins 1970, Frederiksen *et al* 2004, Saino *et al* 2017). This has been linked to climate change, specifically earlier spring warming in temperate systems (Visser *et al* 1998, Visser *et al* 2015). However, we still do not grasp the precise mechanisms behind this trend, as increased predation risk (Borgmann, Conway & Morrison 2013) and incubation costs (Nager, Ruegger & Van Noordwijk 1997) mean early breeding is not inherently beneficial. In this introductory review, I will illustrate why phenology is important to ecological and evolutionary processes in a variety of taxa. Further, I will outline the key evolutionary and ecological questions yet to be resolved in phenology research. The mechanisms shaping phenological strategy and its effect on reproductive success remain unresolved, and yet are crucial to predicting the effects of climate change both across and within populations.

Phenology is broadly important to understand for two main reasons: its role in maximising breeding success through ecological synchrony and as a potential driver of fitness-related trade-offs (Burgess *et al* 2018, Park 2019). These were the primary findings from early investigations of the ecological significance of breeding timing. For example, birds are hypothesised to lay their eggs at a time that maximises food availability and thus offspring survival with tenable costs to the parents, explaining latitudinal variation in breeding phenology among populations (Lack 1950). Since then, such findings have been corroborated in a variety of taxa (Fournier, Thomas & Garland 1999, Visser, Holleman & Gienapp 2006), extending into other phenological phenomena such as migration (Posledovich *et al* 2015).

However, Lack also noted that abiotic variation, specifically in ambient temperatures, could constitute a modifying factor distinct from any direct link between food availability and reproductive strategy. Such a position is key to understanding how wild populations may optimise phenology and maintain reproductive success, as it suggests breeding environment may mitigate or enhance the benefits of breeding timing by driving variation in the abundance and phenology of prey species. This concept of phenological synchrony between a predator and its prey has become central to analysis of variation in phenology and fitness. Populations have an optimal time to begin seasonal reproduction, and deviation from these optima drives declines in reproductive success (Cushing 1969). The resultant term ‘mismatch’, whereby phenology is asynchronous with its ecological optimum, is used today to exemplify how climate change can affect breeding success (Hipfner 2008). Phenological mismatch is a major eco-evolutionary challenge, both in the pressure it places on wild populations and the complex questions presented for researchers.

We now have many examples of climate-associated mismatches linked to population declines. In the willow tit (*Poecile montanus*), earlier caterpillar abundance peaks shrink the optimal provisioning window (Vatka, Rytkönen & Orell 2014), while also reducing the time migratory species have to recover before commencing reproduction (Both *et al* 2010). The yellow-bellied marmot emerges from hibernation earlier in warmer springs, which has been linked to reduced over-winter survival in the following season (Wells *et al* 2022). These examples indicate that large-scale climate shifts drive demographic declines in many consumer taxa. However, questions remain as to why such declines were not sufficiently mitigated by tracking of environmental cues used to maintain phenological strategy and/or phenotypic plasticity.

On an ultimate level, we understand the proliferation of mismatch in the wild to be the product of differing rates of response to environmental change between a consumer population and its prey (Thackeray *et al* 2010). This conclusion is supported by observations that phenologies at lower trophic levels are more sensitive to climate variation (Thackeray *et al* 2016), and thus there is an 'evolutionary lag' as consumers attempt to keep phenological pace with their prey (Cushing 1969, Bründl *et al* 2020). This explains why vulnerability to mismatch in insectivorous passerines is associated with the prevalence of deciduous forest habitat that shapes caterpillar phenology and abundance (Bailey *et al* 2022). These differing rates of response indicate that ecological change which outpaces evolutionary change is the primary reason for the demographic consequences of climate change. However, this presents further questions because not all mismatched consumer populations are suffering for it. The Atlantic herring (*Clupea harengus*) for example, is not declining despite seasonal copepod peaks being a major part of their diet (Donnelly, Caffarra &

O’Neill 2011). What enables some populations to maintain a disparity between advancing phenology optima and the population mean, when we would expect this to represent intensifying directional selection for early breeding?

The apparently lacking adaptative response to mismatch in some populations remains a fundamental evolutionary question in phenology research. This state of evolutionary stability accompanied by high trait variation is termed as a ‘paradox of stasis’ (Hansen & Houle 2004). We can therefore consider the persistence of variable phenological strategies under perceived directional selection for early laying one such ‘paradox’ (De Villemereuil *et al* 2020). Such phenomena have been attributed to opposing selection pressures that are sufficiently strong to counteract each other, thereby maintaining the phenotypic distribution (Bowers *et al* 2016). The implication for phenology is that some other selective force sufficiently incentivises later breeding strategies, or mitigates the fitness advantage of early breeding, to reduce or even arrest evolutionary change.

How much evolutionary change should be occurring in these wild populations? Observations of stasis have been linked to a disparity between the fittest and most frequently observed phenological strategies. However, we cannot conclusively surmise that this alone is maladaptive, or even unusual, in nature (Singer & Parmesan 2010). When only a substratum of individuals display phenology synchronous with the population-level optimum, other individuals may be driven by different optima (Hinks *et al* 2015). In this case, more complex patterns of synchrony with variable environmental conditions may alleviate population-level mismatch, thereby explaining ‘stasis’. Consequently, we arrive at one of the key ecological questions still to be resolved in phenology. What factors maintain variation in phenology and at what scale do they operate? The latter is notable because a lack of evolutionary change may be symptomatic of fine-scale variation in phenological optima between individuals or the habitats they occupy.

Currently, the role of individual variation in phenology selection has received less attention than environmental variation both within and among populations. This can be attributed to both the relative scarcity of long-term datasets incorporating individual-level data (Charmantier & Gienapp 2014) and because many theoretical models in ecology operate on the assumption of a homogeneous population (Crawley & Akhteruzzaman 1988). As a result, incorporation of among-subject variation necessarily involves a substantial increase in model complexity and as already mentioned, data requirements. A further challenge in analysing individual-level variation is that it is often difficult to directly extricate the significance of the individual from that of its environment. Many aspects of individual variation are inherently dependent on the immediate environment. For example, in great tits (*Parus major*), the physiological stress exerted by harsh winters with low food availability is dependent on the competitive ability of the individual, because resource scarcity intensifies interspecific competition (Carrascal *et al* 1998). As such, it seems appropriate to suggest that ascertaining the exact role of environmental variation will develop our understanding of both population and individual-level phenology selection.

Studies positing a significant role of environmental heterogeneity in determining selection on phenology have thus far focused on factors historically thought to vary over coarse scales, such as mean precipitation and population-level ambient temperatures (Van Noordwijk, Mccleery & Perrins 1995, Studds & Marra 2011, Visser *et al* 2015). The effects of these variables on breeding success are often strong, yet once again mismatch is not always accompanied by demographic decline. Moving forward, within-population variation, either among individuals or their habitats, may be an essential point of focus for phenology research. Indeed, it has been suggested that the lack of studies demonstrating a substantiated link between phenology variation and fitness is a lack of both trophic and spatiotemporal scope (Tang *et al* 2016, Thackeray 2016). Studies of consumer phenology have historically been conducted on specific interactions, such as between insectivorous passerines and caterpillars, but it has been found that variation in vegetation also plays a key role in these relationships (Bai *et al* 2012, Søraker *et al* 2022). Simultaneously, our sparse understanding of within-population variation in selection can be attributed to a research bias towards analysing data at the population-level.

In summary, perceived directional selection for early breeding has been linked to declines in wild populations due to mismatch, but this effect is inconsistent in space and time. We have yet to grasp how and why selection on phenology, and therefore the effects of mismatch, could vary within populations, thereby maintaining variation under population-level directional selection. Elucidating the role of environmental variation in driving habitat or even individual-level optima in phenological strategy is key to uncovering the ecological mechanisms maintaining phenology variation. Formulating such conclusions will be a necessary step in predicting how climate change will shape the complex future of life history trait dynamics in different populations.

1.2: Research Objectives

The research presented in this thesis focuses hereafter on two primary knowledge gaps for life history variation within populations. First, do phenology and selection for early breeding vary in space? As already discussed, many investigations of the environmental drivers of phenological strategy have focused on coarse-grain variation in abiotic factors. These variables are therefore sometimes treated as being high in temporal, but not spatial, heterogeneity (Van Noordwijk, Mccleery & Perrins 1995, Hodgson *et al* 2011). While it is important to understand variation over the course of a breeding season or among years, finer-scale spatial variation in phenology, among territories or subpopulations for example, has received relatively little attention. Evidence that phenology, or even phenology selection gradients, vary significantly in space for a population of ecologically comparable individuals would constitute key evidence of fine-scale differences in phenology optima coexisting with population-level directional selection.

My aim in Chapter 2, using a bird population with a significant negative association between phenology and breeding success, is to quantify the degree of spatial variation in phenology and breeding success. I will then use a range of environmental covariates, both biotic and abiotic, to attempt to explain this variation, facilitating discussion of potential ecological mechanisms. This will be accomplished through formulating multivariate models that enable me to simultaneously quantify the explanatory power of environmental covariates on the response and spatial variation. Further, my research objectives include addressing the lack of trophic scope in phenology study by including data from both prey species and the primary producers on which they depend. Primary production has been associated with spatial variation in the phenology of non-herbivorous consumers in recent years (Cole, Regan & Sheldon 2021), and thus forms a potential driver of variation in selection for early breeding in spatially heterogenous habitats.

Another major knowledge gap, which I aim to address in Chapter 3, is that few studies of phenology variation include multiple scales of variation in their analyses. As mentioned, the maintenance of phenology variation under directional selection could be explained by the existence of both population-level and finer-scale phenology optima. It is therefore necessary to construct quantitative frameworks that can account for both of these circumstances simultaneously if we are to substantiate any such evolutionary mechanism. A key objective of my research is to construct modelling frameworks that can a) quantify multiple scales of spatiotemporal variation in phenology and reproductive success and b) use environmental covariates to explain variation at each scale simultaneously, thereby testing for scale dependent ecological mechanisms in phenology. Evidence for such mechanisms would indicate that selection is not operating at a particular scale, and thus it is inappropriate to predicate evolutionary conclusions on a single scale of spatiotemporal variation.

1.3: Expected Outcomes

Chapter 2 will provide one of the first analyses to quantify fine-scale spatial variation in phenology and associated breeding success. The importance of spatial variation has been speculated upon multiple times, but few studies have made it a focus of their analyses. My research will provide an in-depth investigation of how phenology can vary among individual territories within a population, rather than comparing variation among populations. Further, constructing models that can quantify spatial autocorrelation will lend an additional dimension to my analyses. Spatial autocorrelation, or the amount of ‘structure’ in spatial variation, is a well-studied concept but has not been widely applied in phenology. Spatial structuring in phenology and breeding success (or lack thereof) could provide a more substantial basis for concluding that a spatially heterogeneous environment influences selection for early breeding, more so if spatially clumped phenological strategies do not exhibit similar levels of reproductive fitness.

In Chapter 3, my research focuses on comparing multiple scales of spatiotemporal variation in phenology simultaneously. This is a novel pursuit in itself, but more importantly I focus on the relationship between phenology and breeding success as a response variable, rather than modelling each trait individually. Relatively little work has sought to test for direct fitness consequences of phenology variation at fine spatiotemporal scales. I aim to rectify this by using environmental covariates as interaction terms with the relationship between phenology and breeding success. We can directly test whether these covariates affect the reproductive fitness of a given phenological strategy, rather than seeking correlations between the environment and early breeding and/or high reproductive output. This approach will provide a more substantive basis for concluding whether or not the environment drives variation in phenology selection. It is my hope that the outcomes of this research will provide future research with a sound methodological basis for pursuing complex patterns of variation in phenology and other life history traits. A quantitative framework that directly tests the evolutionary and ecological hypotheses central to the concept of within-population variation in selection is essential if we are to move towards predicting climate change driven evolution.

1.4: Study Sites and Species

The research presented here is conducted on a single system of nestboxes in the *Parc Naturel Régional des Pyrénées Ariégeoises*. This montane mosaic woodland is characterised by elevational gradients variable in both size and aspect. The complex habitat structure enables heterogeneity in a range of biotic and abiotic factors, including temperature and vegetation communities. This uniquely detailed snapshot of environmental variation provides an opportunity to test a range of hypotheses for ecological drivers of phenology variation, even at fine spatial resolutions. The study system therefore yields a dataset well-suited to uncovering potential environmental mechanisms for spatial variation in phenology selection when combined with passerine breeding data.

The species that comprise my dataset are found ubiquitously, both in Europe and phenology research. The great tit (*Parus major*) and blue tit (*Cyanistes caeruleus*) are prevalent in a range of habitats. These species do not exhibit strong dependence on specific habitat characteristics (Cowie & Hinsley 1988, Pagani-Núñez, Valls & Senar 2013), and thus are likely to breed throughout the study site. However, numerous studies suggest that there is a great deal of variation in breeding success among habitats, which is of importance to my research. Blue tits and great tits both exhibit increased breeding success in habitats with a prevalence of oak trees, due to improved brood condition (Wilkin, King & Sheldon 2009) and larger clutches (Amininasab *et al* 2016) associated with increased caterpillar abundance. Further, average nestling survival for great tits breeding in pinewoods can be 15% lower than comparable populations breeding in deciduous woodland (Van Balen 1973). These findings may be indicative of spatial variation in selection on phenology. While these birds are habitat generalists, there are clearly environmental biases in their reproductive fitness, suggesting that ecological mechanisms do drive variation in selection. Whether such mechanisms interact directly with phenology and thus selection for early breeding is unresolved.

Chapter 2: Habitat Heterogeneity Influences Fine-scale Spatial Variation in Avian Phenology & Success

2.1: Abstract

Differing rates of response between interacting populations lead to mismatch between the seasonal cycles of breeding consumers and their prey. Some mismatches have been associated with population declines, but we still observe variation in phenological strategy which would seem maladaptive under directional selection for early breeding exerted by these mismatches. Such variation may be the product of spatiotemporal heterogeneity in the environment at fine scales, though empirical evidence for such mechanisms is lacking. Using 7 years of breeding data from Parids in the French Pyrenees, I aimed to investigate: a) the prevalence of fine scale variation in phenology and breeding success and b) the role of territory-level variation in explaining these patterns. I found significant non-random variation in occupancy, but little evidence of environmental effects on phenology or success. However, the effect of phenology on success varied with an environmental driver of occupancy. My findings highlight that environmental mechanisms for phenology variation may be indirect, potentially mediating the fitness consequences of phenology. These results provide future study with important considerations on how to model the effect of the environment on phenology and selection. Implementing such frameworks may facilitate predictions of how climate-driven mismatch may continue to shape phenology variation in future.

2.2: Introduction

Global scale climate change has been linked to significant advancements in life history traits among temperate populations of numerous taxa (Visser *et al* 1998, Visser & Both 2005, Thackeray *et al* 2016), including plants, holometabolous arthropods and birds (Brown, Li & Bhagabati 1999, Visser & Holleman 2001). Large-scale climate effects, such as advanced spring warming, are significant drivers of phenology shifts, such as earlier spring emergence in orange-tip butterfly (*Anthocaris cardamines*) and yellow-bellied marmot (*Marmota flaviventris*) populations (Sparks & Yates 1997, Bonamour *et al* 2019). While this could be interpreted as directional selection for phenology advancement, some evolutionary responses to this selection have been weaker than predicted (Visser *et al* 2015, Bonamour *et al* 2017). At the population level, trophic asynchrony is driven by this disparity in response rates, because longer generation times in consumers compared to their prey generate 'evolutionary lags' (Cushing 1969, Bründl *et al* 2020). The resultant breakdown of spatiotemporal synchrony or 'mismatch' can manifest due to the costs of response to selection for earlier breeding (constraints hypothesis, Nager, Ruegger & Van Noordwijk 1997), or maintaining cue-driven phenotypic plasticity (cues hypothesis, Phillimore *et al* 2016, Gutiérrez & Wilson 2021). Such mismatch can drive population-level declines, potentially accompanied by increased reproductive success in early breeders (Cresswell & Mccleery 2003, Thackeray *et al* 2010).

If phenology is under directional selection, why do we continue to observe a lack of phenotypic change in the phenology of many wild populations? (De Villemereuil *et al* 2020)? One possible explanation for this 'paradox of stasis' is that negative relationships between phenology and fitness vary at fine spatiotemporal scales with the environment. If directional selection gradients are variable across years and/or across space within years, population-level stasis may be symptomatic of variation at the habitat or individual level. Selection for early breeding has been found to be consistent across years. For example, Townsend *et al* 2013 found black throated blue warblers (*Setophaga caerulescens*) under consistent, significant directional selection for early laying across multiple years and even variable spring temperatures. However, a growing body of evidence demonstrating variable responses among populations of the same species under comparable environmental conditions implies ecologically-driven variation in selection gradients (Visser *et al* 2003, Visser *et al* 2015). However, though selection operates on individuals, few studies have investigated the potential for fine-scale heterogeneity to explain this variation (but see Armstrong *et al* 2016). In territorial consumers, where the population is forced to occupy habitat of varying quality, population-level response to directional selection for early breeding may be constrained by such heterogeneity. For instance, poor local food availability prior to laying may constrain early breeding by proportionally increasing the cost of egg formation (Nager, Ruegger & Van Noordwijk 1997). Developing our understanding of how habitat structure influences evolutionary response to directional selection may therefore be key to fully understanding the paradox of stasis.

Territorial songbirds provide an ideal system through which to analyse the role of ecological heterogeneity in variable selection gradients and phenotypic change. Arthropods make up a significant portion of their diet during the breeding season, with distributions that depend on variation in forest structure (Tanabe, Toda & Vinokurova 2001). Therefore, birds must establish a territory of sufficient quality to successfully breed each season (Wilkin *et al* 2006).

Therefore, habitat-driven competition generates considerable within-population variation in habitat characteristics which may help explain phenology variation (Hinks *et al* 2015). Egg laying dates in these species are observed to be spatially variable both within and between wild populations. A 2014 study on Parids found egg-laying in rural and suburban habitats occurred up to several days before conspecifics in associated urban habitats (Solonen and Hildén 2014). In 2003, Sanz found that the negative effect of ambient temperatures on rate of change in pied flycatcher (*Ficedula hypoleuca*) laying dates was stronger in more northernly and westerly populations. However, it has also been noted that variance in lay dates is not adequately explained by environmental factors that are unlikely to vary at small scales, such as temperature and rainfall (Visser *et al* 2015). There is also compelling evidence for lay date variation being driven by individual-level factors, such as body condition and additive genetic effects (Price, Kirkpatrick and Arnold 1988, Evans, Postma & Sheldon 2020).

Habitat-level variation therefore offers a promising avenue for investigation. Indeed, in 2021 Cole *et al* found Parids breeding in habitats with healthy oaks advanced their lay dates by 0.1 days more per year than those in lower quality habitats. Therefore, ecological factors can mediate responses to climate-driven selection, and spatial autocorrelation is a necessary consideration when modelling phenology. As spatially associated habitats are more likely to be similar to each other, I expect to observe autocorrelated spatial distributions of phenology and fitness if fine-scale environmental heterogeneity affects the strength of directional selection. We can assess the impact of habitat-level heterogeneity by using environmental covariates to explain spatial variation and autocorrelation in phenology and fitness. If environmental factors are correlated with phenology and/or fitness and explain spatial variation, we will have a basis for concluding that fine-scale ecological effects are at play. I present a multivariate, mixed effects additive modelling framework that will aim to present new evidence of fine-scale ecological effects on phenology and reproductive success.

This study was conducted on a system of 149 nestboxes in Moulis in Ariége, Southern France, within the *Parc Naturel Régional des Pyrénées Ariégeoises*. The boxes provided life history data from the great tit (*Parus major*) and blue tit (*Cyanistes caeruleus*). I will test how environmental variables explain variation and spatial structuring in nest box occupancy, clutch initiation date and number of successful fledgings (as a measure of reproductive success). In the first instance, I predict significant spatial variation and autocorrelation in occupancy that will indicate heterogeneous territory quality. I can then test whether occupancy is predicted by environmental factors. I consequently predict similar levels of spatial variation and autocorrelation in both phenology and success. Therefore, I also predict a positive relationship, as well as common environmental predictors, among occupancy, phenology and breeding success, in addition to the negative relationship between phenology and success. The outcomes of this study will highlight the capacity of environmental heterogeneity to explain spatial variation in directional selection on phenology. Greater understanding of the ecological interactions that maintain trait variation is essential if we are to grasp the long-term evolutionary implications of climate-driven mismatch.

2.3: Methods

2.3.1: Data collection

Data was sampled from a total of 149 unique woodcrete nestboxes in the spring breeding seasons (March-July) of 2013-2019. These nestboxes were distributed around the commune of Moulis in Ariége, Southern France, within the *Parc Naturel Régional des Pyrénées Ariégeoises*, and all data used were provided by the *Centre National de la Recherche Scientifique* (CNRS). This montane system is dominated by a mosaic woodland landscape, with large forest patches separated by roads, agricultural land, and human settlements. The sampling area is as follows; longitude: 1.08731-1.09555 (°N), latitude: 42.96504-42.97268 (°E), altitude: 448-593 metres above sea level. In order to account for spatial autocorrelation in occupancy, phenology, and reproductive success, WGS84 longitude and latitude (as well as elevation) were determined with precision per nestbox using GPS equipment. The geographical aspect of each habitat's slope was also determined.

Beginning in the third week of March each year, every nestbox was visited every 1-3 days until a confirmed case of occupancy. The species of the occupant(s) was also recorded at this stage. After occupancy was confirmed, nests were visited daily until the first egg was laid. Consequently, clutch initiation date was known with precision. Following this, nest visits returned to every 1-3 days until the onset of incubation. In the first week of incubation a maximum of two more visits were made to check for any predation or abandonment. There were no recorded cases of double-brooding (i.e. a second clutch after a successful first attempt in the same season) in these nestboxes during the study period. Daily nest visits resumed after 11 days of incubation and continued until the third day after hatching. For the first 18 days of chick rearing, the chicks were weighed every few days and capture/recapture of parents at the nestbox was attempted between days 11 and 16 for ringing/identification. After this point, daily nest visits resumed around the predicted fledge date until the final brood size was confirmed. The final dataset comprised 1043 nestbox years.

In order to test the potential of nestbox habitat properties in explaining spatial variation, the density, timing, and diversity of local vegetation were sampled, as localised plant communities are a major source of spatial habitat heterogeneity in temperate systems (Bai *et al* 2012). Vegetation sampling was conducted in the spring of 2017, in a 20m radius around each nestbox. Vegetation densities were determined by a single observer using on-site photos of each habitat. Density levels were categorised either dense, moderate, or sparse for understorey (no visible ground, partial cover, little or no cover), midstorey (4 or more shrubs, 3 or less shrubs, no shrubs) and canopy cover (predominantly or entirely shaded, approximately half shaded or less, 3 or less trees in habitat). Following this assessment, all trees within the 20m radius were identified to species level, including the nestbox tree. These identifications resulted in a dominant (most prevalent) tree species record for each habitat as well as a tree diversity assessment. Tree diversity was categorised as either monospecific, low diversity (one dominant species with 3 or less subordinates), moderate diversity (one dominant species with more than 3 subordinates), or high diversity (3+ species with a similar level of dominance). Finally, a small dataset containing tree budburst dates between 2013-2019 was also provided by CNRS. From this data, the dates of first budding on each nestbox tree were taken, though this only contained a sample of the nestboxes in the study site for a total of 433 nestbox years.

As arthropod populations constitute a major food resource of these birds in this period, I tested to what degree local arthropod abundance predicted spatial variation in occupancy, phenology, and success. Arthropod abundance was sampled from the nestbox habitats during the months of April-July in 2016-2019. In each year, every nestbox habitat was divided into radial zones, beginning with 0-5m from the nestbox up to 20-25m from the nestbox. These zones were sampled in a randomly generated order each year (meaning sampling of zones in the same nestbox habitat was not necessarily consecutive), with no zone being sampled more than once each year. Sampling continued at a rate of approximately 10 samples a day until all nestbox habitats had been sampled at each distance interval in that year. In each case, a locally common tree was identified (a dominant species if possible) and a low branch beaten with a bamboo stick three times over a beating tray. Any arthropods dislodged were transferred to sampling tubes via pooter, or by hand if too large. In each sample, the arthropods found were identified to at least order level and then the total number of individuals captured was recorded.

2.3.2: Data Handling

Various data were then reformatted, and new variables calculated to expand my analyses. First, the base occupancy data was used to calculate a proportion (between 0 and 1) of years in which the nestbox was occupied. This additional variable would represent nestbox occupancy rate as a predictor variable in my modelling. Furthermore, in each nestbox year the number of other occupied nestboxes (neighbour density) within a 2-hectare area was calculated, based on the findings presented in Wilkin *et al* 2006, which suggested density dependent effects on breeding success in great tits are not significantly affected by an increase in territory size beyond this value. Clutch initiation date and tree budburst were both converted to a julian value, using 1st January as 0.

As an unoccupied nestbox cannot provide data here, 582 nestbox years had no value for clutch initiation date or successful fledgings. Two nestbox years also lacked these data due to abandonment or predation before nest completion. Another two were missing data for fledgings due to abandonment or predation between post clutch completion. Consequently, unoccupied nestbox years are not included when modelling with clutch initiation date or successful fledgings as the response variable. Clutch initiation and fledging data were mean centred, and any missing data assigned a value of 0. This affected a total of 7 occupied nestbox years in 2016, 4 in 2017, 16 in 2018 and 20 in 2019. Some nestbox years recorded exceptionally late clutch initiations that were deemed unlikely to be first clutches/attempts. The 23 (5%) latest nestbox years were therefore omitted in the analyses.

There was also a low level of missingness in the arthropod abundance data with some nestbox years having no recorded value for local arthropods. As a result, the arthropod abundance data was mean-centred, and any missing data assigned a value of 0. For the same reason, the nestbox years from 2013-2015 were also assigned values of 0, as arthropod sampling did not take place in those years. Ring ID data was obtained for 328 (72%) occupied nestbox years for females and 257 (57%) for males. Any remaining occupied nestbox years were assigned a sequential dummy ID, and unoccupied nestbox years were assigned a 0 for both ring ID variables (Individual IDs were not used in occupancy modelling). Finally, as the budburst data for the nestbox trees was taken from only a sample of nestboxes, the mean date of first budding for each recorded species of nestbox tree was calculated in each year. These were then assigned to each nestbox year based on the dominant tree species in that habitat. 4 nestbox years were still missing a budburst value following this, and so were given a mean date of first budding based on their nestbox tree species.

2.3.3: Statistical Modelling

All coding for the mapping and analysis of data was conducted in R version 4.2.0 (RStudio Team 2015). A set of generalised additive mixed effects models (GAMM) using the 'mgcv' and 'gamm4' packages (Wood 2011, Bates *et al* 2015, Wood, Scheipl & Wood 2017) were used to test for spatial variation and autocorrelation in occupancy, clutch initiation date and number of successful fledgings. Occupancy as the response was given as a binary 0 or 1 with a binomial error structure. Clutch initiation date and fledging models were specified with a Gaussian error structure. Additive modelling is an effective method of highlighting spatial autocorrelation by identifying significance and non-linearity in spatial terms (Guisan, Edwards Jr & Hastie 2002). By fitting a bivariate (longitude & latitude), single-smoothed spatial variable, this non-linearity measure can be used to test the significance of spatial autocorrelation in the response. A series of spatial variation maps (see results) were produced using the package 'gratia' (Simpson & Singmann 2018) using the draw() function. This was repeated for each of the three response variables during the following model selection process. All environmental covariates varied significantly in space ($p<0.05$), with the exception of arthropod abundance ($p=0.66$).

My null models included Nestbox ID and sample year as random effects with no fixed effects, as simple measures of spatiotemporal variation. Models for clutch initiation and fledging also included each parent's ring ID as random effects. These models where then further developed using a forward selection process.

In each phase, predictors are added to the models on top of the best fitting model from the previous step. Akaike's Information Criterion (AIC) was used to determine model fit, removing any predictors that significantly worsened model fit (AIC increased by at least 2). In the first phase, the bivariate spatial autocorrelation term was added. In the next phase, nestbox elevation and habitat slope aspect were added to the model as linear predictors. In the models using clutch initiation date and fledging numbers as the response, occupancy rate, occupant species and neighbour density were also included as linear predictors. Additionally, the fledging models included clutch initiation date as a non-linear predictor (using a single smooth spline) as I predicted extremely early laying to be detrimental to success even under directional selection. The third selection phase incorporated vegetation factors as predictors. Understorey, midstorey and canopy densities along with local tree diversity were included as ordinal factors at this stage, and budburst was added as a linear predictor. The effect of local arthropod abundance was tested as a linear predictor in the final phase. This phase was completed by removing any non-significant predictors that did not significantly improve model fit (AIC reduced by at least 2) and testing for interactions between remaining model predictors. I then tested for interactions in the effects of significant predictors of occupancy and the effect of occupancy rate on clutch initiation date, as well as the effect of clutch initiation date on successful fledging numbers.

2.4: Results

2.4.1: Nestbox Occupancy

The overall occupancy rate for nestboxes between 2013-2019 was 44% (occupied n = 454 (blue tit n =296, great tit n = 158), vacant n = 589). The lowest recorded rate of occupancy among occupied nestboxes was 14% (1 year out of 7) and a total of 8 out 149 nestboxes were occupied in all 7 years of the study period. 12 nestboxes were not occupied at all between 2013-2019. My null GAMM found more variation between nestboxes than years in occupancy in the absence of fixed effects (Nestbox ID variance: 0.77, Year variance: 0.04). There was also significant spatial autocorrelation when nestbox coordinate was added as the only fixed effect (Nestbox location: $\chi2=24.3$, df=7.39, p=0.001, Figure 1D). This spatial autocorrelation was explained by the effects of elevation and slope aspect, suggesting that these parameters explained all non-random spatial variation in the occupancy data (Table 1).

Nestbox elevation negatively predicted occupancy (logit-scale estimate: -0.02, SE: 0.01, Figure 1A) as did habitat slope aspect (logit-scale estimate: -0.003, SE: 0.001, Figure 1B) reflecting increased occupancy on south facing slopes. Canopy density also negatively predicted occupancy (logit-scale estimate: -0.5, SE: 0.2) as nestboxes in habitats with sparse canopies (3 or less trees) had significantly higher occupancy than nestboxes in other habitats (logit-scale estimate: 0.7, SE: 0.28, p=0.01, Figure 1C). However, canopy density did not explain spatial autocorrelation, even when elevation and aspect were removed from the model. The effects of understorey density, midstorey density, mean budburst and tree diversity were non-significant and significantly worsened model fit. The effect of local arthropod abundance did not significantly worsen model fit despite its non-significance but was still removed in the last model selection step. No significant interactions were found between the significant predictors of occupancy. For a breakdown of model selection steps and associated maps, consult: https://jharris2211.shinyapps.io/PhenoApp/

Table 1: The minimal adequate model for occupancy of nestboxes in Moulis, French Pyrenees. The fixed effects section provides a list of all predictors that significantly improve model fit (Akaike's Information Criterion (AIC) reduced by at least 2) and covariate type: S for spline-smoothed continuous predictors, L for linear predictors, and O for ordinal factors. The random effects section provides the variances among unique nestbox IDs and among years. Additionally, the nestbox location smooth random effect indicates the amount of variance in random slopes of the non-linear relationship between nestbox location and the response.

Fixed Effects	d.f.	χ^2	p-value
Nestbox Location (S)	2	4.13	0.13
Elevation (L)	1	11.53	<0.001
Aspect (L)	1	6.02	0.01
Canopy Density (O)	2	6.12	0.047
Random Effects	**Variance**		
Nestbox ID	0.54		
Year	0.04		
Nestbox Location Smooth	1.1x10^{-7}		

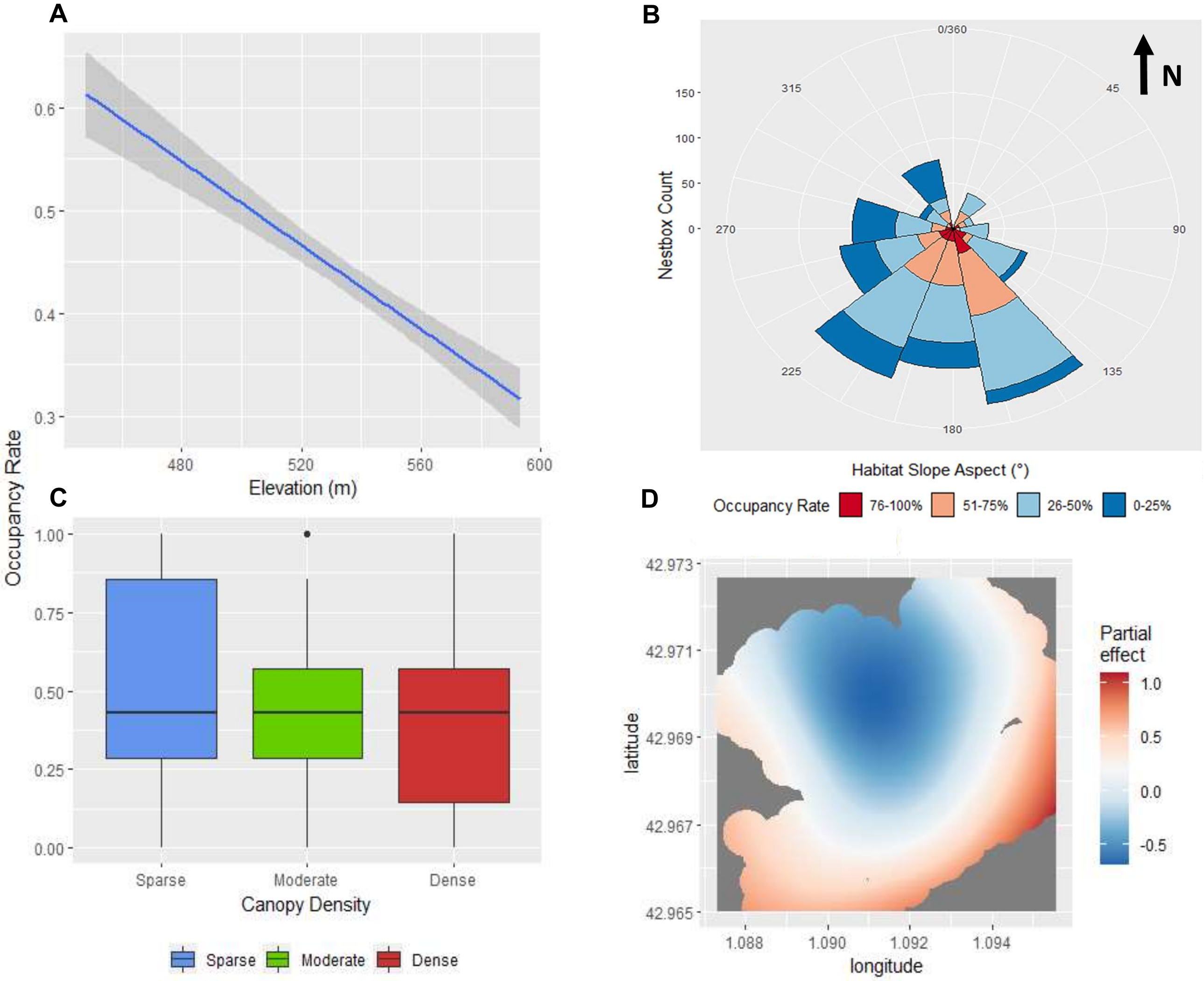

Figure 1: Effects of nestbox elevation (A), habitat slope aspect (B) and local canopy density (C) on nestbox occupancy in nestboxes near Moulis in the French Pyrenees between 2013-2019. Additionally, the spatial autocorrelation of occupancy variation in the site is displayed (D), indicating a significant level of non-randomness (df=7.39, p=0.001) in occupancy. The 'partial effect' scale indicates the slope of the relationship between nestbox location and occupancy throughout the site. Nestboxes at higher elevations were significantly less likely to be occupied (logit-scale estimate: -0.02, SE: 0.01, p<0.001). There was also significantly increased occupancy on south facing slopes (logit-scale estimate: -0.003, SE: 0.001, p=0.01). Nestboxes in habitats with sparse canopies (3 or less trees) had significantly higher occupancy than other habitats (logit-scale estimate: 0.7, SE: 0.28, p=0.01).

2.4.2: Clutch Initiation Date

The earliest observed clutch initiation was on the 26th of March 2019, while the latest observed was 11th of June 2013. This range varied between years, with the smallest being 28 days in 2015 and the largest being 70 days in 2014. The year with the earliest mean clutch initiation was 2017 at 7th of April and the latest mean clutch initiation was 24th of April in 2013. Clutch initiation date was significantly different between the two occupant species (One-Way ANOVA: $F_{1,430}$=9.54, p=0.002) with blue tits laying a mean of 2 days earlier than great tits. Consequently, GAMMs for clutch initiation controlled for the effect of occupant species.

My null GAMM found that nestbox ID only accounted for 2% of variance in clutch initiation dates, indicating relatively little spatial variation. Further, there was no significant spatial autocorrelation observed in clutch initiation dates (Nestbox location: F=1.44, df=2, p=0.24). Occupant species significantly predicted clutch initiation date (Table 2). Significantly later clutch initiation was observed in great tits than in blue tits (estimate: 1.91, SE: 0.63, Figure 2). Model fit was significantly worsened by inclusion of understorey density, tree diversity and local arthropod abundance, and their effects did not significantly predict variation in clutch initiation. Nestbox occupancy rate, elevation, habitat slope aspect, neighbour density, midstorey density, canopy density and mean budburst did not significantly improve or worsen model fit, nor did they significantly predict clutch initiation date. As such these factors were not removed until the last model selection step. No significant interactions were found between the significant predictors of clutch initiation date, nor between the effects of occupancy and its predictors. For a breakdown of model selection steps and associated maps, consult: https://jharris2211.shinyapps.io/PhenoApp/

Table 2: The minimal adequate model for clutch initiation dates recorded from nestboxes in Moulis, French Pyrenees. The fixed effects section provides a list of all predictors that significantly improve model fit (Akaike's Information Criterion (AIC) reduced by at least 2) and covariate type: S for spline-smoothed continuous predictors and C for categorical factors. The random effects section provides the relative variances among unique ringed individual IDs, nestbox IDs, and among years. Additionally, the nestbox location smooth random effect indicates the amount of variance in random slopes of the non-linear relationship between nestbox location and clutch initiation date.

Fixed Effects	d.f.	F	p-value
Nestbox Location (S)	9.15	1.59	0.11
Species (C)	1	9.14	0.003
Random Effects	**Variance**		
Female Ring ID	19.26		
Male Ring ID	3.04		
Nestbox ID	9.82×10^{-9}		
Year	7.19		
Nestbox Location Smooth	13		
Residual	10.62		

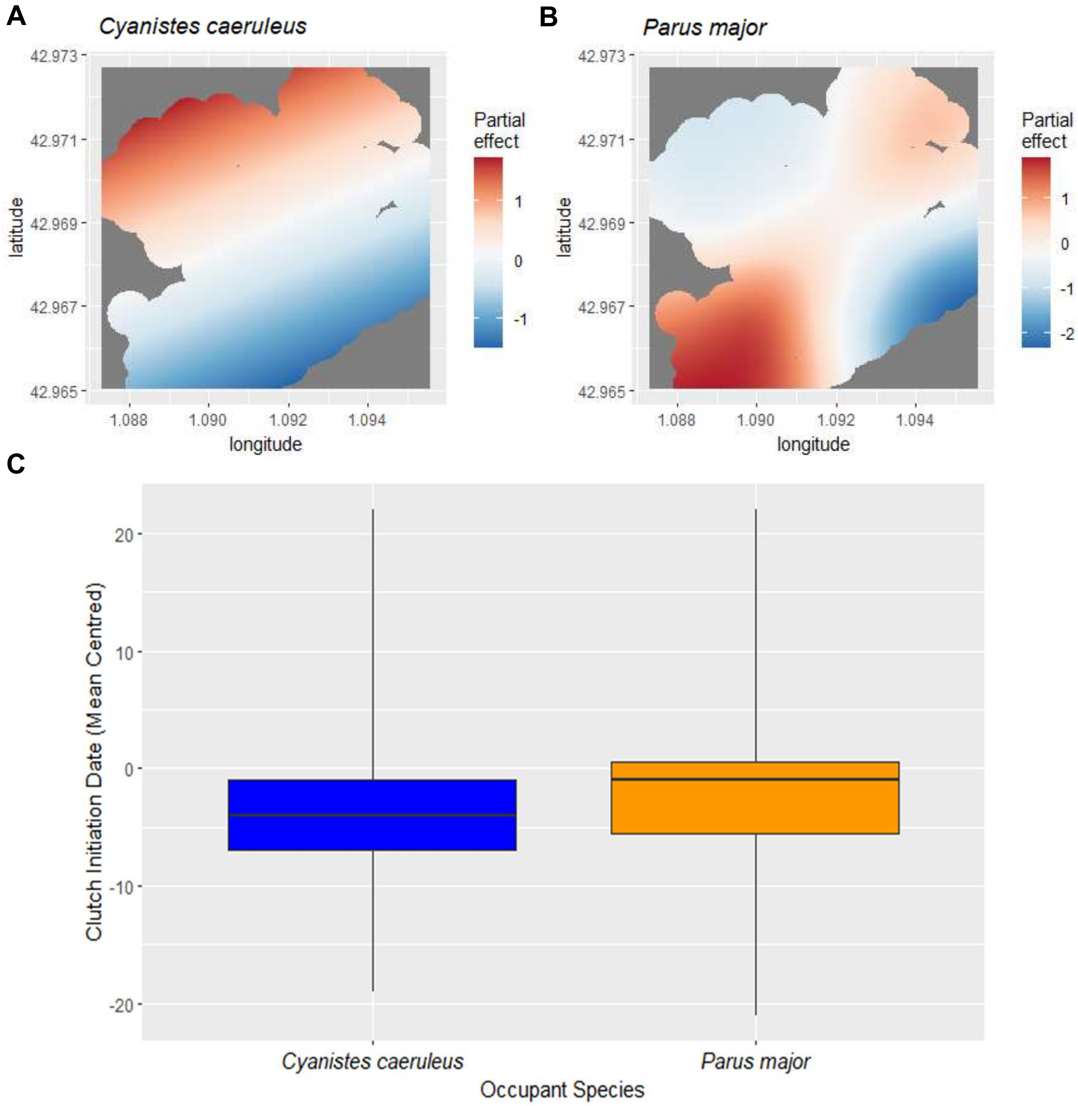

Figure 2: Spatial autocorrelation in clutch initiation dates (A & B) of nestboxes near Moulis in the French Pyrenees between 2013-2019, as well as the effect of occupant species (C). The distributions indicate a non-significant degree of spatial autocorrelation in both species. The ‘partial effect’ scale indicates the slope of the relationship between nestbox location and clutch initiation dates throughout the site. Great tits laid significantly later than blue tits (estimate: 1.91, SE: 0.63, p=0.003).

2.4.3: Fledging Success

The number offspring successfully fledged between 2013-2019 ranged between 1 and 11 fledgings, with an overall mean of 5 successful fledgings. Failure to fledge any offspring whatsoever (when occupied and clutch completed) was recorded in 37 nestbox years. The number of offspring fledged differed significantly between great tits and blue tits (One-Way ANOVA: $F_{1,430}$=20.38, p<0.001), with blue tits fledging a mean of 1.32 more offspring than great tits. As such, GAMM analysis controlled for the effect of occupant species on number of successful fledgings.

The null GAMM found that nestbox ID accounted for only 3% of variance in number of successful fledgings, indicating relatively little spatial variation. However, I also found significant spatial autocorrelation in number of successful fledgings (F=3.41, df=2, p=0.03). Additionally, clutch initiation date and occupant species were significant predictors of fledgings but did not explain the spatial autocorrelation (Table 3). Great tits fledged significantly less offspring than blue tits (estimate: -1.24, SE: 0.3, Figure 3C).

The effects of elevation, habitat slope aspect, canopy density and local arthropod abundance did not significantly predict variation in number of successful fledgings and all significantly worsened model fit. The effects of nestbox occupancy rate, neighbour density, midstorey density, mean budburst and tree diversity on fledgings were also non-significant, but neither significantly worsened nor improved model fit. As such these effects were not removed until the final model selection phase. There were no significant interactions between the predictors of fledging numbers. However, when investigating whether the effect of clutch initiation date was dependent on the predictors of occupancy, a significant interaction was found with canopy density (included as a by variable (Figure 3D, Wood & Wood 2015)). For a breakdown of model selection steps and associated maps, consult: https://jharris2211.shinyapps.io/PhenoApp/

Table 3: The minimal adequate model for number of successful fledgings recorded from nestboxes in Moulis, French Pyrenees. The fixed effects section provides a list of all predictors that significantly improve model fit (Akaike's Information Criterion (AIC) reduced by at least 2) and covariate type: S for spline-smoothed continuous predictors, C for categorical factors and I for an interaction (see Wood & Wood 2015 for information on 'By Variables'). The random effects section provides the relative variances among unique ringed individual IDs, nestbox IDs and among years. Additionally, the nestbox location smooth random effect indicates the amount of variance in random slopes of the non-linear relationship between nestbox location and number of successful fledgings.

Fixed Effects	d.f.	F	p-value
Nestbox Location (S)	2	4.48	0.01
Species (C)	1	17.69	<0.001
Clutch Initiation Date (By Canopy Density) (I)			
Sparse	2	2.81	0.06
Moderate	1	0.11	0.74
Dense	1	21.06	<0.001
Random Effects	**Variance**		
Female Ring ID	1.5		
Male Ring ID	0.28		
Nestbox ID	0.14		
Year	0.07		
Nestbox Location Smooth	Effective 0		
Clutch Initiation Date (By Canopy Density)			
Sparse	6.18		
Moderate	Effective 0		
Dense	$2.89x10^{-8}$		
Residual	5.72		

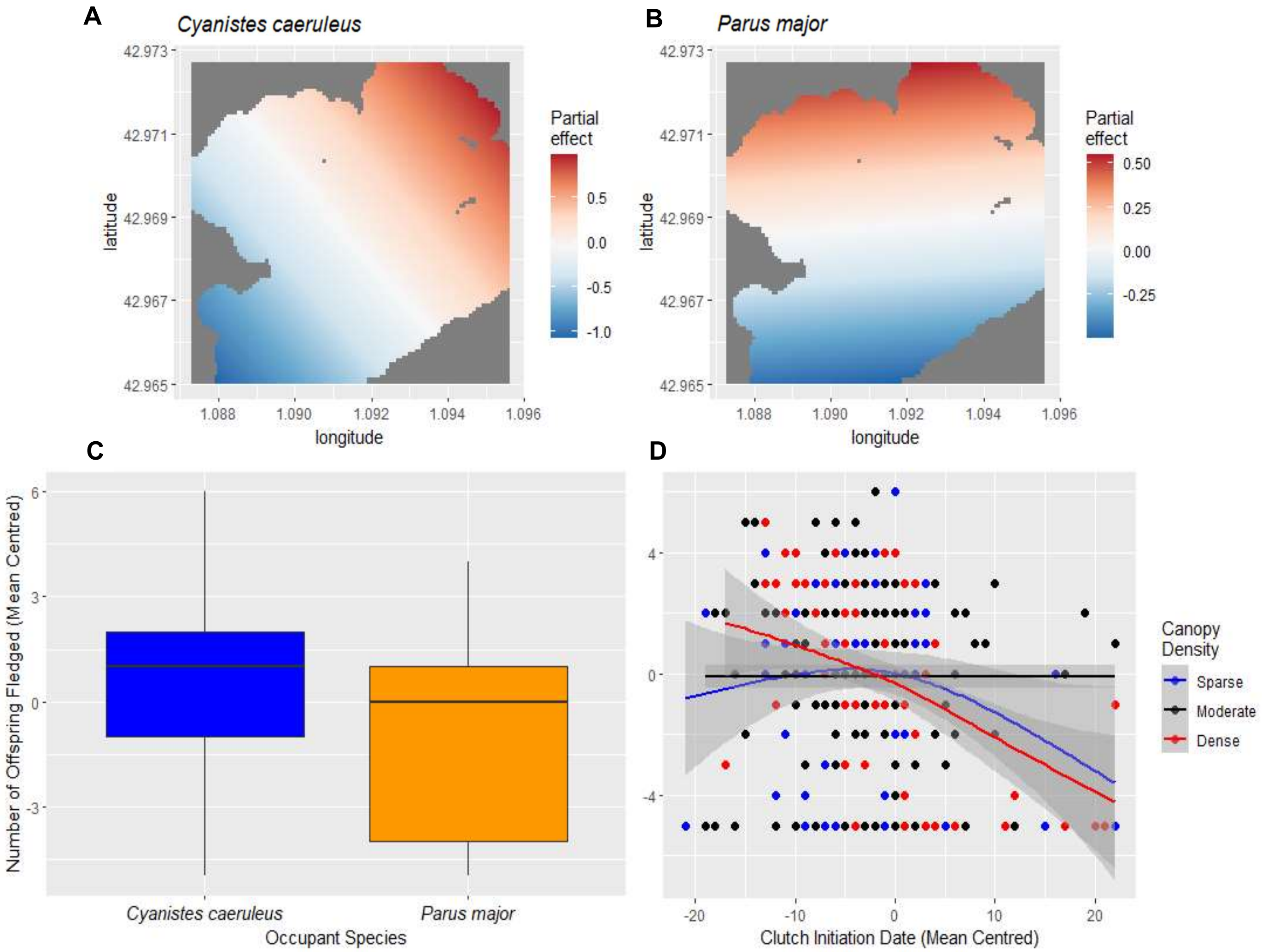

Figure 3**:** Spatial autocorrelation in numbers of successful fledgings (**A** & **B**) from nestboxes near Moulis in the French Pyrenees between 2013-2019, and the effects of occupant species (**C**) and clutch initiation date on successful fledgings, which interacts with local canopy density (with 95% confidence intervals) (**D**). The distributions indicate a significant degree of spatial autocorrelation overall (F=3.41, df=2, p=0.03). The 'partial effect' scale indicates the slope of the relationship between nestbox location and successful fledgings. Great tits fledged significantly less offspring than blue tits (estimate: -1.24, SE: 0.3, p<0.001). Furthermore, clutch initiation date significantly, negatively predicted number of successful fledgings, though only in habitats with dense canopies (F=1, df=21.06, p<0.001).

2.5: Discussion

I confirmed that there is a negative relationship between clutch initiation date (phenology) and fledging numbers (success). Further, I present new evidence of an ecological effect on phenology selection. Phenology selection was most negative in habitats with dense canopy cover, and negligible in habitats with moderate cover. Contrary to my prediction of similar spatial autocorrelations between response variables, I found no significant evidence of occupancy, phenology or success explaining spatial autocorrelation in each other. Occupancy was the only variable with significant autocorrelation that was explained by environmental predictors. Further, I found little evidence of spatial variation in either phenology or success, with nestbox ID accounting for <1% of final model variance in both cases. Even before the addition of fixed effects, these accounted for 2% and 3% of variances in phenology and success, respectively.

Finding an interaction between an environmental variable and the effect of phenology on success furthers our understanding of phenology selection. Significant ecological correlates of the negative relationship between phenology and fitness may not directly predict phenology or success. Analyses of fine-scale variation in phenology selection may be enhanced by a broader view of the reproductive cycle that accounts for environmental effects both preceding and throughout the breeding season. Examples of this are already evident in studies of migratory phenology, which find significant effects of preceding winter conditions (Eichorn *et al* 2009, Sullivan *et al* 2016). Previous work finds that territoriality and consequent variation in habitat quality experienced by a population improves reproductive fitness by facilitating early breeding (Szymkowiak 2013), which I reinforce by finding an interaction between an occupancy predictor and reproductive success. However, I did not find a significant association between occupancy itself and phenology/success. If we do not see the highest success or earliest breeding in the most popular territories, how do we interpret a significant effect of an occupancy predictor on selection for early laying?

Competition for the most popular territories may be sufficiently strong that it constrains any positive association between occupancy rate and reproductive success. A 2017 study analysing the relationship between occupancy and phenology found that blue tits in nestboxes with fewer and more distant neighbours laid significantly earlier (Serrano-Davies, Barrientos & Sanz 2017). In my analyses however, neighbour density did not predict phenology or success. Even so, such constraints may be driven by birds occupying natural cavities (Robertson 1990), which my data do not account for. It could be concluded that the fitness consequences of canopy density are independent from its relationship with occupancy. However, variance among slopes of clutch initiation date on success in sparse canopy habitats (which had the highest occupancy rates) accounted for almost 45% of model variance. This result may indicate that the observed relationship between phenology and success in these habitats is repeatable, and therefore a less ‘risky’ reproductive investment. A proclivity towards risk-averse breeding strategies may be evidence of bet-hedging in this population. Simons 2011 posited that evidence of environmentally-correlated, within-population variance in the fitness of trait phenotypes (in this case phenology) could constitute evidence of bet-hedging strategy if such variance maximises population fitness. Therefore, I recommend further investigations integrating this within-population framework with population-level analyses of fitness trends, to validate minimising of environment-driven unpredictability in breeding success. Multi-scale analyses could also explain the significant spatial autocorrelation remaining in my model if the lack of non-linearity in success indicates non-random spatial variation over larger spatial gradients.

No environmental predictors significantly predicted phenology or success, so I suggest that individual-level variation (Sydeman & Eddy 1995, Blackmer *et al* 2005) is a more promising avenue than habitat-level variation for identifying direct effects on phenology and success. My clutch initiation analyses support this, as approximately 36% of model variance was attributable to differences among individual females. Effects of body condition and breeding experience on phenology, both of which have been found before (Winkler & Allen 1996, Winkler *et al* 2020), are feasible. However, lay date variation may still depend on breeding environment. Female body condition is constrained by environmental factors such as local food availability and predation risk (Clinchy *et al* 2004, Zanette *et al* 2013). In the case of food availability, it is surprising that I found no significant effects of local arthropod abundance, though this may be due to the nature of the arthropod sampling protocol. Numerous key prey species for Parids are canopy-dwellers that disperse vertically (Ulyshen 2011), potentially making the area around nestboxes unrepresentative of their distribution.

Nevertheless, my framework could be expanded upon by the inclusion of endogenous, individual-level variables in conjunction with aforementioned population-level inference. For phenology analyses in particular, incorporating variation both within and between individual birds (and any interaction between them) will be essential to devising models with the explanatory power to formulate predictions on how climate-driven mismatches will shape phenology variation. Few studies have demonstrated direct empirical links between fine-scale environmental variation and phenological strategy, and my results would suggest that this is because direct ecological effects on reproductive timing and success do not operate at the habitat-level. I therefore recommend that the variable of interest to studies of variation in lay date selection should be the effect of phenology on success, rather than solely testing for direct effects of the environment on phenology or success.

Direct effects of the environment may operate at much larger spatial scales, such as temperature, rainfall (Visser *et al* 2015) or photoperiod (Lambrechts & Perret 2000) or be correlated with a population's ability to track environmental change and engage in adaptive plastic response, as found in Cole et al 2021. However, neither phenology nor success was predicted by elevation or aspect. Therefore, although elevational gradients in ambient temperature drive spatial variation in both avian lay date and fecundity (Badyaev & Ghalambor 2001, Camfield, Pearson & Martin 2014), and increased exposure to sunlight and reduced moisture on south facing slopes may affect perceived ambient temperature (Correira *et al* 2015 & Zapata-Rios *et al* 2016), it is unlikely that the fine-scale occupancy variation I observed was related to temperature. The actual elevation range in this site is less than 200m, and so any expected change in ambient temperatures between habitats at the extremes should not be in excess of 2°C, similar to the ranges of various studies that have demonstrated temperature-driven phenology change (Visser, Holleman & Caro, Shave *et al* 2019, Shipley *et al* 2020). If this occupancy variation is not based on ambient temperature driving variation in phenology, further work is needed at the proximate level.

Elevation was correlated weakly, but significantly, with a number of other environmental variables (See Table S1). If occupancy variation is indicative of variation in habitat quality, this effect may be the product of a combination of other habitat-level differences that are not individually strong enough to provide a significant effect. The question of why occupancy variation appears independent of phenology remains open, however. Despite this, my multivariate framework effectively dissected spatial variation, autocorrelation and environmental effects that have the potential to explain it. The occupancy analyses exemplify this because I was able to identify that, of the three variables predicting occupancy, only elevation and aspect explained the significant autocorrelation. As a result, I highlight that some environmental effects are non-randomly distributed in space, while others are not. Failing to account for this could lead to bias in effect estimates that would significantly impede disentangling significant habitat and individual-level effects on life history traits (Dormann 2007). The framework tackles this challenge, estimating spatial variation and autocorrelation therein using spatial terms that are transferrable between systems (data permitting) and allow direct estimation of the relative importance of different covariates in explaining autocorrelation. Such resources are needed to identify what role fine-scale variation in the environment plays in constraining population-level response to selection for early breeding. Understanding how within-population variation in selection response drives mismatch is vital to formulating robust conclusions on how life histories will continue to evolve under pressure from climate change.

I aimed to present evidence of fine-scale environmental effects on phenology and success, which I was able to do through a multivariate, mixed effects approach that quantifies spatial variation, autocorrelation, and the explanatory power of environmental covariates. The relationship between clutch initiation date and fledgings is significantly variable based on an environmental correlate of occupancy. Perhaps few studies have found empirical evidence of environment-driven variation in lay date selection because such variables may not have direct correlational relationships with phenology or fitness. However, I also find evidence of individual-level variation determining phenological strategy and unexplained non-random spatial variation in reproductive success. Future study would be enhanced by expanding on my framework to incorporate multi-scale analysis of individual, habitat, and population-level effects on selection for early breeding. My findings elucidate environmental influence on within-population variation in selection, which may drive these observations of stasis. Building on this is necessary to understand and predict how populations will respond to increasing selective stress from climate-driven mismatch.

Chapter 3: Scale Dependent Heterogeneity Shapes Variation in Selection for Early Breeding Across Multiple Scales

3.1: Abstract

Understanding how populations inhabiting seasonal environments respond to climate change is a major challenge. As these environments can be heterogeneous in both space and time, we must establish the role of the environment in maintenance of variation in phenology, which can have major fitness consequences. The ecological mechanisms through which different phenological strategies remain viable in the face of climate driven selection remain unclear. I tackle this by quantifying variation in the strength and shape of selection gradients at multiple scales. Using data from a system of nestboxes in the French Pyrenees, I modelled the association between lay date and fledging numbers in blue and great tits at three different scales. First, lay dates were spatially autocorrelated, but fledging numbers were not, driving spatiotemporal variability in the relationship between them. I found this to be the result of significant variability in selection for early breeding among nestboxes (driven by nest failure) and years (driven by annual variation in local temperatures). These results were not accounted for by phenology or elevation, highlighting complex, fine-scale heterogeneity in the fitness of phenological strategy. I highlight that scale dependent effects on the relationship between phenology and fitness can lead to fine-scale variability in fitness outcomes. These findings indicate that mismatch may be driven by localised phenological optima that broad scale analyses may overlook, though resolving the role of individual-level variation and any interaction with habitat-level variation remains a priority.

3.2: Introduction

A fundamental aim of evolutionary and population ecology is to understand and predict how environmental change shapes trait variation in wild populations (Russell *et al* 2012). Global climate change has become an area of focus in this regard (Buckley & Kingsolver 2012, Straile, Kerimoglu & Peeters 2015) due to its well-established impact on phenology (Visser & Holleman 2001, Thackeray *et al* 2016, Renner & Zohner 2018). Seasonal ecological events, such as breeding and migration in birds (Visser et al 1998), insects (Stefanescu 2001), and mammals (Sheriff, Buck & Barnes 2015), depend on maintaining synchrony with dynamics of other ecologically important populations (e.g., prey). When interacting populations respond to environmental change at different rates, the resulting ‘phenological mismatch’ may have fitness consequences, driving variation in both the reproductive fitness of individuals and/or vital rates of populations (Van de Pol & Bailey 2019, Vriend *et al* 2023). Declines of up to 90% have been observed in breeding Pied Flycatchers (*Ficedula hypoleuca*) when mismatch with caterpillar abundance peaks is strongest (Both *et al* 2006). Further, individually mismatched female Parids have been found to be 50% less likely to double-brood and lay smaller clutches, though notably this was not accompanied by a population-level decline in recruitment (Reed, Jenouvier & Visser’s 2013). Such results can be interpreted as directional selection for early breeding driven by mismatches (Visser *et al* 2021). Despite this, variation in phenology and associated reproductive fitness remains prevalent in the wild.

Spatiotemporal variation in a population’s environment is thought to incentivise variable phenological strategies (Te Marvelde *et al* 2012, Visser et al 2015), but few studies have provided clear examples of such links (but see Cole, Regan & Sheldon 2021). Variation in the fitness of a given phenological strategy may not be directly indicative of mismatch but rather variation in phenology optima on the basis of an individual's qualities and/or those of its local environment. Proximate understanding of phenology variation within populations has been hampered by a lack of spatiotemporal scope (Tang *et al* 2016). The level of variation observed in phenology can depend on the data's spatiotemporal resolution. Analysing differences among populations can yield an inference that places less importance on environment-driven variance compared to analysing differences among individuals across populations (Park, Newman & Breckheimer 2021). We may observe this because some population-level modelling theoretically assumes that a level of homogeneity is present among subjects (Crawley & Akhteruzzaman 1988). This may lead to unreliable conclusions on phenology variation within species (McLean, Van Der Jeugd, Van De Pol 2018) and study systems if these subjects experience significant environmental heterogeneity at fine spatiotemporal resolutions. In such circumstances, within-population variation could indicate that different phenological strategies are adaptive specifically under localised environmental conditions (Frederiksen *et al* 2004). These 'scale dependent' effects could therefore explain phenology variation maintenance if fine-scale heterogeneity is important in mitigating or avoiding phenological mismatch within populations.

Small passerines such as Parids breeding in temperate habitats depend on synchrony with seasonal abundances of arthropod prey to maximise reproductive success (Verhulst & Tinbergen 1991). Even so, studies of temperate passerine phenology have not shown that mismatch consistently explains variation in the fitness of ecologically comparable populations and individuals. Willow warblers (*Phylloscopus trochilus*) in the northern UK experienced an increase of 60% between 1994-2012, while southern populations experienced a 30% decline (Morrison *et al* 2016). As latitudinal variation in mismatch with prey is coarse in spatial scale (Burgess *et al* 2018), mismatch alone is unlikely to explain this disparity between phenologically similar populations. Tree swallow (*Tachycineta bicolor*) populations under directional selection for early breeding showed little evidence of adjustment to match with seasonal food peaks, as unpredictable food abundance peaks during the laying period were more influential (Dunn *et al* 2011). Therefore, spatiotemporal variation in environmental characteristics may incentivise fine-scale variation in phenology, even under population-level directional selection for early breeding. As such, this study aims to provide evidence of spatiotemporal variation in selection on phenology at fine scales, which would explain maintenance of such variation. I can achieve this by modelling reproductive (fledging) success as a function of phenology (clutch initiation date), while allowing for variation at multiple spatiotemporal scales.

My analysis, based on nestbox data from across a southern region of the French Pyrenees, will employ a mixed-effects additive framework to model multiscale variation in the phenology-fledging success relationship (as a proxy for selection). I predict significant variation among individual nestboxes (indicative of localised optima), nested within a lesser degree of variation observed among six discrete study sites. Further, I expect variation in the phenology-success relationship among years, due to interannual variation in weather patterns during temperate springs (Lopez-Moreno & Vicente-Serrano 2007). In the same vein, the environmental covariates are drawn from sources that can be expected to exhibit spatiotemporal variation. Ambient temperatures are expected to be significantly associated with interannual variation, while elevation and habitat slope aspect are predicted to explain spatial temperature differences (Correia *et al* 2015, Zapata-Rios *et al* 2016). To capture the influence of biotic environmental variation, vegetation around the nestboxes is included. Plant communities are a source of spatial habitat heterogeneity (Bai *et al* 2012) that can indicate habitat quality and therefore abundance of key arthropod prey. As such, I predict vegetation data to explain nestbox-level variation in selection for early breeding.

My findings will advance phenology research by demonstrating that fine-scale spatiotemporal variation in selection on phenology can be observed alongside directional selection for early breeding. More broadly, I hope to elucidate how scale dependent effects of environmental heterogeneity can enhance inferences of phenology variation by incorporating multiple scales of variation simultaneously. In turn, we will have gained valuable insight into how the environment enables a range of phenological strategies, maintaining variation under apparent directional selection associated with mismatch. Formulating such conclusions is essential if we are to construct robust projections of how this phenomenon will shape the future of seasonal ecological cycles in the wild.

3.3: Methods

3.3.1: Data collection

Breeding data from great tits (*Parus major*) or blue tits (*Cyanistes caeruleus*) was sampled from 370 unique woodcrete nestboxes distributed across Ariége, Southern France, within the *Parc Naturel Régional des Pyrénées Ariégeoises* between 2013-2019. All data used were provided by the *Centre National de la Recherche Scientifique* (CNRS). This montane system is dominated by large forest patches separated by roads, agricultural land, and human settlements. My system comprises 6 study sites covering various elevations. WGS84 longitude, latitude and elevation were determined for each nestbox using GPS equipment. The geographical slope aspect at each nestbox was also recorded. Temperature loggers near each site recorded ambient air temperature every 30 mins throughout the year (see Table S1 for exact sample site boundaries and logger locations).

Beginning in the third week of March each year, each nestbox was visited every 1-3 days until occupancy was confirmed. Nests were visited daily until the first egg was laid to determine clutch initiation date and then every 1-3 days until the onset of incubation. In the first week of incubation a maximum of two more visits were made to check for predation or abandonment. Daily nest visits resumed after 11 days of incubation and continued until the third day after hatching. A final visit at the predicted fledge date confirmed final brood survival. There were no confirmed cases of second clutches following a successful first clutch in these nestboxes during the study period. The dataset comprised 2449 nests, with 328 nestboxes being represented in all 7 years. The remaining 42 were absent in some years due to being damaged or moved to a different site, though no nestbox was present in less than 3 years.

As localised plant communities are a major source of spatial habitat heterogeneity in temperate systems (Bai *et al* 2012), vegetation sampling was conducted in the spring of 2017, in a 20m radius around each nestbox. Vegetation densities were determined by a single observer using on-site photos of each habitat. Density was categorised as either dense, moderate, or sparse for understorey (no visible ground, partial cover, little or no cover), midstorey (4 or more shrubs, 3 or less shrubs, no shrubs) and canopy cover (predominantly or entirely shaded, approximately half shaded or less, 3 or less trees in habitat). Further, all trees within the 20m radius were identified to species level. From these data a dominant (most prevalent) tree species and tree diversity assessment were derived. The latter was categorised as either monospecific, low diversity (one dominant species with 3 or less subordinates), moderate diversity (one dominant species with more than 3 subordinates), or high diversity (3+ species with a similar level of dominance). Finally, tree budburst dates were recorded between 2013-2019. The dates of first budding on each nestbox tree were checked for during nestbox surveys, though this did not occur for all the nestboxes in the study site, giving budburst dates for a total of 915 nests. Consequently, the mean date of first budding for each recorded species of nestbox tree was calculated in each year. These were then assigned to each nestbox year based on the dominant tree species in that habitat.

For each nest the number of other occupied nestboxes (neighbour density) within a 2-hectares was calculated. Density-dependent effects on breeding success in great tits are not significantly affected by an increase in territory size beyond this value (Wilkin et al 2006). Clutch initiation date and tree budburst were both converted to a Julian date, using 1st January as day 0. As temperature data recorded at a single location near each site, daily mean and maximum temperatures were calculated per site and year using temperature records for March – June. This variable is hereafter referred to as a site and season-specific mean/maximum of temperature in the rearing period each year.

Clutch initiation/fledging data was unavailable for 17 occupied nests due to abandonment or predation before nest completion. Another 3 nests were missing data for fledging numbers due to abandonment or predation between post clutch completion. Unoccupied nests are not included in my modelling. Clutch initiation date and fledging data were centred on overall mean, and any missing data assigned a value of 0 (i.e., the mean). A small number of nests with exceptionally late laying were deemed unlikely to be first clutches; hence the 50 (5%) latest nests were omitted in the analyses as well as one very early outlier. The final sample for modelling was 946 nests (Blue tit n=560, great tit n=386).

3.3.2: Statistical Modelling

All analyses were conducted in R version 4.2.0 (R Core Team 2022). I first established whether there was significant non-random spatial variation in clutch initiation date and fledging number using Moran's I Test for spatial autocorrelation (Paradis & Schliep 2019). Following this, I modelled the relationship between clutch initiation date and fledgling number. I first confirmed that the overall relationship between clutch initiation date and fledgling number is negative using a simple linear model with mean-centred clutch initiation date as a covariate. Then a Generalised additive model (GAM) was used to ascertain whether nonlinearity (which may be indicative of spatiotemporal variation in the slope of the phenology-fledging relationship) is also present. Based on these (see below), I constructed generalised additive models using package 'mgcv' (Wood 2011, Wood & Wood 2015) in which I allowed the intercept and slope of the relationship between clutch initiation date on fledgling number to vary among nestboxes, sites and years simultaneously. I modelled the nonlinear effect of clutch initiation data on fledgling numbers with a Gaussian error structure, including random effects smoothers to allow for variation in the intercept and slope of this relationship.

Elevational gradients can generate considerable environmental variation in temperature gradients and vegetation communities, which may drive variation in phenology and fledgling numbers. My model therefore included a decomposed tensor interaction between clutch initiation date and elevation (decomposed meaning both the main nonlinear effects were also included in the model). This served as the null model, against which the effects of the following environmental covariates were tested: Habitat slope aspect; mean ambient temperature; maximum ambient temperature; understorey; midstorey and canopy densities; local tree budburst date and local tree diversity. Each covariate was added to the model individually, with its own tensor interaction with clutch initiation date. Categorical predictors were instead included as 'by' variables (see Wood & Wood 2015) for the main effect of clutch initiation date. Hence the model never exceeded 3 nonlinear fixed effects (clutch initiation date, elevation & one of the above) and two interaction terms in complexity. I smoothed all non-interaction fixed effects using a thin plate spline (Wood 2003).

3.4: Results

The nestbox occupancy rate between 2013 - 2019 was 41%. Clutch initiation dates varied between -23 Julian days in 2016 and 25 Julian days in 2016 and 2019. Clutch initiation dates varied most in 2016 with 48 days between the first and last recorded clutch initiations. The smallest range, observed in 2015, was 29 days. Fledgling numbers recorded between 2013-2019 ranged between 1 and 11, with an overall mean of 5. Complete failure to fledge (in nestboxes with a completed clutch) was observed in 171 nests.

Moran's I Test indicated that clutch initiation dates were significantly spatially autocorrelated (Moran's I: 0.02 ± 0.003, $p<0.001$), whereas fledgling numbers displayed a non-significant degree of spatial autocorrelation (Moran's I: 0.005 ± 0.003, $p=0.073$). Further, there was a significantly negative relationship between clutch initiation date and fledging success ($\beta \pm SE = -0.07 \pm 0.01$, $F_{1,944}$

= 24.44, p<0.001; Figure 4A), within which informative nonlinearity was present (ΔAIC between LM and GAM = 10.7; Figure 4B).

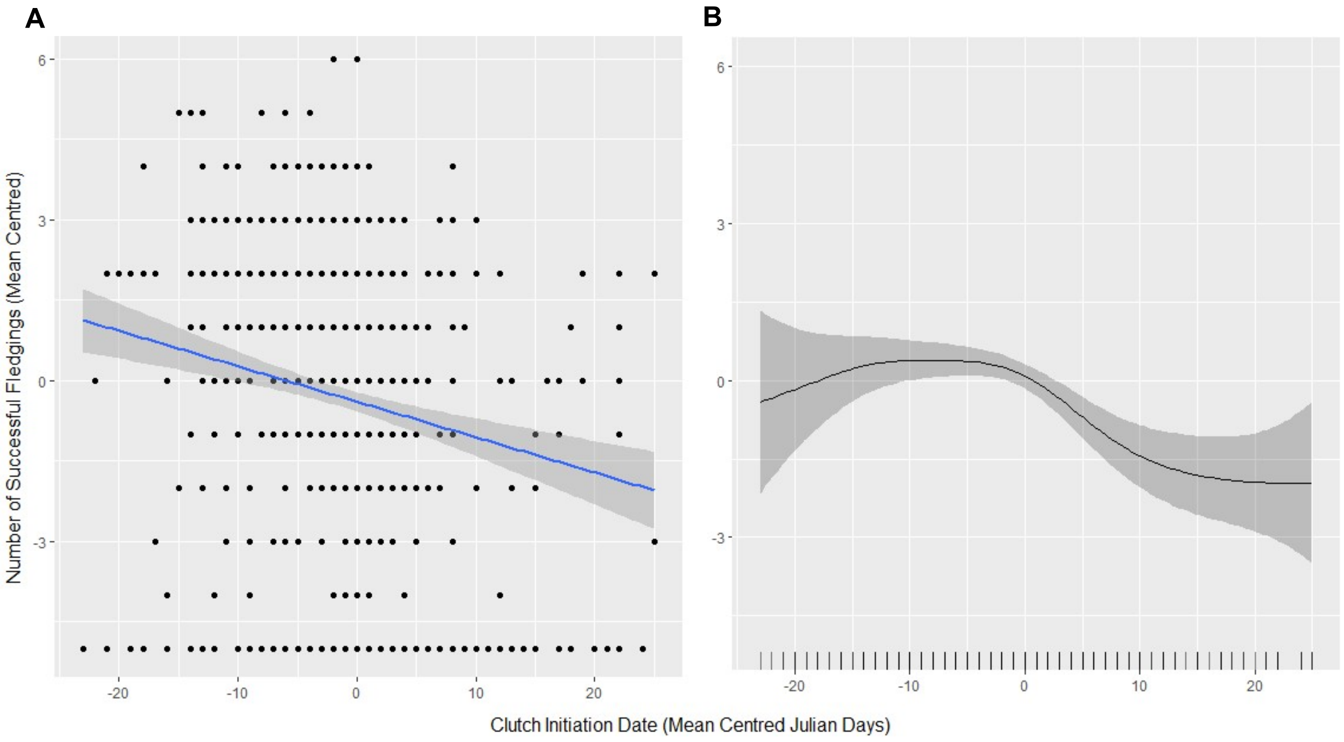

Figure 4: The modelled linear (A) and nonlinear (B) relationship between clutch initiation dates and numbers of successfully fledged chicks in breeding attempts of Parids in the French Pyrenees between 2013-2019. Data points are represented by dark circles in A and by the x-axis rug in B. The nonlinear relationship represents a better fit for these data, as evidenced by an AIC reduction of 10.7.

To decompose any variation in this negative, non-linear relationship, I incorporated the random effects of nestbox, site and year, while controlling for the (nonlinear) effect of elevation. The effect of nestbox elevation on number of fledglings was non-significant and clutch initiation date remained a significant predictor of the number of fledglings when elevation was included. I also found significantly variable random intercepts among study sites, slopes among nestboxes and both among years (Table 4; Figure 5).

Table 4: Generalised Additive Model (GAM) of the nonlinear effects of clutch initiation date, nestbox elevation and a tensor interaction between the two on the number of successful fledgings in breeding attempts of a population of Parids in the French Pyrenees between 2013-2019. The model also allowed for random intercepts and slopes among individual nestboxes, study sites and years. The 'e.d.f' column indicates the degree of nonlinearity in the fixed effects, as well as the variability among subject-specific intercepts/slopes in the random effects.

Predictor Variable	e.d.f.	F	p-value
Clutch Initiation Date	4.6	2.4	0.045
Nestbox Elevation	4	1.6	0.17
Clutch Initiation Date * Nestbox Elevation	1	0.2	0.64
Random Effects:			
Nestbox ID (intercepts)	10.9	0.03	0.34
Nestbox ID (slopes)	35.6	0.2	0.01
Site (intercepts)	1.9	1.4	0.01
Site (slopes)	0.8	0.3	0.17
Year (intercepts)	5.2	5.6	0.001
Year (slopes)	4.6	8.8	<0.001

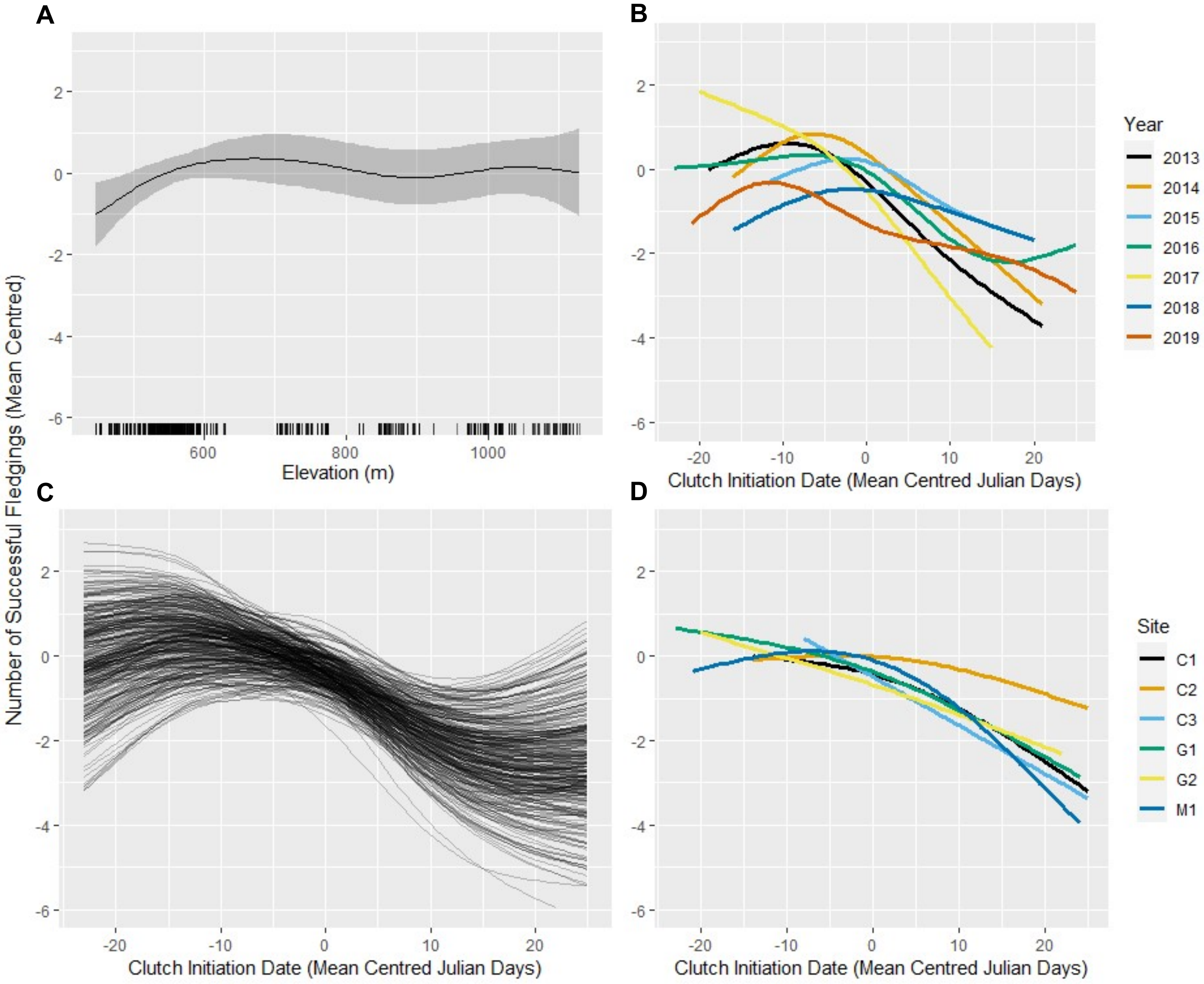

Figure 5: Fledgling numbers of breeding attempts in wild Parid populations in the French Pyrenees between 2013-2019, as a nonlinear function of elevation (A) and clutch initiation date, with subject-specific relationships among individual years (B), nestboxes (C) and study sites (D). Elevation data points are represented by the x-axis rug in A. Each fitted line in C represents an extrapolated trend from a single nestbox. The effect of elevation on fledging success was non-significant (p=0.17), while the effect of clutch initiation date was significant (p=0.045). Further, the model found significantly different random slopes among nestboxes (p=0.01), random intercepts among study sites (p=0.01) and both among years (p=<0.001).

Site and season-specific mean daily temperature was a significant predictor of fledging success (Figure 6) even while controlling for elevation and clutch initiation date, with the inclusion of temperature improving model fit (ΔAIC = 6.1). However, there was no significant interaction with clutch initiation date. No other environmental covariates significantly predicted fledgling numbers (Table 5) or improved model fit.

Table 5: Generalised Additive Model (GAM) of the nonlinear effects of clutch initiation date, site and season specific mean daily temperature, nestbox elevation and tensor interactions between the latter two and the former on the number of successful fledgings in breeding attempts of a population of Parids in the French Pyrenees between 2013-2019. The model also allowed for random intercepts and slopes among individual nestboxes, study sites and years. The 'e.d.f' column indicates the degree of nonlinearity in the fixed effects, as well as the variability among subject-specific intercepts/slopes in the random effects.

Predictor Variable	e.d.f.	F	p-value
Clutch Initiation Date	3.2	2.1	0.1
Nestbox Elevation	4.6	1.7	0.14
Clutch Initiation Date * Nestbox Elevation	1	0.1	0.79
Site and Season Specific Mean Daily Temperature	2.4	6.5	0.001
Clutch Initiation Date * Site and Season Specific Mean Daily Temperature	2.8	1	0.45
Random Effects:			
Nestbox ID (Intercepts)	12.1	0.04	0.31
Nestbox ID (Slopes)	32.7	0.2	0.01
Site (Intercepts)	2	1.5	0.01
Site (Slopes)	1	0.4	0.18
Year (Intercepts)	0.9	0.2	0.4
Year (Slopes)	4.1	3.6	<0.001

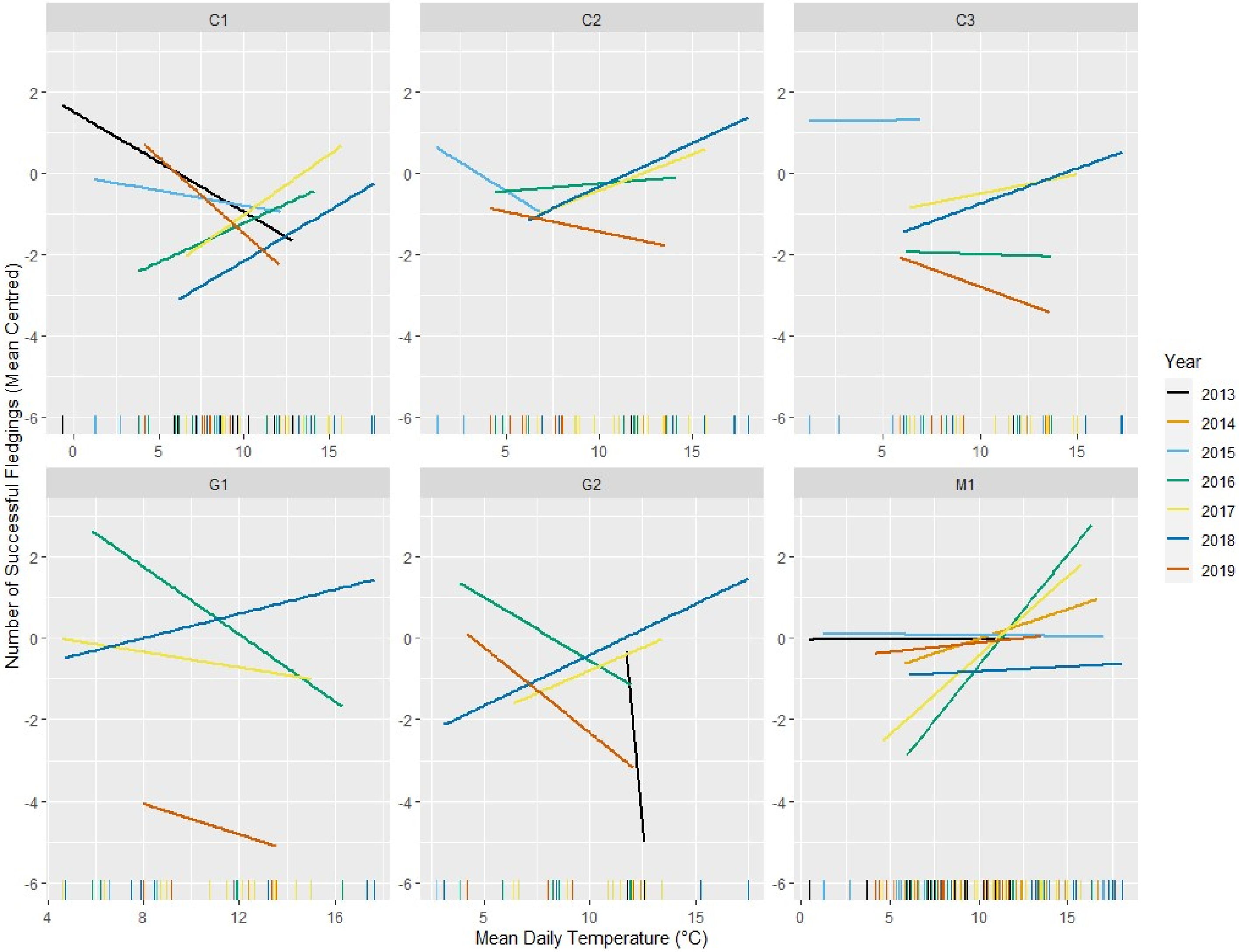

Figure 6: Numbers of successful fledgings in breeding attempts of wild Parid populations in the French Pyrenees between 2013-2019, significantly predicted by the mean of daily temperatures in each site and each year (p=0.001). Temperature data points are represented by the x-axis rugs. Where a fitted line does not appear for a given year in a given site, this is due to a lack of temperature data from that site in that year.

Models were also fitted to data from which nests where no young were fledged was omitted. This provided largely similar results, but the variation in the slope of the relationship of fledgling number and clutch initiation date was lower among sites, years and especially nestboxes (Tables S2 & S3; Figures S1 & S2).

3.5: Discussion

My analyses found significant spatial autocorrelation in clutch initiation dates, but not fledging numbers and these two variables had a nonlinear negative relationship. I consequently predicted that this relationship would vary at different spatiotemporal scales, with variation among individual nestboxes being most prominent. This prediction was validated, though variation among study sites was limited. I found significantly variable slopes among nestboxes and years, both of which were explained by variation in rate of nest failure. I also found significantly variable intercepts among sites and years; the latter partly explained by ambient temperature variation. Temperature also significantly predicted fledging success even when controlling for elevation which, contrary to my predictions, displayed little association with clutch initiation date or fledging success. Further, I found no evidence of local vegetation explaining variation in the phenology-success relationship at the nestbox level, and in general there was little evidence of spatial variation in biotic factors predicting phenology selection gradients.

It is important to view my findings through the lens of the first result, that spatial autocorrelation was present in clutch initiations but not fledging. If clutch initiation dates are non-randomly distributed in the study sites, but this is not linked directly to fitness outcomes, why are spatially proximate lay dates significantly more likely to be similar? Non-random spatial variation in lay dates has previously been linked to environmental factors, such as oak condition (Cole, Regan & Sheldon 2021) and tree budburst phenology (Hinks *et al* 2015). In these cases, these are spatially variable cues for prey abundance peaks, which may consequently drive phenology variation. However, studies testing for spatially distributed fitness outcomes as a consequence of such interactions are vanishingly rare (but see Gienapp & Bregnballe 2012 & Gordo *et al* 2013). Since none of the environmental covariates showed significant interactions with clutch initiation date on fledging success, spatial autocorrelation in phenology is unlikely to reflect occupancy of optimal breeding habitat. This population is comprised of territorial individuals, and thus many will not breed in an 'ideal' habitat (Christman 2001). The rest of my findings on the phenology-success relationship must therefore be interpreted in the context that the spatial distributions of phenology and fitness are explicit from one another. Therefore, the negative relationship observed between phenology and fledging success for this population as a whole may not be representative of many individual habitats. I further reinforced my prediction of strong variation among nestboxes, as the link between phenological strategy and its fitness consequences is expected to show strong spatial heterogeneity.

However, it is inappropriate to suggest that this autocorrelation is entirely divorced from fitness consequences. While it is true that I observed higher reproductive fitness in early breeders, both the earliest and latest breeding attempts diverge nonlinearly from this trend. This indicates that early breeding is not a wholly reliable indicator of high reproductive fitness. Individual female fitness has a significant role in driving the increased success of early phenological strategies (Sydeman & Eddy 1995). However, the nonlinear relationship I observed suggests that earlier phenology and increased reproductive fitness are not absolutely consecutive. As such, the lack of spatial autocorrelation in fledging success may be due to differences in fitness of individual early breeders. If an environmental cue stimulates early breeding, it is unlikely that all local breeders are: a) equally well-equipped to meet the associated physiological demands of egg production (Nager, Ruegger & Van Noordwijk 1997) and incubation (Drent, Fox & Stahl 2006); and b) equally sensitive to such cues (Thackeray *et al* 2016). Therefore, in areas dominated by early breeders (giving rise to autocorrelation in phenology), lower quality individuals may still breed early. Findings that insectivorous passerines adjust laying date in response to density of competitors (Ahola *et al* 2012, Møller *et al* 2018) further support this notion. For some individuals, the costs of early breeding may be outweighed by the fitness consequences of being outcompeted by higher quality females better equipped to pay those costs.

Variable fitness outcomes for similarly timed breeding attempts could constitute evidence of scale dependent effects (whereby some ecological factor(s) are more influential at a particular spatiotemporal scale, Frederiksen *et al* 2004) on the success of phenological strategy. I found such evidence at the nestbox level. I observed significant variability in fitness outcomes for early and late breeders, with an overall negative trend between phenology and fledging success. This is important evidence that optimisation of phenological strategy may be driven by territory-level optima within populations. Fine-scale variation in the effect of phenology on success may relax selective pressure on individuals with lower phenotypic plasticity (Bonamour *et al* 2019) and/or sensitivity to phenologically important environmental cues (Thackeray *et al* 2016), enabling some maintenance of reproductive fitness. Directional selection for early laying therefore does not preclude individuals or habitats with optima different from the population mean. I provide evidence of fine-scale maintenance of phenology variation, as scale dependent mechanisms may be acting within this population as a buffer against the selective pressure exerted by climate-driven mismatch (Reed *et al* 2013, Visser *et al* 2021).

However, nestbox-level variation in the slope of phenology on fledging success was non-significant when nest failures were removed from the model. Slopes among nestboxes were most variable at the extremes of the distribution, suggesting nest failure was most prominent in the earliest and latest breeding attempts. An elevated risk of nest failure in these attempts may provide an explanation for a prolonged disparity between the population-level phenology mean and optima. For early breeders increased risk of nest predation (Borgmann, Conway & Morrison 2013), due to reduced vegetation cover for example (Eggers, Griesser & Ekman 2008), could explain this failure rate. Therefore, my observations of variable success in early breeding attempts could be indicative of opposing selective forces operating at fine spatial scales. If fine-scale variation in nest failure leads to a decoupling of directional selection from population-level response, this could explain what has been previously described as ‘evolutionary stasis’ in avian lay dates (Bonamour *et al* 2017). Response to selection for early breeding in some populations is weaker than predicted (Merilä, Sheldon & Kruuk 2001, Pujol *et al* 2018), which may be an evolutionary consequence of diverse selection gradients within populations (De Villemereuil 2020). I build upon such hypotheses here by demonstrating that variation in phenology could be maintained by stabilising, scale dependent effects of nest failure risk occurring across space within populations.

Nest failures also explained significant interannual variation in the slope of the phenology-success relationship. Further, significantly different intercepts among years were non-significant when controlling for the effect of site and season specific mean ambient temperature. Years with the steepest decline in fledging success over the course of the season (e.g., 2017) were warm with relatively little variation, while colder temperatures in 2015 were associated with a weaker decline (Figures S3 & S4). Extreme weather variation at fine temporal scales is an established driver of avian phenological strategy (Glądalski *et al* 2016, Regan & Sheldon 2023). Considering nest failure's role in interannual variation, a phenological mechanism driven extreme abiotic variation is plausible, leaving little room for plastic responses (Reed *et al* 2010). Contrary to my predictions however, I did not find evidence of a spatial temperature effect. Elevation did not interact with clutch initiation date or temperature. Aspects of forest structure can shape variation in the rate of warming at finer spatial scales (De Frenne *et al* 2021, De Pauw *et al* 2022), potentially decoupling the association between elevation and temperature. Therefore, the effect of temperature on fitness may be independent of phenology. The passage of time is only evolutionarily meaningful when important environmental cues are temporally correlated (Visser 2008). These birds may therefore be synchronous with optimal temperatures that occur variably at fine spatiotemporal scales. It is unclear however, whether scale dependent temperature effects are widely responsible for mitigating response to mismatch.

Overall, the study has found that simultaneous analyses of multiple scales of variation can effectively highlight evidence of spatiotemporal variation in selection for early breeding. Variable rates of nest failure in similarly timed breeding attempts could contribute to maintenance of phenology variation even under perceived directional selection for early breeding. However, evidence for direct environmental effects on the relationship between phenology and breeding success was limited. Future study should aim to extricate the effects of individual-level factors in maintaining phenology variation. Frameworks such as ours provide an ecologically relevant null model from which to incorporate individual variation, as evidenced by my nestbox-level analyses. I have shown multiscale modelling to be a useful resource in uncovering the ecological mechanisms through which phenology variation, and thus mismatch, persists. Such methods may be essential for formulating projections of how climate change will continue to shape seasonal breeding ecology in the wild.

Chapter 4: General Discussion

4.1: Identifying Variation in Phenology and Fitness

Phenological mismatch does not consistently elicit the expected evolutionary response. Why are some populations evidently less vulnerable to the demographic consequences phenological mismatch than others? It is a long-established notion that environmental heterogeneity has a significant role in maintaining phenology variation (Visser *et al* 2015). Even so, substantive evidence of such ecological mechanisms for variation in mismatch-driven selection remain scarce. My research has highlighted multiple potential reasons for the longevity of this knowledge gap.

In Chapter 2, my analyses of spatial variation in and environmental predictors of successful fledging numbers provided a key outcome of this thesis. The significant, negative association between phenology and breeding success was dependent on canopy density, even when no environmental variables directly predicted either clutch initiation date or fledging numbers. This result ultimately constitutes evidence of environmentally-driven spatial variation in selection for early breeding, as different habitats displayed different selection gradients. More broadly my findings here show that, to elucidate the role of the environment in maintaining phenology variation, the shape of the phenology-success relationship is our variable of primary interest. I did not find any direct environmental effects on either clutch initiation date or fledging numbers, but this interaction is a notable example of indirect fitness consequences of environmental variation.

Insufficient understanding of the ecological mechanisms maintaining phenology variation has been attributed to a lack of both trophic and spatiotemporal scope

(Thackeray 2016). My first set of findings indicate the importance of the latter, as investigating the effects of fine-scale spatiotemporal heterogeneity provided evidence of variable selection gradients. Phenology research has typically been focused on variation among populations with coarse-scale abiotic differences in temperature (Cresswell & Mccleery 2003, Solonen and Hildén 2014). Building on this, I have focused on the role of within-population variation, down to the level of individual habitats. Future phenology research would benefit from a holistic spatiotemporal approach, incorporating multiple scales of variation. In conjunction with analysing the relationship between phenology and breeding success, rather than each characteristic individually, we can more precisely identify potential candidates for ecological mechanisms maintaining phenology variation and thus mismatch.

4.2: Scale Dependent Selection on Phenology

The utility of multiscale analyses is twofold, however. Not only can we observe within and among-population variation simultaneously, but also test for scale dependence (i.e., ecological mechanisms operating at specific spatiotemporal resolutions). Future study may therefore uncover ecological mechanisms in phenology through multiscale analyses, and this is exemplified by Chapter 3. In highlighting significant spatiotemporal variation in selection for early breeding occurring at multiple scales, I was able to determine that interannual variation in the relationship between clutch initiation date and fledging numbers was partly explained by local temperatures, even when controlling for elevation. Spatiotemporally complex warming patterns may alter the strength and shape of selection for some breeders even among consecutive breeding seasons. Therefore, we can surmise through multiscale analyses that directional selection for early breeding at the population level can reasonably coexist with phenology variation within populations.

One scale of variation not addressed in my analyses is that between individual birds, particularly females. Key questions remain regarding selection for early breeding at the individual level (Van de Pol & Wright 2009, Frigerio *et al* 2021). Specifically, do earlier breeders attain higher reproductive fitness, or do higher quality individuals breed earlier? We must disentangle whether the negative association between phenology and fitness is driven by high quality individuals who can pay the costs of early breeding (Sergio *et al* 2007) versus early breeders maximising benefit from their breeding environment prior to seasonal deterioration (Perrins 1970). Though my dataset was not fully equipped to tackle such questions, they remain a vital consideration moving forward if we are to gain a proximate understanding of phenology variation maintenance.

4.3: Concluding Remarks

The research presented here is provides important evolutionary and ecological conclusions that develop our understanding of key proximate challenges in phenology and life history research. Further, I set out how further study can quantitatively tackle some of these challenges. A major aspect of my work is the focus on variation within populations which, whether considered apart from or alongside population-level patterns, has been key to elucidating that environmental effects on selection for early breeding can be indirect and highly heterogeneous in both space and time. As such, if we are to understand and eventually predict how climate change and associated mismatches will impact wild populations, incorporating the variable relationship between phenology and success into multiscale frameworks is key.

Appendices

Table S1: Boundaries of six nestbox study sites located across the Ariége region of the French Pyrenees, as well as the locations of associated thermologgers from which site-specific temperature data was recorded.

Site	Longitude	Latitude	Elevation Range (m)	Thermologger Coordinates	Thermologger Elevation (m)
C1	1.04122-1.04786°N	42.9339-42.9409°E	555-630	1.04224°N, 42.93394°E	604
C2	1.04823-1.05415°N	42.9308-42.9328°E	702-774	1.05398°N, 42.92444°E	847
C3	1.0532-1.06692°N	42.9161-42.926°E	818-1108	1.06162°N, 42.91706°E	1110
G1	0.9025-0.92043°N	42.9478-42.9526°E	971-1129	0.90218°N, 42.95363°E	1193
G2	0.91655-0.91802°N	42.9417-42.9458°E	957-1034	0.91688°N, 42.94706°E	1002
M1	1.08731-1.09555°N	42.965-42.9727°E	448-593	1.0939°N, 42.96865°E	565

Table S2: Generalised Additive Model (GAM) of the nonlinear effects of clutch initiation date, nestbox elevation and a tensor interaction between the two on the number of fledgings in successful breeding attempts (at least 1 chick fledged) of a population of Parids in the French Pyrenees between 2013-2019. The model also allowed for random intercepts and slopes among individual nestboxes, study sites and years. The ‘e.d.f’ column indicates the degree of nonlinearity in the fixed effects, as well as the variability among subject-specific intercepts/slopes in the random effects.

Predictor Variable	e.d.f.	F	p-value
Clutch Initiation Date	2.3	4.5	0.003
Nestbox Elevation	4.1	1.7	0.14
Clutch Initiation Date * Nestbox Elevation	1.5	0.7	0.56
Random Effects:			
Nestbox ID (Intercepts)	19.9	0.07	0.21
Nestbox ID (Slopes)	1.7	0.01	0.41
Site (Intercepts)	3	3.3	<0.001
Site (Slopes)	1.2×10^{-8}	<0.001	0.62
Year (Intercepts)	5.1	4.6	<0.001
Year (Slopes)	2.2	0.9	0.16

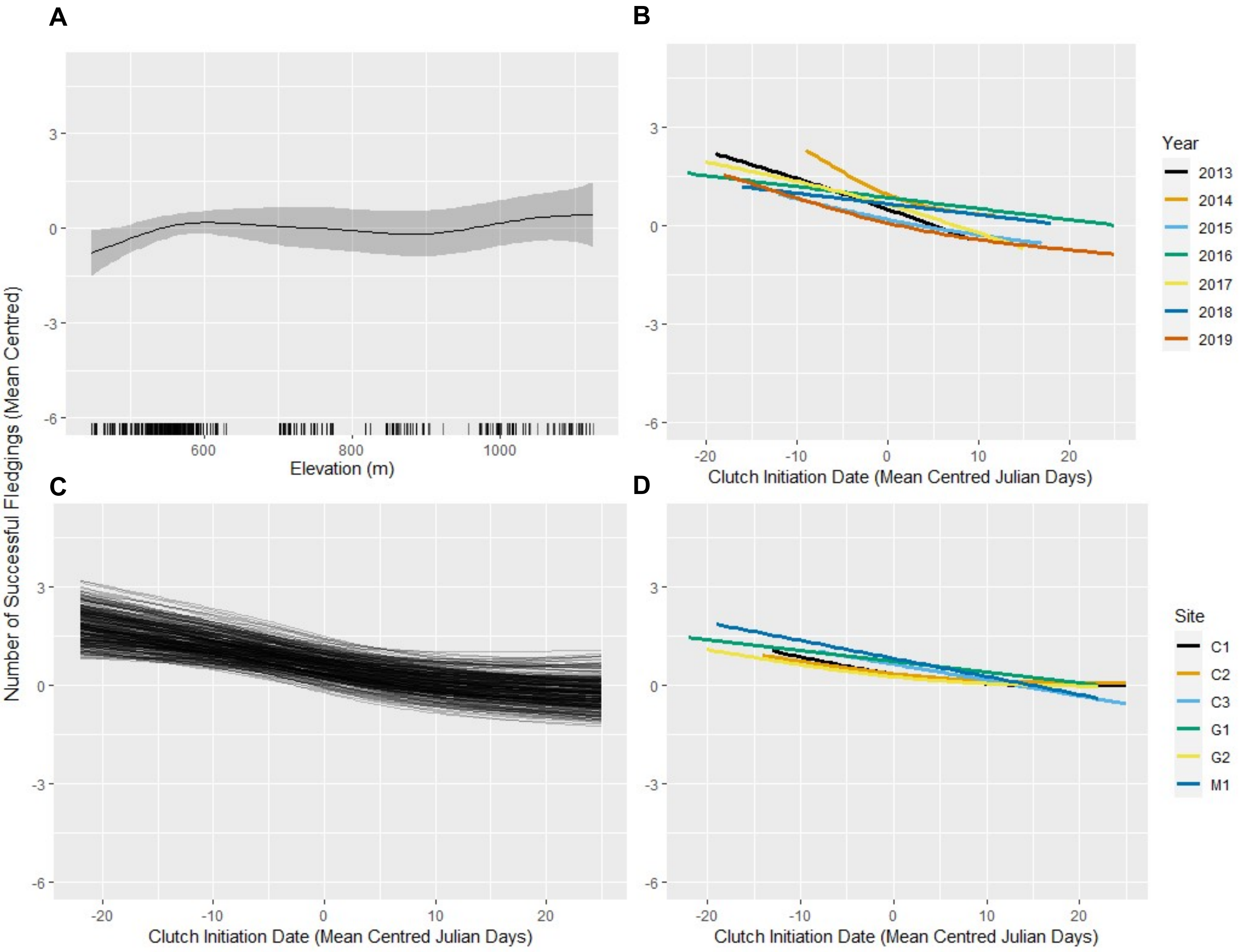

Figure S1: Fledgings of successful breeding attempts (at least 1 chick fledged) in wild Parid populations in the French Pyrenees between 2013-2019, as a nonlinear function of elevation (**A**) and clutch initiation date, with subject-specific relationships among individual years (**B**), nestboxes (**C**) and study sites (**D**). Elevation data points are represented by the x-axis rug in **A**. Each fitted line in **C** represents an extrapolated trend from a single nestbox. The effect of elevation on fledging success was non-significant (p=0.17), while the effect of clutch initiation date was significant (p=0.045). Further, the model found significantly different random slopes among nestboxes (p=0.01), random intercepts among study sites (p=0.01) and both among years (p=<0.001).

Table S3: Generalised Additive Model (GAM) of the nonlinear effects of clutch initiation date, site and season specific mean daily temperature, nestbox elevation and tensor interactions between the latter two and the former on the number of fledgings in successful breeding attempts (at least 1 chick fledged) of a population of Parids in the French Pyrenees between 2013-2019. The model also allowed for random intercepts and slopes among individual nestboxes, study sites and years. The ‘e.d.f’ column indicates the degree of nonlinearity in the fixed effects, as well as the variability among subject-specific intercepts/slopes in the random effects.

Predictor Variable	e.d.f.	F	p-value
Clutch Initiation Date	3.2	2.3	0.06
Nestbox Elevation	4.5	1.7	0.14
Clutch Initiation Date * Nestbox Elevation	1.4	0.5	0.68
Site and Season Specific Mean Daily Temperature	3.5	3.1	0.02
Clutch Initiation Date * Site and Season Specific Mean Daily Temperature	4.6	0.6	0.66
Random Effects:			
Nestbox ID (Intercepts)	25	0.1	0.15
Nestbox ID (Slopes)	2.2	0.01	0.39
Site (Intercepts)	3.2	3.6	<0.001
Site (Slopes)	6.4×10^{-8}	<0.001	0.63
Year (Intercepts)	1.9	0.4	0.23
Year (Slopes)	2.5	0.9	0.08

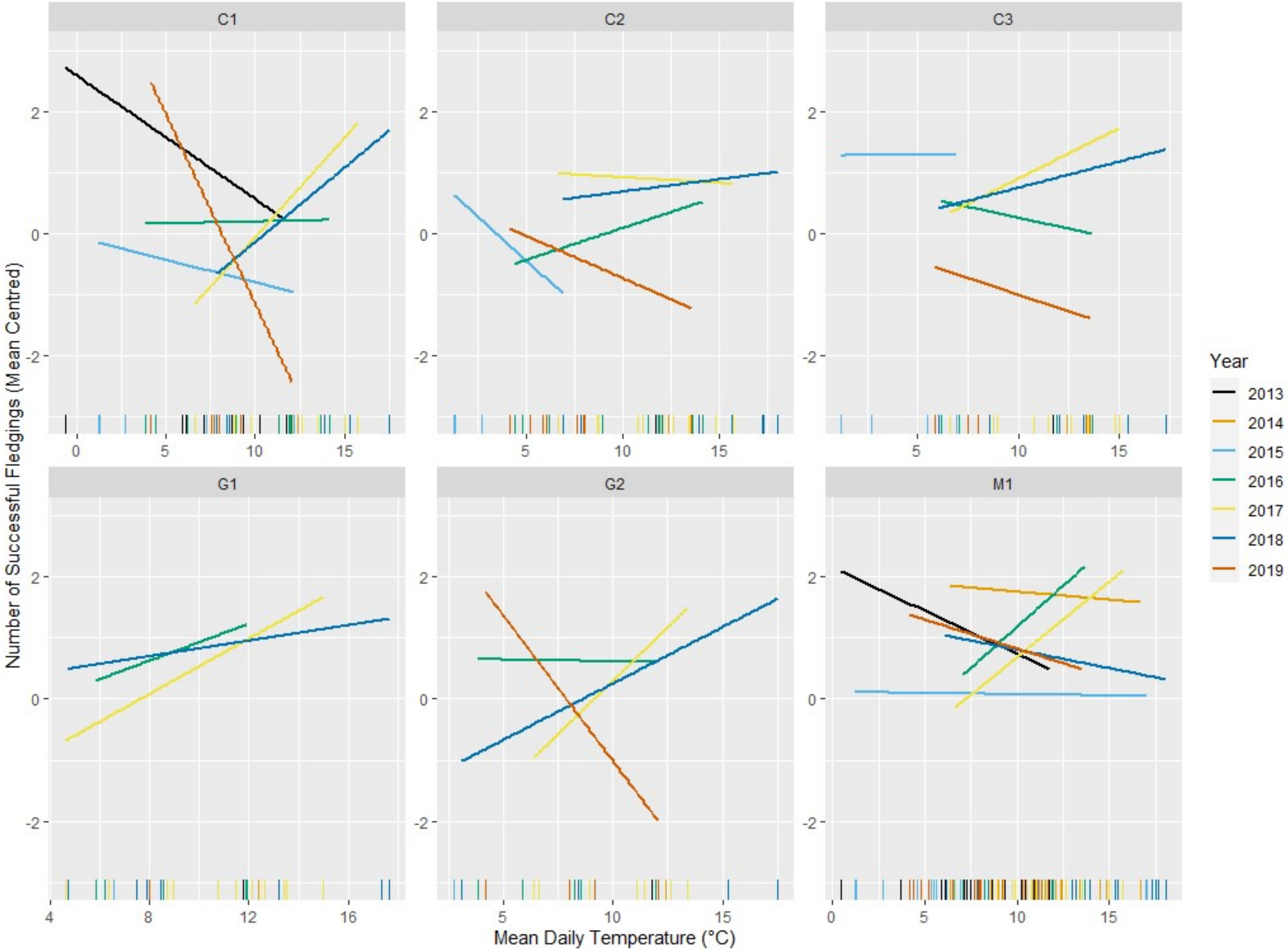

Figure S2: Numbers of successful fledgings in successful breeding attempts of wild Parid populations in the French Pyrenees between 2013-2019, significantly predicted by the mean of daily temperatures in each site and each year ($p=0.02$). Temperature data points are represented by the x-axis rugs. Where a fitted line does not appear for a given year in a given site, this is due to a lack of temperature data from that site in that year.

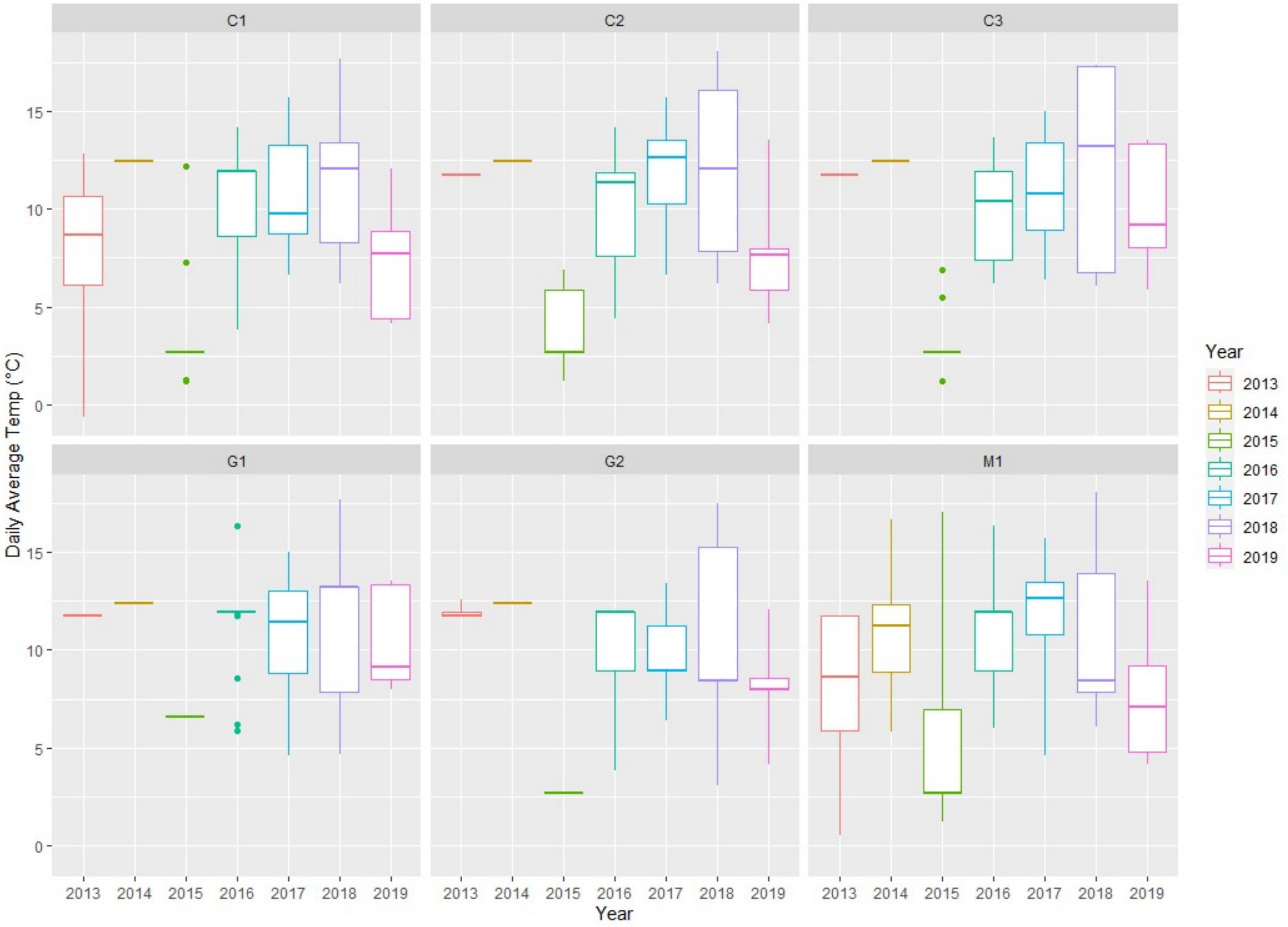

Figure S3: Daily mean temperatures (± 1 S.E.) observed in a system of nestboxes in the French Pyrenees between 2013-2019. The temperature values are drawn from the observed incubation and rearing period (late March - June) of great (*Parus major*) and blue tits (*Cyanistes caeruleus*) across six study sites. These sites occupied a range of elevational gradients, and each site was associated with a single temperature logger (Table S1). Sites with little variation and/or numerous outliers indicate that large amounts of data were missing for that year, and so a year-specific mean value has been imputed for missing records.

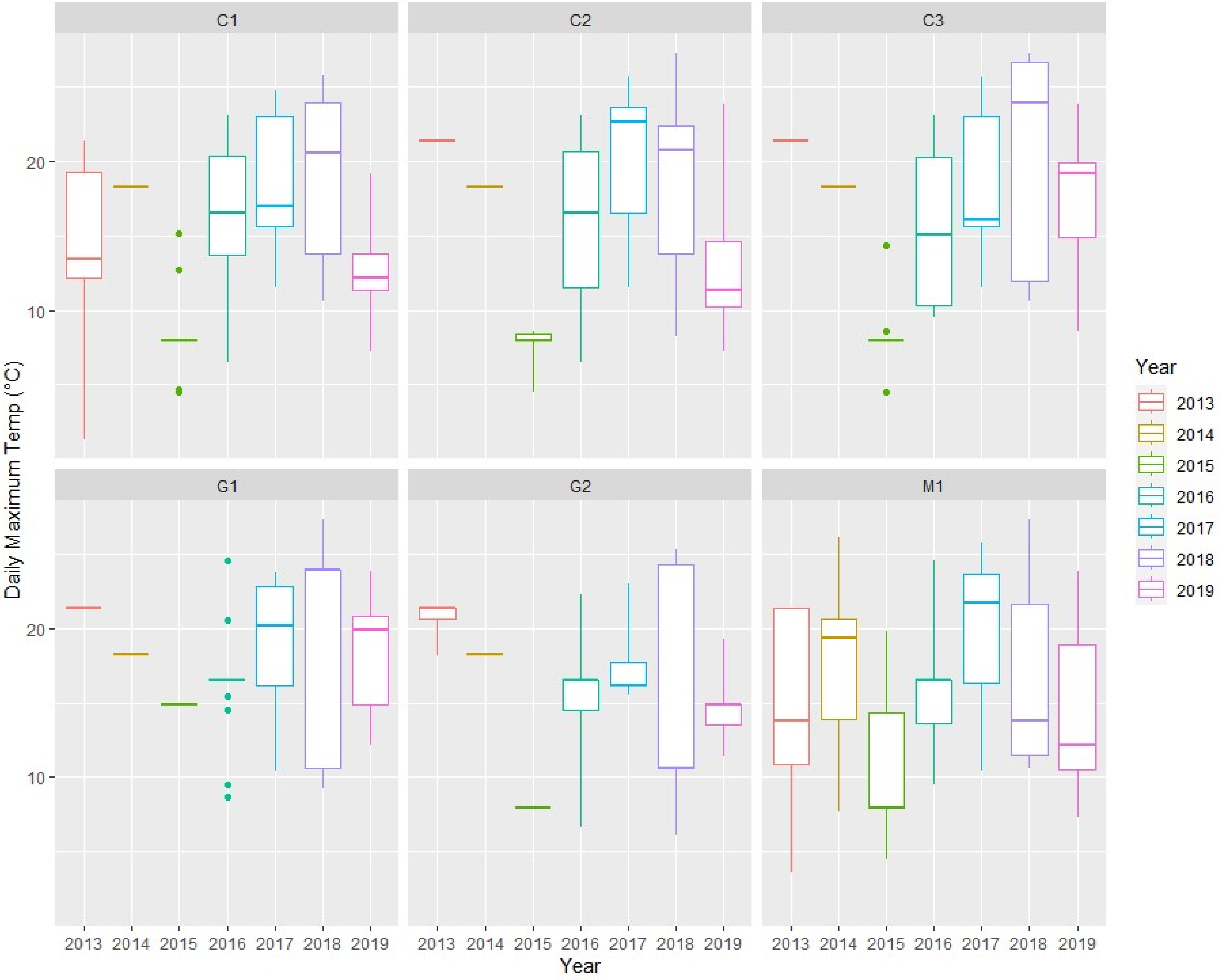

Figure S4: Daily maximum temperatures (± 1 S.E.) observed in a system of nestboxes in the French Pyrenees between 2013-2019. The temperature values are drawn from the observed incubation and rearing period (late March - June) of great (*Parus major*) and blue tits (*Cyanistes caeruleus*) across six study sites. These sites occupied a range of elevational gradients, and each site was associated with a single temperature logger (Table S1). Sites with little variation and/or numerous outliers indicate that large amounts of data were missing for that site in that year, and so a year-specific mean value has been imputed for missing records.

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