Territory-level temperature influences settlement decisions, breeding phenology and productivity in three forest passerine birds

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Abstract

1. Temperature is a key determinant of breeding phenology in temperate zone birds, with increasing spring temperature across years or large geographic gradients known to advance timing of breeding. It is less well understood how localised, territory-scale temperature variations effect territory occupation, breeding phenology and productivity, primarily due to a lack of fine-scale temperature data.

2. We examine the influence of temperature at the territory-scale, and its interaction with mean annual temperature, on territory selection and breeding outcomes of three co-occurring forest passerine bird species; two long-distance migrants (pied flycatcher *Ficedula hypoleuca* and wood warbler *Phylloscopus sibilatrix*) and one resident (blue tit *Cyanistes caeruleus*); all species dependent on seasonal invertebrate food for reproductive success.

3. Spring temperature was recorded at intersections of a 150m^2 grid encompassing 417 ha of forest in South-West England 2015-18, with temperature across the study area interpolated from this point data. Breeding phenology and productivity from 672 nests across the three species was quantified, and general linear models used to examine the influence of territory temperature on breeding phenology and productivity.

4. All three species exhibited significant trends in reproductive traits associated with territory-scale temperature. Pied flycatchers settled in cooler territories first, where they raised more fledglings. Blue tits laid larger clutches in warmer territories in warm years and always laid earlier at warmer territories irrespective of annual mean temperature. Contrastingly, pied flycatcher and wood warbler breeding phenology was earlier at warmer territories in cool years and cooler territories in warm years, with wood warbler clutch size responding similarly to this interaction. Greater previous

breeding experience and increased territory quality also predicted earlier breeding phenology and higher productivity for pied flycatchers.

5. Our results show that local-scale spatial variation in temperature is associated with spatial variation in territory occupancy, breeding phenology and productivity in forest passerines. We suggest that the two migrant species may be best synchronised with their prey requirements in cooler years at a local population level while resident blue tits match local phenology at lower trophic levels across all years, potentially advantageous under warmer predicted climate change scenarios.

Introduction

Temperature plays a key role in determining the timing of breeding of temperate zone bird species (Crick & Sparks, 1999; Dunn & Møller, 2013). In warmer years, and at generally warmer locations, breeding phenology occurs earlier, and under recent climate change average breeding phenology has advanced over time for many species (Both et al., 2004; McLean, Lawson, Leech, & van de Pol, 2016; Parmesan & Yohe, 2003; Phillimore, Leech, Pearce-Higgins, & Hadfield, 2016). An increase of 1°C has been demonstrated to advance breeding phenology by 3-5 days in a range of birds (McLean et al., 2016; Phillimore et al., 2016; Socolar, Epanchin, Beissinger, & Tingley, 2017). Functionally, this trend to breed earlier is to maintain temporal synchrony with key prey resources (Burgess et al., 2018). Prey synchrony is particularly important for single-brooded insectivorous birds (e.g. tits *Paridae*, flycatchers *Ficedulidae*, leaf warblers *Phylloscopidae*) breeding in highly seasonal environments such as deciduous forests (Burgess et al., 2018; Visser, van Noordwijk, Tinbergen, & Lessells, 1998). Asynchrony with this prey peak can reduce fledgling number and quality, negatively impacting fitness, with such asynchrony termed trophic mismatch (Both, Bouwhuis, Lessells, & Visser, 2006; Miller-Rushing, Høye, Inouye, & Post, 2010).

While the effect of average temperature on breeding phenology across years and geographic gradients is well established, effects of subtler localised intra-annual temperature variation is less understood. This is primarily due to a lack of studies collecting fine-scale within-site temperature data alongside bird breeding data, despite this being the scale relevant to individual birds (Hinks et al., 2015). It is therefore unknown how territory settlement, breeding phenology and breeding outcome are influenced by territory-scale temperature. It has been shown that within-nest temperature can modify breeding phenology (Simmonds, Sheldon, Coulson, & Cole, 2017), and that fine-scale temperature is a strong predictor of localised species distribution (Frey, Hadley, & Betts, 2016). Phenological timings that may be influenced by territory-scale temperature variation include the date of arrival, date of nest building initiation and first egg laying date, while breeding parameters that may be sensitive include clutch size and productivity. In the same breeding locations resident species with similar ecological requirements to long-distance migrants often commence breeding earlier (Källander et al., 2017; Samplonius et al., 2018). With a warming spring climate this difference can become more divergent (Haest, Hüppop, & Bairlein, 2020; Samplonius et al., 2018) suggesting fine-scale temperature may determine breeding onset differently between migrants and residents as well as differing patterns of territory occupancy at a local scale.

Understanding the influence of temperature on territory occupation, breeding phenology and outcome could indicate how optimally timed a population is. As tree and caterpillar phenology is well synchronised with fine-scale temperature (Buse, Dury, Woodburn, Perrins, & Good, 1999; van Asch, Salis, Holleman, van Lith, & Visser, 2012), locally warmer territories will show advanced phenology in lower trophic levels than cool territories (Cole, Long, Zelazowski, Szulkin, & Sheldon, 2015; Hinks et al., 2015). If breeding always commences earlier in warmer territories this could indicate successful thermal niche tracking, where a well-timed population is able to track the local phenology of lower trophic levels (Dobrowski, 2011; Socolar et al., 2017). However, if within a

woodland breeding occurred earlier in cooler territories relative to warmer territories with earlier prey phenology, then the average population consequence would be later than optimal timing as late breeders (either through late arrival, lower quality or competition) will be forced to occupy the remaining warmer territories with the greatest levels of mismatch. If breeding commences earlier in warmer territories in cool years, and in cooler territories in warm years, this would suggest that average population timing is optimal in cool years but suboptimal (late) in warm years.

Examining a population's breeding phenology across a temperature gradient requires few assumptions to be made about precise optimal dates or specific prey items compared to studies focussed on dates. Optimal synchrony between bird species breeding in the same locality may vary due to different prey requirements and developmental needs of young. The ephemeral invertebrate peak in deciduous woodland that several single-brooded passerine species are commonly assumed to depend on are moth caterpillars (Burgess et al., 2018; Visser et al., 1998). However, the most well studied species of this system (blue tit *Cyanistes caeruleus*, great tit *Parus major* and *Ficedula* flycatchers) breed at overlapping but different times to one another (Burgess et al., 2018; Samplonius et al., 2018), and so within any single year and locality breeding timing across these bird species will encompass peaks of different prey species at different nestling developmental stages. Timing breeding to match peak demands of nestlings to the caterpillar peak can have little impact on fledging mass or productivity in some species (Mallord et al., 2017; Maziarz & Wesołowski, 2010; Wesołowski & Neubauer, 2017), while it does in others (Both, Bijlsma, & Visser, 2005; Visser et al., 1998), suggesting differences in prey requirements. Whether breeding is timed to the same or different optima, a preference for breeding in cooler territories first would indicate local population-level mistiming. It would also suggest that the birds were adjusting territory selection and breeding phenology due to the local phenological stage (Hinks et al., 2015; Hušek, Lampe, & Slagsvold, 2014; Shutt et al., 2019), in addition to purely relying on temperature as a causal cue of breeding time (Caro, Schaper, Hut, Ball, & Visser, 2013; Verhagen, Tomotani, Gienapp, & Visser, 2020).

In this study, we investigate how territory-scale temperature variation over four years within a 417ha woodland affects territory settlement, breeding phenology, clutch size and productivity of three single-brooded co-occurring insectivorous woodland passerine bird species: pied flycatcher *Ficedula hypoleuca*, blue tit and wood warbler *Phylloscopus sibilatrix*. All three are similarly sized, primarily single-brooded, spring-breeding species. We hypothesise that as these migrants tend to breed later than residents (Samplonius et al., 2018; Slagsvold, 1976), and later breeding in warm years increases mismatching (Burgess et al., 2018), that in warm years migratory species will be less optimally timed compared to resident species, selecting cooler territories first and showing lower productivity in warm territories.

Materials and methods

This study was conducted at East Dartmoor National Nature Reserve in Devon, South-West England, UK (50.60°N -3.73°E) over four breeding seasons 2015-2018. Habitat across the reserve is relatively uniform and dominated by sessile oak *Quercus petraea* with a European holly *Ilex aquifolium,* and rowan *Sorbus aucuparia* understory and a European bilberry *Vaccinium myrtillus* field layer. The study area extends linearly approximately 5 km along a steep-sided river valley in the north, with a 150ha woodland containing two shallow stream valleys in the south, together resulting in slopes at different aspects and an altitudinal range of 60-300m.

Breeding bird data

Throughout the study area, 309 wooden nestboxes with a 32 mm entrance hole were available each year and monitored annually throughout the bird breeding season April-June. Nestbox checks were made at least weekly and more frequently at some nest stages to determine species occupancy,

date of first nesting material, date of first egg laying, completed clutch size and the number of successful fledglings (productivity) for each breeding attempt. Date of first nesting material was taken as the date of the first nest check that found fresh nesting material for nests that ultimately had a clutch of eggs laid in, with nests found half complete (cup shape evident) or more over the maximum 7 days inspection interval assigned the mid-point between the two visits. All species were assumed to lay one egg per day (Lundberg & Alatalo, 2010; Perrins, 1979), with the first egg date back-calculated from incomplete clutches recorded at nest inspections. Clutch size records the total number of eggs laid that were incubated, and the number fledged was the number alive at the last visit pre-fledging minus the number found dead at the first visit post-fledging.

The date of spring arrival by territorial male pied flycatchers to nestboxes was also recorded from the first week in April. Territorial activity, such as singing, alarm calling and inspection of nestboxes, was observed on alternate mornings, and the presence of, colour and position of any rings and variable plumage characteristics such as forehead patch size were recorded. These were cross-referenced against males captured at the same nestboxes later in the breeding season. Male arrival date to a territory was taken as the mid-point between the survey prior to the first observation of a male and the survey when first observed. This is a common method used for pied flycatchers (Bell, Harouchi, Hewson, & Burgess, 2017; Potti, Camacho, Canal, & Martinez-Padilla, 2018) and its accuracy has been verified with geolocator tracking data (Both, Bijlsma, & Ouwehand, 2016). Nearly all breeding male and female pied flycatchers were captured annually and are marked with a unique metal numbered ring upon first capture, enabling the frequency of breeding over an individuals' lifetime to be determined, including for years prior to 2014 using data collected prior to the present study. Between 2015-2018, 320 pied flycatcher and 315 blue tit nesting attempts were monitored.

Wood warbler nests were also monitored throughout the breeding seasons 2015-2018. Wood warblers are ground nesting and were located by observing parental behaviour, with the location of

175 each nest determined by GPS and visited every 3-4 days. First egg-laying dates were determined
176 from visits during egg laying assuming that one egg is laid per day. A total of 37 wood warbler nests
177 were monitored during the study period.
178
179 **Temperature data**
180
181 Between 2015-2018 96 temperature dataloggers (Thermachron iButton DS1921G) were placed
182 throughout the study area at each intersection of a 150m grid. Each was attached to a tree 1.5m
183 above ground level in a waterproof standard sized plastic container with three drilled holes to
184 provide air circulation (Shutt et al., 2019). Temperature dataloggers recorded temperature hourly to
185 an accuracy of 0.5°C. Additionally, 22 higher-sensitivity temperature dataloggers (Thermachron
186 iButton DS1922L) that record temperature to an accuracy of 0.0625°C were attached alongside 22 of
187 the lower resolution dataloggers on the same trees with the same aspect in a non-random way to
188 maximise coverage of the entire study area.
189
190 We used temperatures recorded between Julian days 97 and 132, which encapsulates the spring
191 temperature sensitivity window previously estimated for blue tit and pied flycatcher egg laying for
192 the study area (Samplonius et al., 2018). Data from temperature dataloggers with more than 16
193 missing hourly data points within the focal period within a year were discarded as incomplete (n=25,
194 from a total of 333). Additionally, data from temperature dataloggers recording at least one
195 measurement beyond the extreme credible temperature bounds within the focal period (<-8°C or
196 >35°C) were discarded for the year in question as unreliable or faulty (n=9). As all faulty dataloggers
197 were the higher sensitivity model, and data from high sensitivity dataloggers are not directly
198 comparable with data from low sensitivity dataloggers, the unaffected higher resolution datalogger
199 data were used to determine the accuracy of their paired low sensitivity datalogger only and were
200 excluded from all other analyses (n=56). Paired high sensitivity and low sensitivity dataloggers gave

very similar readings (interquartile range <0.2°C despite recording on different sensitivities with a possible correct error range of 0.25°C), whereas the variation across the entire study area was much higher (interquartile range >0.6°C in each year), providing confidence that local temperature differentials across the study area correspond to genuine local temperature variation rather than datalogger inaccuracy. Temperature means across the focal period were used and a total of 257 datalogger mean readings remained over the four-year period after this quality control (87 in 2015, 54 in 2016, 56 in 2017, and 60 in 2018).

All spatial analysis was conducted within R version 3.6.3 (R Core Team, 2018) using the raster, gstat and tmap libraries. The data from each remaining low sensitivity temperature datalogger within each year was then projected to its geographical location and temperature across the study area interpolated using inverse distance weighting (Gräler, Pebesma, & Heuvelink, 2016) raised to the power two. The inverse distance squared weighting power was decided upon after investigating the ability of the data to predict known temperature points in a 'leave one out' validation routine of powers between one and four (root-mean-squared-error of P1 = 0.467, P2 = 0.447, P3 = 0.453, P4 = 0.461). Temperature differentials for each nestbox and wood warbler nest location were then extracted from the resultant heatmap raster (Gräler et al., 2016). On inspection, the heatmap differential rasters for each year were highly consistent in both spatial pattern and variance and so an interannual differential mean was used which we term the local temperature differential. This allows determination of whether territories were in a relatively cool or warm area within the overall study area and afforded greater differential consistency as not every temperature datalogger position recorded data in all years.

Statistical analysis

226 General linear models (GLM) were constructed to assess the effects of local temperature differences
227 on measures of breeding success for this system. Not all breeding parameters were assessed as a
228 response variable for each of the three bird species due to lack of data. Five breeding parameters
229 were used: date of male arrival to breeding territory and date of nest building initiation (both pied
230 flycatcher only), date of first egg laying, clutch size and productivity (number of fledglings) (all three
231 species). All dates are reported as April days (days from the 1st April, e.g. 25th April = day 25). For
232 wood warblers, as nests were often found discovered after eggs had been laid, if date of first egg
233 laying was not recorded but date of hatching was, first egg date was inferred by subtracting the
234 mean number of days (n=18) between first egg date and hatching date across those nests where
235 both were recorded, from hatching date where first egg date was not recorded. All analyses were
236 conducted in R version 3.6.3 (R Core Team, 2018).
237
238 Response variables were tested by Bayesian GLMs (Hadfield, 2010) with annual mean temperature,
239 local temperature differential, territory quality, previous breeding experience and the interaction
240 between annual and local temperature as fixed predictor variables. Continuous predictor variables
241 were mean centred for ease of interpretation and model functioning (Schielzeth, 2010). Each model
242 was run for 100,000 iterations with the first 10,000 discarded as burn-in with a Gaussian error
243 structure, with both response data and model traces visually inspected to ensure the fit was
244 acceptable. Year was not included as a random predictor variable as it correlated perfectly with
245 annual mean temperature for each data point, however it was included in additional, unreported
246 models for each response to ensure its omission did not significantly influence results.
247
248 Territory quality was inferred from the proportion of years each nestbox had been occupied by
249 nesting pied flycatchers or blue tits out of the total number of years each nestbox was available
250 since 1980 and until 2018. Long-term nestbox/territory occupancy patterns have previously been
251 shown to provide a clear correlate of territory quality, with more frequently occupied territories of

higher quality (Potti et al., 2018; Sergio & Newton, 2003). We used the occupancy rate since 1980 as both nestbox number and bird population size had by this year stabilised after nest box provisioning started incrementally from 1955. Territory quality could not be included as a predictor variable for wood warbler as this species does not use nestboxes and therefore territories could not be ascribed long term occupancy rates. Individual breeding experience was defined as the number of years an individual had previously been captured breeding in the population. Previous breeding experience could not be included as a predictor variable for blue tit or wood warbler due to incomplete data on parental identity. For pied flycatcher date of arrival, male breeding experience was included as a fixed effect, whereas in all other models female breeding experience was used, as females build the nests, lay the eggs and provide the majority of parental care in pied flycatchers (Lundberg & Alatalo, 2010). Pairwise correlation between fixed effects was assessed and as all were <0.18 this suggested no issue with colinearity within the models, with the most significant correlation being that higher quality territories tended to have cooler local temperature differentials.

Results

Local spring temperature varied by around 2°C from the coldest to warmest areas across the study area with colder areas at the higher elevations of Yarner Wood in the south and Neadon Cleave in the north, and warmer areas at lower elevations along the River Bovey in Lustleigh Cleave (Fig 1). This pattern was spatially consistent across all four years. Variation in mean spring temperature between years was observed, with 2018 the warmest (mean = 10.7°C) and 2016 the coolest (mean = 9.2°C).

Male pied flycatchers returning from migration in spring occupied the coolest territories first, irrespective of the relative mean annual temperature, with our model predicting arrival to the coolest territories on 12th April and warmest territories on 20th April (Table 1, Fig 2a). There was also

an interaction effect of local temperature on the timing of nest building initiation; in cool years nests were initiated significantly earlier at warmer territories, with this pattern reversed in warm years with nests initiated earlier at cooler territories (Table 1, Fig 2b). This temperature effect on the timing of nest building did not translate into an effect on the timing of egg laying or clutch size (Table 1). Productivity varied by 1.7 chicks per nest attempt across the temperature gradient, with productivity higher at the coolest territories compared to the warmest territories (5.6:3.9 fledglings per attempt respectively) (Table 1, Fig 2c). This latter effect was strongest is cool years, while in warm years productivity was similar irrespective of the local temperature (Table 1, Fig 2d).

For resident blue tits, higher local temperatures predicted a significant advancement of five days in the timing of egg laying between the coolest and warmest territories (Table 1, Fig 2e). There was also an interaction effect of local temperature on clutch size, with cooler territories predicted to have substantially larger clutches in cool years, while in warm years warmer territories were predicted to have slightly larger clutches (Table 1, Fig 2f). There was no significant effect of local temperature on blue tit productivity, although the interaction effect was in the same direction as for clutch size (Table 1). In warm years, blue tits laid eggs earlier (-2.22 days/°C) and had higher productivity (+0.78 fledglings/°C) (Table 1).

There were significant effects of local temperature interactions on migratory wood warbler breeding parameters. In cooler years, eggs were predicted to be laid substantially earlier at warmer territories than cooler territories, whereas in warmer years the opposite was true, with eggs laid earlier at cooler territories (Table 1, Fig 2g). Wood warbler clutches were also significantly larger at cooler territories in warmer years, and at warmer territories in cooler years (Table 1, Fig 2h). There was no significant effect of local temperature on wood warbler productivity (Table 1).

303 Previous breeding experience also affected pied flycatcher breeding parameters. Males with more
304 experience arrived earlier (-0.81 days/year experience, Table 1, Fig 3a) and females with more
305 experience laid larger clutches (+0.17 eggs/year experience, Table 1, Fig 3b) earlier in the year (-0.93
306 days/year experience, Table 1, Fig 3C). In higher quality territories pied flycatchers also initiated
307 earlier nest building (21st April: 1st May, Table 1, Fig 3d) and egg laying (6th May: 12th May, Table 1,
308 Fig 3e) and produced more fledglings (3.9: 5.4 fledglings per attempt, Table 1, Fig 3f), with figures at
309 the two extremes of territory quality found in our study. Territory quality showed no significant
310 relationship with blue tit breeding parameters (Table 1).
311
312 **Discussion**
313
314 This study demonstrates multiple relationships resulting from territory-level spatial variation in
315 temperature to differences in territory occupancy, breeding phenology, clutch size and productivity
316 for three insectivorous woodland birds. The patterns show that within a 417ha woodland both
317 migratory and resident species either select breeding territories where territory temperature best
318 matches breeding phenology, with these locations differing between cold and warm years, and/or
319 show fitness benefits in relation to the temperature of the territory occupied. In cold years, when
320 vegetation and invertebrate phenology is expected to be latest (Burgess et al., 2018), pied flycatcher
321 nest building and wood warbler egg laying commenced earlier in warmer territories, with larger
322 clutch sizes for wood warbler and blue tit. In warm years, when vegetation and invertebrate
323 phenology is earlier (Burgess et al., 2018), cooler territories were preferred by the migratory
324 species', being associated with earlier nest building by pied flycatchers, and earlier egg laying and
325 larger clutch sizes in wood warblers. Territory-scale temperature also influenced pied flycatcher
326 productivity across years, with 1.7 more fledglings predicted per nest in the coolest territories
327 compared to the warmest. This pattern was driven by considerably higher productivity in cool

territories in cooler years, suggestive of a negative effect on productivity from trophic mismatch in relatively warmer territories in cool years.

Temperature impacts on breeding phenology

Male pied flycatchers returning from Africa settled in cooler territories first, with nest building also beginning first in cooler territories in warm years, with this pattern reversed in cold years. Our measure of arrival was only for males as these are more conspicuous, but our method of estimating nest building initiation is frequently used as a proxy for female arrival date (Potti & Montalvo, 1991; Visser et al., 2015) as pairing and nest building can commence on the day of female arrival (Potti & Montalvo, 1991). Making that assumption, our results suggest that both male and female pied flycatchers may partly base territory selection on territory temperature, with the territories selected first by the earliest arriving birds those most likely to have a better match with prey phenology. In warmer years migration timings may constrain earlier arrival (Both & Visser, 2001) with the implication that in warm years later arrivals are constrained to breed in the warmest territories and be more likely mismatched with prey. In cooler years the local population overall is therefore better phenologically matched.

Territory and female mate selection is well studied, with males establishing territories first and females selecting breeding territories held by males based on either habitat quality (Alatalo, Lundberg, & Glynn, 1986), or male traits (Sirkiä & Laaksonen, 2009). Territory choice can be further influenced by information obtained from heterospecifics, for example from cues related to occupancy and density patterns of resident species (Forsman, Hjernquist, Taipale, & Gustafsson, 2008) or inspecting multiple nest sites upon arrival (Schuett, Järvistö, Calhim, Velmala, & Laaksonen, 2017). Our study suggests fine-scale temperature is another key determinant of territory choice in pied flycatchers.

Egg laying date in our three study species is constrained by photoperiod (Caro, Lambrechts, Balthazart, & Perret, 2007; Lambrechts & Perret, 2000) and environmental factors (Shutt et al., 2019), and is strongly related to spring temperature at larger spatial scales (Both & Visser, 2001; Phillimore et al., 2016; Schaper, Rueda, Sharp, Dawson, & Visser, 2011), with laying starting later at cooler locations such as higher latitudes and elevations (Burgess et al., 2018; Sanz, 1998), but examination at local scales is rare. We found spatial variation in laying date with regards to local temperature for both wood warbler and blue tit. Wood warblers started egg laying substantially earlier at warmer territories in cooler years and cool territories in warmer years. Previous work on wood warblers showed a strong relationship between the temperature of the pre-laying period and laying date at larger spatial scales, with earlier laying associated with higher pre-laying temperatures (Wesołowski & Maziarz, 2009). We find the same pattern at the territory scale in cool and average years, providing further support that temperature is a cue to wood warbler laying. However, in warm years the opposite pattern occurs, which may indicate phenological mismatch within the local population in warm years as later breeders are occupying the warmest (and thus most phenologically advanced) territories, possibly due to these being the only ones remaining once earlier breeders have occupied the better-matched, cooler territories.

Higher territory temperature linearly predicted earlier egg laying in resident blue tits, similar to that found across longer gradients of space and time but with a slightly shallower slope to other estimates (McLean et al., 2016; Phillimore et al., 2016). Our results are consistent with temperature being a direct cue for blue tit breeding phenology (Shutt et al., 2019; Verhagen et al., 2020; Visser, Holleman, & Caro, 2009) and that this cue applies at a very localised scale. No significant temperature relationship for lay date was found for pied flycatcher, suggesting temperature may not be a direct cue to egg laying in this species. Pied flycatcher egg laying date shows less spatial and inter-annual variation compared with arrival phenology (Nicolau et al., 2021), indicating that in years

with early arrival, individual birds can nest build well in advance of egg laying. Our results on the effects of territory scale temperature on breeding phenology suggest that warming springs may be more favourable to resident blue tits than migrant pied flycatchers and wood warblers at this locality.

Temperature impacts on clutch size

We found spatial variation related to temperature in clutch size for wood warbler and blue tit, but not for pied flycatcher. Wood warbler clutch size followed a similar pattern to the breeding phenology of this species with regards to local temperature, being larger at cool territories in warm years, and at warm territories in cool years, with clutch size therefore larger in territories selected earlier for breeding. The effect of territory temperature on clutch size may therefore help to explain why wood warbler clutch size declines seasonally (Grendelmeier, Arlettaz, Gerber, & Pasinelli, 2015). Although wood warblers do not time breeding to match caterpillar peaks (Maziarz & Wesołowski, 2010; Wesołowski & Maziarz, 2009), if higher clutch sizes are indicative of better phenological synchrony to their own invertebrate prey peaks these results imply that wood warblers may be late matched in warm years and search for their optimal territory level temperature locally (Frey et al., 2016), refined within territories by nest site preferences such as by slope and distance from forest edge (Pasinelli, Grendelmeier, Gerber, & Arlettaz, 2016). Blue tit clutch size showed the opposite interaction, with larger clutches in warm territories in warm years and cool territories in cool years. Blue tits time breeding to match caterpillar phenological peaks (their principle prey) (Shutt et al., 2020; Wesołowski & Rowiński, 2014), and our results indicate that blue tit breeding phenology might be early in cool years and better matched birds breed in cooler territories. As blue tit clutch size does not vary with woodland habitat or geography but by annual variation (Shutt, Bolton, Cabello, Burgess, & Phillimore, 2018), annual temperature could be an important factor determining the quality of the breeding year for blue tits.

Temperature impacts on productivity

There were no territory-level temperature effects on productivity in either blue tit or wood warbler, but pied flycatchers showed a strong response, fledging 1.7 more chicks in cool compared to warm territories, with this effect strongest in cool years. Higher productivity from cooler territories suggests cooler territories have a better match with invertebrate prey abundance in this species. Cooler territories conferring greater productivity may also explain why these territories are occupied first by both male and female pied flycatchers upon arrival. There may be a greater risk of mistiming breeding in warmer springs due to lower levels of local variation in tree budburst (Denéchère et al., 2019).

Non-temperature impacts: territory quality and individual experience

For pied flycatcher our models also controlled for other factors that may influence nest building: clutch size and productivity. Higher territory quality predicted earlier nest initiation and egg laying, and higher productivity, supporting the general validity of using the simple indirect proxy of long-term occupation trends to indicate territory quality (Potti et al., 2018; Sergio & Newton, 2003), particularly for measuring territory quality in relatively homogeneous habitats when habitat composition and structural preferences can be hard to determine or differentiate. The spatial pattern of temperature across the study area was consistent, and the territories that were relatively cool in 2015-2018 had the highest pied flycatcher occupancy rates since 1980, showing that cool territories have been preferentially selected for almost 40 years. The models also indicated that adult flycatchers with greater previous breeding experience (i.e. older individuals) tended to arrive earlier in spring (male experience), lay eggs earlier and lay larger clutches (both female experience).

This is concordant with other studies (Both et al., 2016; Potti, 1998), and is indicative of more experienced parents having higher nesting success.

Conclusions

Territory-level temperature variations within a single site have profound effects on the breeding decisions and outcomes of all three passerine bird species studied. Resident blue tit breeding phenology responds linearly to increasing territory temperatures similar to responses across large-scale geographic and annual temperature gradients (Phillimore et al., 2016). Migrant pied flycatchers and wood warblers, on the other hand, may be responding to small-scale phenological cues at lower trophic levels, and local populations may be late timed in warm years. Current climate change scenarios potentially favour resident blue tits that track local phenology well across all years, over the two migrant species which may be best synchronised in cool years. As avian distributions are limited by thermal breeding niches (Socolar et al., 2017), this may contribute to shaping breeding distribution and abundance of these species, with southern populations possibly impacted to a greater extent by climate change (Both et al., 2006). For populations of declining long-distance migrant species, including pied flycatcher and wood warbler in the UK (Massimino et al., 2019), knowledge of territory and thermal preferences and their influence on fecundity and productivity could be used to help maintain distribution and population size by informing woodland management and the locations of conservation interventions.

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Author contributions

JDS, SCB and MDB conceived the study; SCB, FB, JC, MEH and MDB collected the field data; JDS curated and analysed the data; JDS and MDB wrote the first draft of the manuscript, with SCB and FB also contributing critically to later drafts; MDB managed the project.

Data availability statement

Data will be made publicly available in the Dryad Digital Repository upon manuscript acceptance.

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652 **Figures and tables**
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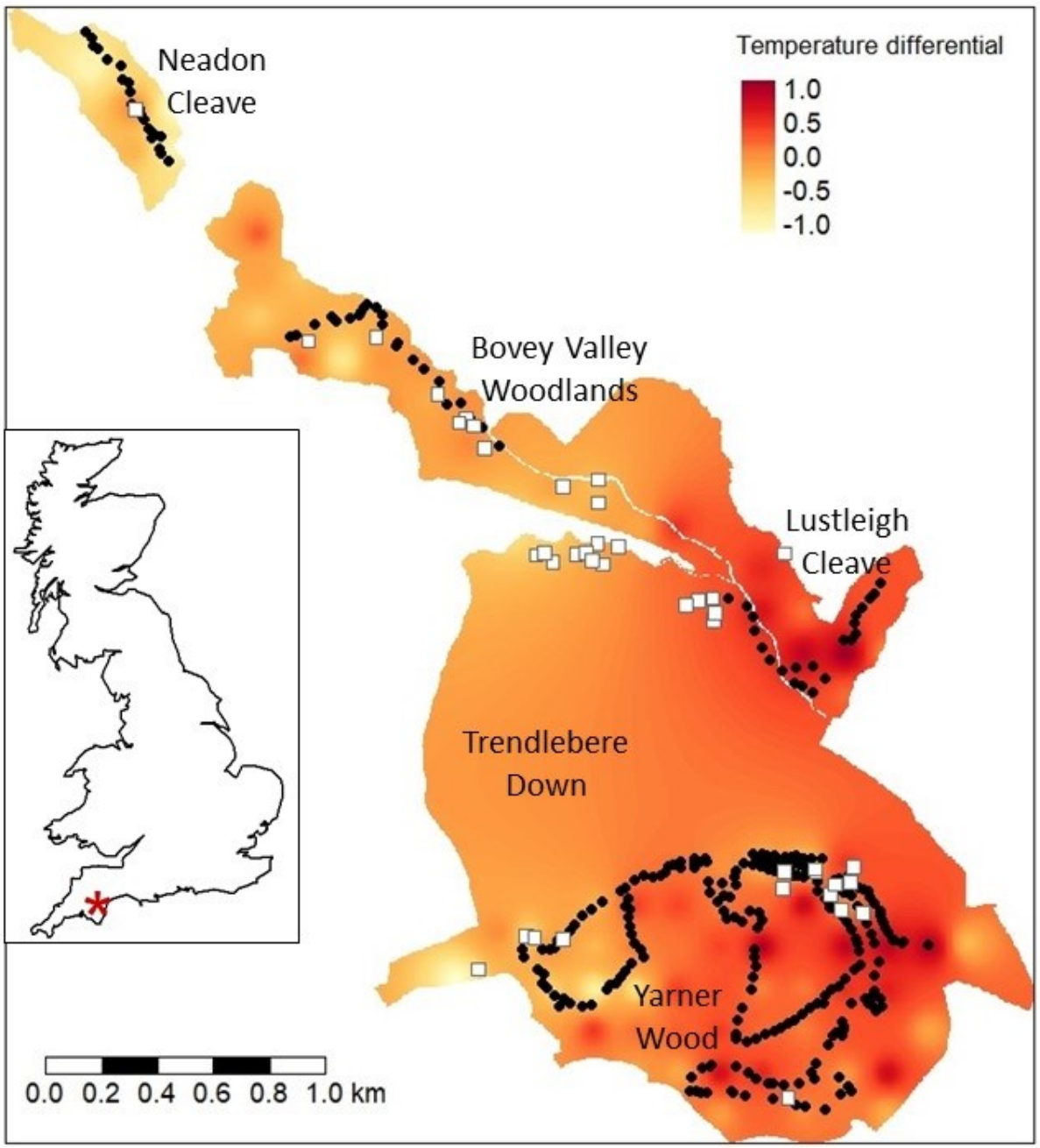

654
655 **Figure 1** Map of the study area (East Dartmoor National Nature Reserve, Devon, UK), showing its
656 location within Great Britain (inset, red star), the location of nestboxes (black points) and wood
657 warbler nests (white squares), the local names of sections of the reserve, and the relative local
658 temperature differential throughout.

Table 1 The effects of temperature, territory quality and breeding experience on reproductive phenology and outcomes in three forest passerine species. All results are taken from Bayesian GLM's, with slope estimates and credible intervals for each fixed term, with significance asterisks for significant terms (pMCMC ≤0.05* ≤0.01** ≤0.001***). Yearly temperature and territory quality are mean centred, breeding experience relates to males for arrival date but females for all other measures, and the temperature interaction is between yearly temperature and territory temperature.

Fixed Term	Arrival Date	Nest Initiation	Egg Laying Date	Clutch Size	Productivity
			Pied Flycatcher		
Intercept	15.97 (15.18 – 16.77)	25.16 (24.25 – 25.99)	38.59 (37.90 – 39.37)	6.80 (6.70 – 6.90)	4.75 (4.49 – 5.01)
Yearly Temperature	1.22 (-0.08 – 2.54)	-0.69 (-2.09 – 0.70)	-1.01 (-2.22 – 0.23)	-0.11 (-0.28 – 0.05)	-0.09 (-0.53 – 0.36)
Territory Temperature	4.27 (1.99 – 6.51) ***	0.94 (-1.46 – 3.36)	0.37 (-1.63 – 2.37)	-0.18 (-0.47 – 0.08)	-0.93 (-1.65 - -0.21) *
Temperature Interaction	2.84 (-0.60 – 6.23)	4.38 (0.36 – 8.39) *	-0.49 (-4.11 – 2.74)	0.16 (-0.30 – 0.63)	1.19 (0.00 – 2.38) *
Territory Quality	-4.18 (-9.22 – 1.37)	-11.34 (-17.28 - -5.58) ***	-6.57 (-11.45 - -1.68) *	0.28 (-0.36 – 0.96)	1.76 (0.00 – 3.49) *
Breeding Experience	-0.81 (-1.55 - -0.07) *	-0.49 (-1.24 – 0.24)	-0.93 (-1.55 - -0.28) **	0.17 (0.08 – 0.25) ***	0.02 (-0.20 – 0.24)
			Blue Tit		
Intercept			24.45 (23.47 – 25.50)	8.46 (8.23 – 8.69)	3.14 (2.76 – 3.56)
Yearly Temperature			-2.22 (-3.89 - -0.48) *	0.20 (-0.19 – 0.60)	0.78 (0.10 – 1.48) *
Territory Temperature			-3.02 (-5.89 - -0.24) *	-0.57 (-1.21 – 0.06)	-0.77 (-1.93 – 0.28)
Temperature Interaction			0.10 (-4.71 – 5.12)	1.22 (0.17 – 2.33) *	1.46 (-0.47 – 3.35)
Territory Quality			-2.33 (-8.21 – 3.35)	0.34 (-0.95 – 1.65)	1.31 (-0.95 – 3.73)
			Wood Warbler		
Intercept			49.92 (45.12 – 55.08)	5.59 (5.23 – 5.94)	2.99 (2.02 – 3.94)
Yearly Temperature			2.57 (-6.54 – 11.40)	0.35 (-0.28 – 0.97)	0.09 (-1.56 – 1.89)
Territory Temperature			-3.53 (-25.31 – 17.68)	0.11 (-1.33 – 1.40)	-1.68 (-5.41 – 2.10)
Temperature Interaction			51.59 (13.58 – 91.09) *	-2.82 (-5.23 - -0.50) *	-0.44 (-7.06 – 5.86)

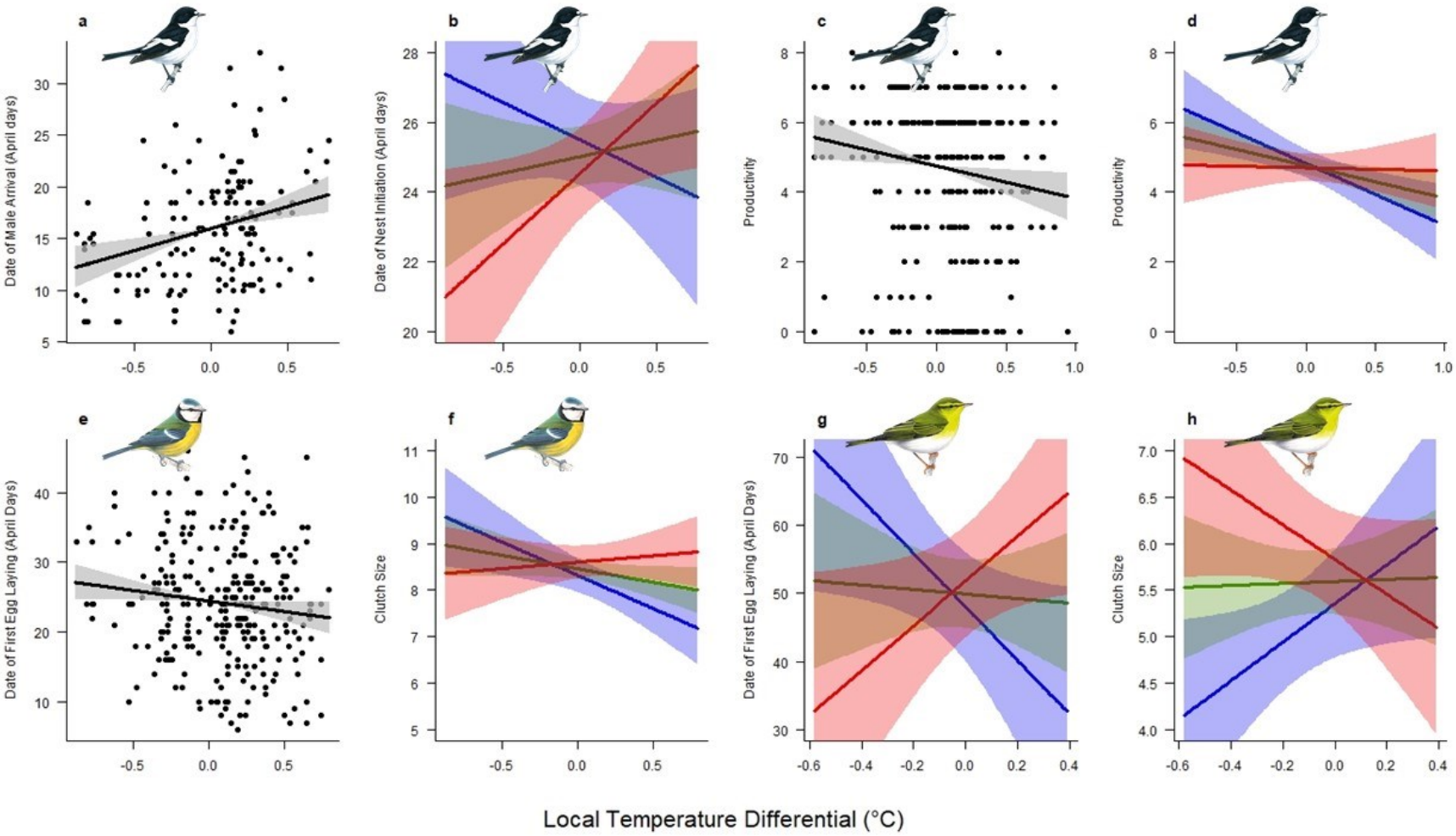

Figure 2 Illustrating the significant effects of territory temperature on the breeding parameters of three woodland passerine species: (a-d) pied flycatcher (e-f) blue tit (g-h) wood warbler. Figures a, c and e show significant single predictor linear effects (solid black line) along with 95% credible intervals (grey shading). Figures b, d and f-h show significant interaction linear effects (solid lines) and 95% confidence intervals (shading) in a cold (blue, -0.7°C below mean interannual temperature), average (green, mean interannual temperature) and warm (red, +0.7°C above mean interannual temperature) example year. Bird drawings reproduced with permission from Mike Langman, RSPB Images.

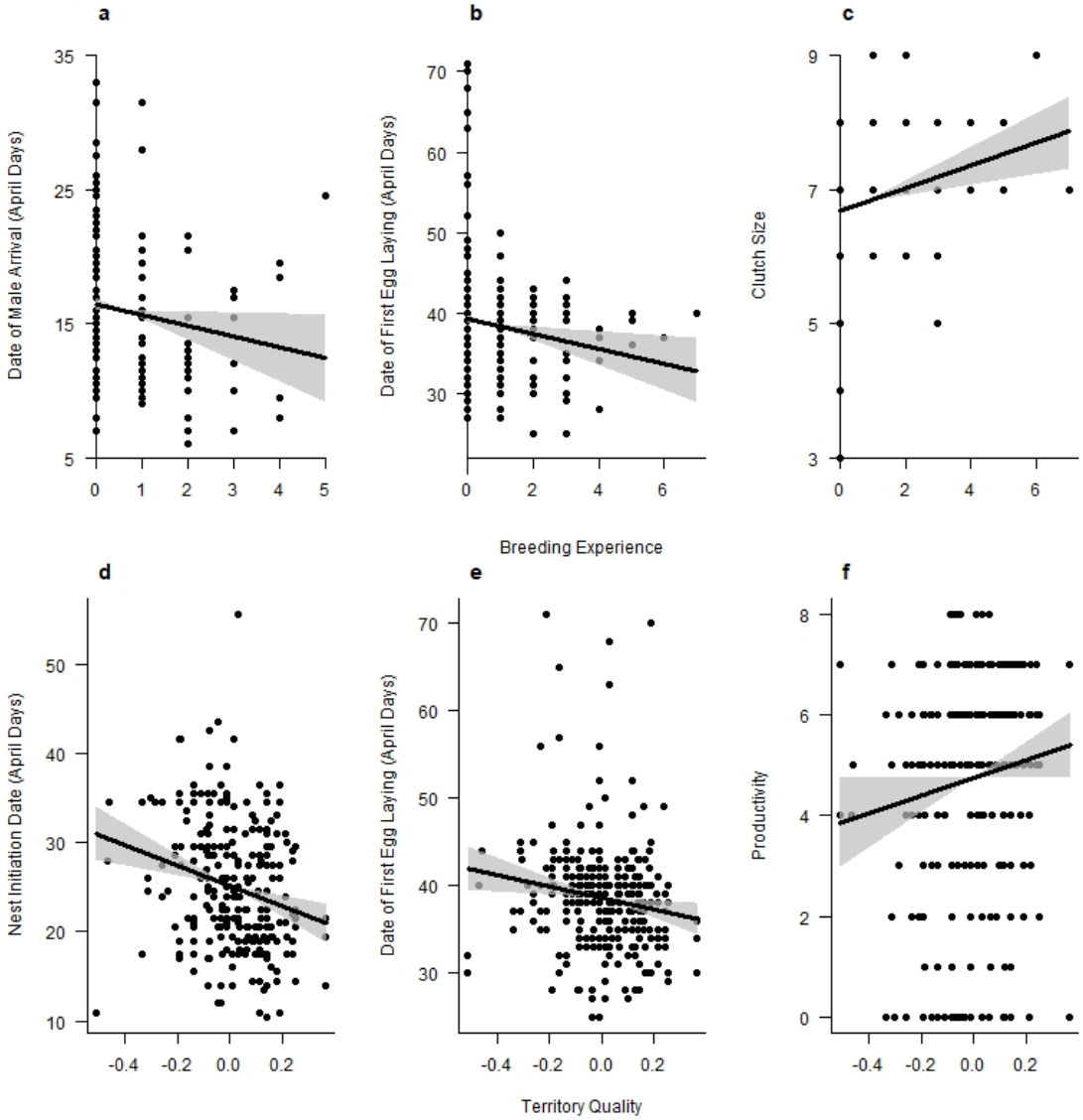

Figure 3 Illustrating the significant effects (solid black lines) of breeding experience (a male and b-c female) and territory quality (d-f) on the breeding parameters of pied flycatcher, along with 95% credible intervals (grey shading).