



CONTEXT-DEPENDENT CHANGES IN THE WEIGHTING OF ENVIRONMENTAL CUES THAT INITIATE BREEDING IN A TEMPERATE PASSERINE, THE CORSICAN BLUE TIT (*CYANISTES CAERULEUS*)

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ABSTRACT.—Birds use local environmental cues to fine-tune the timing of egg laying such that the nestling period normally coincides with the local peak in food availability. Ambient temperature, vegetation phenology, and insect phenology are often considered the most likely cues, but no previous studies have explicitly compared and partitioned their relative effects. We used confirmatory path analyses and a long-term study of Blue Tits (*Cyanistes caeruleus*) to identify and measure the relative weighting of the causal paths that link laying date to spring phenology and temperature in deciduous and evergreen oak forests on Corsica. Path analysis showed that the effects of temperature and vegetation phenology vary between forest types and season. In deciduous oak forest, where females lay eggs early in spring, phenology of vegetation or insects sets the laying date. In evergreen oak forest, where breeding occurs later in the season, females shift from a predominantly phenology-based cue system to a predominantly temperature-based cue system. This plasticity in the decision process allows birds to minimize the risk of mismatching breeding date with the optimal time window and may be critical in allowing birds to track human-induced environmental change. Received 15 December 2008, accepted 16 May 2009.

Key words: Blue Tit, *Cyanistes caeruleus*, environmental cues, temperature, timing of breeding, vegetation phenology.

Changements dépendants du contexte dans la pondération des repères environnementaux qui induisent la reproduction chez un passereau des régions tempérées, *Cyanistes caeruleus*

RÉSUMÉ.—Les oiseaux utilisent des repères environnementaux à l'échelle locale pour synchroniser la ponte des œufs de façon à ce que la période de soins aux jeunes coïncide avec le pic local de disponibilité de la nourriture. La température ambiante, la phénologie de la végétation et la phénologie des insectes sont souvent considérées comme étant les repères les plus plausibles, mais aucune étude n'a à ce jour explicitement comparé ni partitionné leurs effets relatifs. Nous avons utilisé une analyse confirmatoire des pistes et une étude à long terme portant sur *Cyanistes caeruleus* afin d'identifier et de mesurer le poids relatif des coefficients de piste qui relie la date de ponte à la phénologie du printemps et à la température dans les forêts de chênes à feuillage persistant et caduc en Corse. L'analyse des pistes a démontré que les effets de la température et de la phénologie de la végétation varient entre les types de forêts et les saisons. Dans les forêts de chênes à feuillage caduc, où les femelles pondent leurs œufs tôt au printemps, la phénologie de la végétation ou des insectes règle la date de ponte. Dans les forêts de chênes à feuillage persistant, où la reproduction se produit plus tard en saison, les femelles passent d'un système de repères principalement basés sur la phénologie à un système de repères basés surtout sur la température. Cette plasticité du processus de décision permet aux oiseaux de minimiser le risque de décalage entre la ponte et la fenêtre de temps optimale. Ceci peut revêtir une importance critique en permettant aux oiseaux de suivre les changements environnementaux d'origine anthropique.

THE TIMING OF annual breeding is a crucial determinant of reproductive success, individual fitness, and population performance, particularly in insectivorous passerine birds (Perrins 1970). By synchronizing hatching with the narrow time window

of maximal food abundance, parents can enhance their reproductive success through an increase in offspring growth rate and body condition, survival to fledging, and subsequent recruitment into the breeding population (e.g., van Noordwijk et al. 1995,

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Naef-Daenzer and Keller 1999, Tremblay et al. 2003, Thomas et al. 2007). Breeding pairs may also directly benefit from a reduction in the energetic cost and workload associated with chick provisioning, ultimately increasing adult survival and maximizing individual reproductive opportunities (Thomas et al. 2001a, b).

The timing of breeding has major demographic consequences, so it is important to understand how individuals track nondirectional interannual variation in the optimal breeding date (Przybylo et al. 2000, Wilson and Arcese 2003) or repeated directional shifts that result from human-induced climate change (Crick et al. 1997, Visser et al. 2003, Bradshaw and Holzapfel 2006). The hypothalamic-pituitary-gonadal axis appears to be primed by a genetically determined response to photoperiod that prepares the reproductive system and opens the time window in which gonadal recrudescence, ovulation, copulation, and egg laying may later occur (Lambrechts and Perret 2000, Coppack 2007). However, the exact date of egg laying in a given year and locality appears to be determined by local environmental features (hereafter “cues”; “local” refers to the spatial scale perceived by breeding individuals during their daily movements). Females perceive these cues and accelerate or retard egg production to fine-tune breeding phenology to local conditions (Caro et al. 2009). This phenotypic plasticity in breeding date has come under increasing scrutiny because the reliability of the available information, the accuracy of cue interpretation, and the plasticity of the response determine whether individuals and populations are able to track the yearly variation in the timing of peak food abundance and, hence, the optimal breeding date (Visser et al. 1998, Sanz et al. 2003, Both et al. 2006).

At the population level, interannual variability in breeding date can be large. In two Blue Tit (*Cyanistes caeruleus*) populations that we have studied for 15 and 32 years (hereafter “Muro” and “Pirio,” respectively; see Blondel et al. 2006), mean laying date for first eggs varies by 22 days at Muro and 16 days at Pirio between years. This variability is by no means uncommon (e.g., Sanz 1998, Fargallo 2004). Photoperiod is fixed for a given locale, so variation in local conditions, most probably during the period of gonadal recrudescence and follicular maturation, must determine interannual variation in breeding date. Females most likely use food availability, temperature, or the phenology of spring vegetation and insects to adjust breeding date, but other cues may exist (see Visser and Lambrechts 1999, Bourgault et al. 2006).

Food availability during the pre-laying period could affect body condition in females and, thus, potentially facilitate or impede gonadal and follicular development (Perrins 1970, Williams 2005). However, food supplementation experiments on parids during the pre-laying period have either shown no effect (Clamens and Isenmann 1989, Ramsay and Houston 1998) or advanced laying date by ≤ 5 days (Svensson and Nilsson 1995, Nager et al. 1997, Ramsay and Houston 1997; for a review, see Meijer and Drent 1999). Because the effect of food supplementation is far less than that of interannual and between-individual variation in laying date, food abundance probably plays only a secondary role in setting the timing of breeding. We recently confirmed that experimental food supplementation does not affect laying date in the Muro and Pirio populations (Bourgault et al. 2009), so hereafter we focus on temperature and phenology as the primary determinants of breeding date.

Temperature during the pre-laying period may have two possible effects. By reducing thermoregulatory costs, increasing temperatures may place females in a more positive energy balance, allowing them to invest more energy and material (lipids and protein) in follicle development and egg production (Ward 1996, Stevenson and Bryant 2000, Saino et al. 2004). Current temperature may indicate future temperatures, such that females can use current temperature to predict the time of bud burst, leaf production, and the future peak in the abundance of herbivorous insect prey such as caterpillars (Visser and Lambrechts 1999). Numerous studies have described the correlation between some measure of local temperature and laying date (e.g., van Balen 1973, Perrins 1979, Perrins and McCleery 1989). More recently, others have sought to refine this relationship by examining patterns of increasing spring temperatures and their effect on laying date (e.g., Gienapp et al. 2005; Visser et al. 2006, 2009). Studies of the relationship between temperature and breeding often imply that temperature has a direct effect on laying date (i.e., that individuals rely on temperature information when making breeding decisions).

Although temperature and laying date are correlated, the link between the two may be indirect, leading to the erroneous conclusion that breeding individuals use temperature to determine laying date. Temperature is an important determinant of vegetation phenology, affecting the spring development of buds, the timing of bud burst, and the emergence of young leaves. The development of buds and leaves, in turn, determines the availability of a whole suite of herbivorous insects, including but not restricted to caterpillars, that emerge and develop in concert with the local vegetation (Buse and Good 1996, Chmielewski and Rotzer 2001, van Asch et al. 2007). Birds may use spring vegetation and insect phenology as a cue for timing life-cycle events. For example, McGrath et al. (2009) showed that some birds use flowering phenology to assess food availability when choosing where to settle during spring migration.

Vegetation may provide reliable information about future conditions, particularly the abundance of folivorous insects, such as caterpillars, for at least two reasons. First, spring bud development is based on the integration of spring temperatures over a relatively long time frame, which dampens the effects of transient warm or cold spells (Hunter and Lechowicz 1992, Chuine 2000). Second, the timing of peak abundance of folivorous insects such as caterpillars is causally related to vegetation phenology. Caterpillars do not emerge, survive, and develop to a large size until buds burst and young, tender leaves are available. Caterpillars feed primarily on young leaves that are relatively unprotected by secondary compounds (Buse and Good 1996, Jones and Despland 2006), so the timing of the caterpillar peak is tightly correlated with the growth of young leaves that immediately follows bud burst.

Temperature, phenology, and laying date are clearly related, but the structure of this simple web of variables and the nature of the relationships cannot be determined by simply examining the correlation matrix. Temperature could determine spring vegetation and insect phenology and laying date separately, with no direct link between phenology and laying date (Fig. 1, upper panel). Alternatively, temperature could determine phenology, which in turn sets laying date, with no direct link between temperature and laying date (Fig. 1, lower panel). Any observed correlation between phenology and laying date in the former model or between

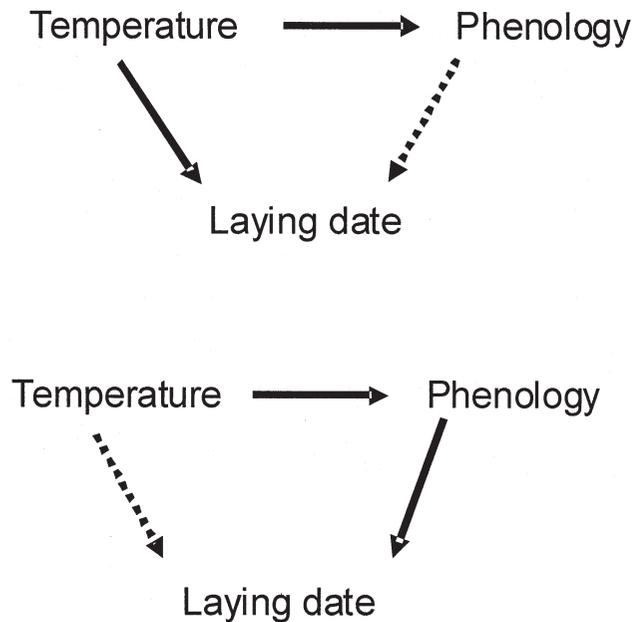


FIG. 1. Hypothesized causal path diagrams linking temperature, spring phenology, and laying date in Blue Tits. Arrows indicate the direction of causality assumed in each model. Solid lines indicate paths with coefficients greater than zero, and dotted lines indicate coefficients equal to zero.

temperature and laying date in the latter model does not imply cause and effect. Confirmatory path analysis, however, is able to determine the causal nature of paths that link variables and thus differentiate correlation from cause and effect.

We used confirmatory path analysis and data on laying date from two populations of Blue Tits in Corsica to examine how laying date is related to spring temperatures and vegetation phenology. This research provides critical information on how passerine birds may adjust breeding in the face of directional climate change by identifying the causal paths that link laying date and environmental cues.

METHODS

Study sites and field measures.—Our analyses are based on data from long-term study of two resident Blue Tit populations in northern Corsica. One population (Muro; 42°33'N, 08°54'E; 350 m elevation) inhabits a north-facing valley dominated by deciduous Downy Oak (*Quercus humilis*) forest, where females lay in early April. The other population (Pirio; 42°34'N, 08°44'E; 250 m elevation) inhabits a west-facing valley dominated by evergreen Holm Oak (*Q. ilex*), where females lay in early May. For detailed descriptions of breeding phenology in these two populations, see Blondel et al. (2006) and Lambrechts et al. (1997).

At each site, 100–150 concrete nest boxes offer nesting sites and are occupied by 45–100 breeding pairs in a given year. During spring we visited nest boxes every 1 to 5 days to monitor nest construction and the date of the first egg, which we call “laying date.” We omitted clutches that were initiated 30 days after the first clutch in a year in each population, because these are usually

second clutches. In a given year, first clutches, including some replacement clutches, span 27.1 ± 6.9 (SD) at Muro and 23.8 ± 4.2 days at Pirio. Our analyses are based on 14 years of breeding data at Muro and 21 years of data at Pirio.

Spring phenology.—We used the date of peak caterpillar frass fall as a quantitative measure of spring phenology (we justify our use of this variable below). At Muro (14 years) and Pirio (21 years), as well as at two secondary sites (Grassa, evergreen oak: 3 years; Pioggiola, deciduous oak: 1 year), we monitored frass fall in 15–20 (0.25-m²) collectors placed under the forest canopy and collected at 3-day intervals (for methods, see Zandt 1994). Once cleaned of debris and weighed, frass fall (mg m⁻² day⁻¹) provides a reliable index of the timing of peak caterpillar availability in a given habitat and year (e.g., Zandt 1994, Naef-Denzer and Keller 1999, Tremblay et al. 2003, Simon et al. 2004, Thomas et al. 2007), although variation in temperature may affect the strength of the correlation between frass fall and caterpillar biomass (Tinbergen and Dietz 1994). Evergreen oak habitat (Pirio and Grassa) offers a brief and low-amplitude peak in caterpillars, whereas deciduous oak habitat (Muro and Pioggiola) offers a broader, high-amplitude peak, which places a premium on synchronizing breeding to the caterpillar peak in evergreen habitats (see Thomas et al. 2001b, Tremblay et al. 2003).

Of course, caterpillar peak dates cannot be the cue used by birds to time egg laying, because caterpillars emerge and develop after eggs are laid. However, caterpillar peak dates correlate with the spring phenology of vegetation and the insect populations that increase in concert with bud development and burst. The peak in caterpillars that typically occurs well after egg laying is simply the culmination of a series of phenological events that accompany bud development during the period when females must integrate environmental cues and initiate egg laying. To verify that caterpillar peak date reliably corresponds to spring phenology occurring ~1 month earlier, we measured the phenology of 10–25 oak trees at Muro (3 years) and Pirio (4 years), as well as at one additional “early” evergreen oak habitat (Grassa; 3 years) and one high-altitude “late” deciduous oak forest (Pioggiola; 1 year). We scored the phenological stage of oak buds at least once weekly until leaves opened according to Du Merle and Mazet’s (1983) scale of bud development from 1 (winter dormancy) through 5 (bud burst) to 8 (full leaf development).

Spring temperature.—We obtained daily temperatures (maximum, minimum, mean) from a weather station at the Calvi airport. We also placed temperature data loggers (iButton thermochrons; model 1922L; Maxim Integrated Products, Sunnyvale, California) in 10 nest boxes at each site between 2004 and 2006 and programmed them to record temperatures at 3-h intervals. Using these local temperature data from Muro and Pirio, we refined local predictions based on the Calvi airport data. We calculated mean temperatures at Muro as $T_{\text{Muro}}^{\circ} = 1.129 * T_{\text{Calvi}}^{\circ} - 2.101$ ($r^2 = 0.99$, $P < 0.001$) and at Pirio as $T_{\text{Pirio}}^{\circ} = 1.093 * T_{\text{Calvi}}^{\circ} - 2.789$ ($r^2 = 0.92$, $P < 0.001$).

We used mean daily temperature at each site, taken during the month preceding average laying date for each site (March for Muro and April for Pirio) because this temperature measure was more tightly correlated with laying date than daily maxima or minima (P. Bourgault unpubl. data). Numerous studies (e.g., van Balen 1973, Perrins and McCleery 1989, Nager and van Noordwijk

1995, Meijer et al. 1999, Nussey et al. 2005, Visser et al. 2009) have shown that mean temperature during the general period preceding laying date influences laying date; however, the exact period over which birds might integrate temperature data remains uncertain. For this reason, we first ran our analyses using mean daily temperature for all consecutive 2-, 3-, or 4-week time windows to find the highest correlation between temperature and laying date and to determine whether the outcome was sensitive to the measurement period. Results were similar for all tested periods, but mean temperature during the first 3 weeks of March at Muro and the last 2 weeks of April at Pirió displayed the highest correlation with laying date, so we used these periods, which represent the best and most biologically relevant temperature measures, in our analyses.

Path models.—In a path model (i.e., without latent variables) there are three possible orientations between any two variables (X , Y): (1) X and Y are independent (no arrow), (2) $X \rightarrow Y$, or (3) $X \leftarrow Y$. Because our models involve three variables, the total number of logically possible models is $3^3 = 27$. However, we can exclude some models *a priori*. First, given that temperature and spring phenology are unconditionally correlated as well as conditionally correlated on laying date and that spring phenology cannot cause temperature, we can fix one path as temperature \rightarrow phenology. Second, it is impossible that the date of egg laying can cause either temperature or spring phenology, so either the laying date is independent of the other two variables or, if there is a causal path, it must be toward the laying date. This leaves only four possible

models for consideration (Fig. 2). The fourth model cannot be statistically tested by path analysis, because it makes no claims of independence or partial independence, but it can be accepted if all other possible models are statistically rejected. Model 1 proposes that laying date is independent of both the temperature and phenology cues. In model 2, laying date is caused only by temperature, the spring phenology being causally irrelevant because it is only indirectly correlated with the laying date, in that the two have a common cause (temperature). In model 3, temperature affects spring phenology, which in turn sets laying date. Therefore, the causal cue for egg laying is phenology, and temperature is only an indirect cause. Model 4 assumes that both temperature and phenology represent causal cues for egg laying. Therefore, temperature has both a direct and an indirect effect on laying date. Note that because model 4 is nested within models 2 and 3, if either of these models provides a nonsignificant lack of fit then model 4 must be nonsignificant as well. The contrary is not true. If both temperature and phenology are causal cues, models 2 and 3 will not fit but model 4 will.

The cause–effect linkages between the variables in models 1, 2, and 3 impose constraints on the covariances and partial covariances between them, and the inferential test determines whether the hypothesized constraints exist in the empirical data. If the causal process generating the data follows the one proposed by the model, the constraints in the model will be mirrored in the data and the associated P value will be nonsignificant ($P > 0.05$). Alternatively, if the constraints in the model do not agree with the

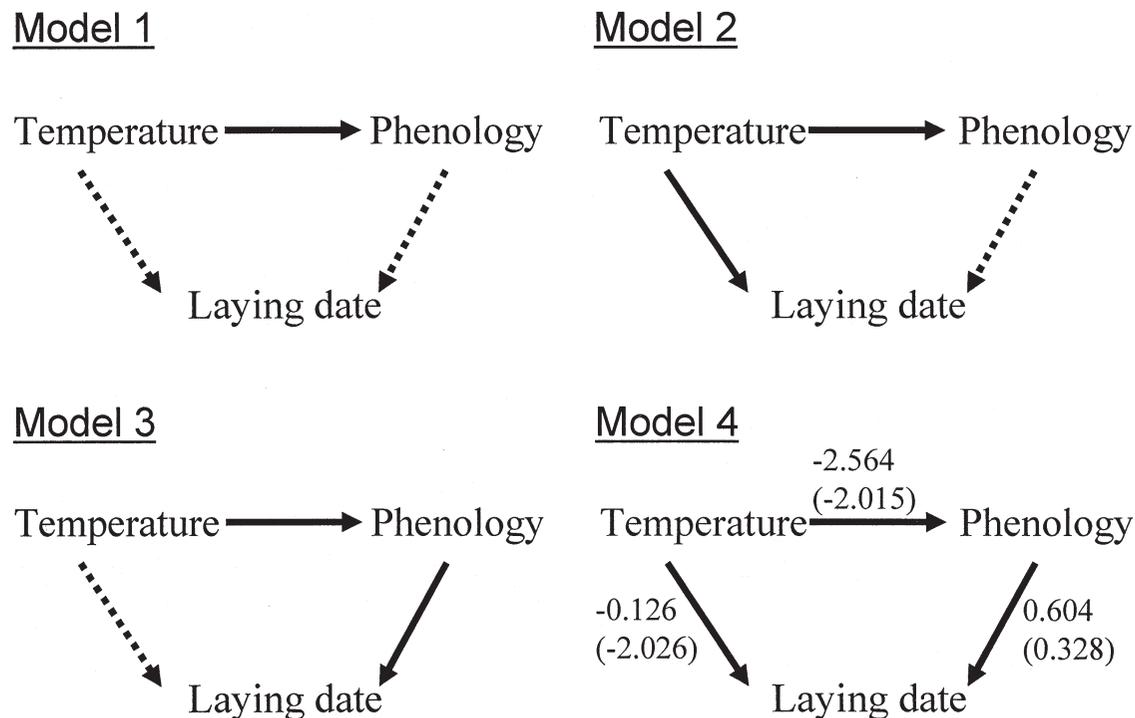


FIG. 2. Four possible cause–effect linkage models linking environmental variables (temperature and phenology) to laying date in Blue Tits. Arrows indicate the direction of causality assumed in each model. Solid lines indicate paths with coefficients greater than zero, and dotted lines indicate coefficients equal to zero. Values for model 4 are path coefficients for each direct causal path at both sites. Coefficients for Pirió are in parentheses, and those for Muro are not.

TABLE 1. Results of linear mixed models testing the relationship between laying date and two environmental cues, spring phenology and temperature, in Blue Tits breeding in deciduous oak forest (Muro) and evergreen oak forest (Pirio), with female identity included as a random term.

Term	<i>t</i>	Coefficient ± SE	<i>P</i>	df
Muro				
Temperature	0.29	-0.12 ± 0.63	0.94	1 and 544
Phenology	3.45	0.60 ± 0.17	<0.001	1 and 544
Pirio				
Temperature	-3.41	-2.03 ± 0.59	<0.001	1 and 1,200
Phenology	2.54	0.33 ± 0.13	0.01	1 and 1,200

generating process, the patterns of covariation predicted by the model will show significant lack of fit to the data, allowing us to reject the model ($P < 0.05$).

Our data have a clear hierarchical structure, with repeated laying dates per individual over years, and spring phenology occurs only once per year. The partial dependences generated by the nested structure make classical confirmatory path analysis inappropriate. Instead, we used mixed models (Pinheiro and Bates 2000) to test our four path models using d-separation tests (Shipley 2000a, b, 2003). A d-separation test consists of deriving a basis set of conditional independence relationships predicted given the topological structure of the path model that predicts all other predicted patterns of correlation and partial correlation among the observed variables; these are shown in Table 1. If a d-separation claim in the basis set predicts that the independence of two variables X and Y is conditional on another variable Z (written as " $X \perp\!\!\!\perp Y \mid Z$ "), then the partial slope associated with X of a mixed model regression of Y on $X + Z$ will not be significantly different from zero. The entire basis set (and therefore the entire model) is tested using the $C = -2 \sum \ln(p_i)$ test statistic, in which p_i is the null probability associated with the i^{th} d-separation claim in the basis set. If all the predicted patterns of independence and conditional independence correctly exist in the data, then C is distributed as a chi-squared statistic with $2k$ degrees of freedom, where k is the number of d-separation claims in the basis set.

Given the data structure, it is impossible to directly determine the relative weighting of each variable when more than one causal variable exists, as is the case in model 4. In this situation, Shipley (2009) showed that the appropriate test is a mixed-effects model.

RESULTS

The culmination of bud development (stage 5, bud burst) is closely correlated with caterpillar peak date (Fig. 3; $r = 0.984$), and study sites fall along a single line. In a general linear model, there is no effect of forest type ($t = 0.58$, $df = 7$, $P > 0.05$) and there is no phenology*forest-type interaction ($t = 0.15$, $df = 7$, $P > 0.05$). Caterpillar peak date provides a uniform and reliable measure of spring phenology in evergreen and deciduous oak forests. Here, we use the term "spring phenology" to refer to the timing of the ecological processes that accompany the development of vegetation, although our statistical analyses are based on caterpillar peak date.

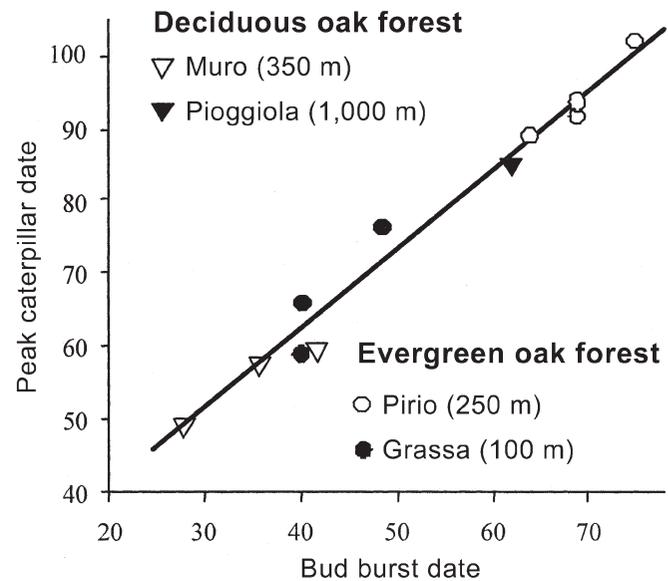


FIG. 3. Relation between bud burst date and peak caterpillar date in March (1 = 1 March; $F = 279.79$, $df = 1$ and 9 , $P < 0.001$, $r = 0.984$) during 2005–2007 at Muro, 2004–2007 at Pirio, 2005 at Pioggiola, and 2005–2007 at Grassa. Elevations, which are responsible for the between-site differences within forest type, are in parentheses.

Laying date, phenology, and spring temperature are all strongly correlated at Muro and Pirio (Fig. 4). A conventional linear mixed model analysis (Table 1) reveals that laying date at Muro depends on phenology alone, despite the correlation between temperature and laying date (Fig. 4). At Pirio, however, laying date is set by both a positive effect of spring phenology and a negative effect of spring temperature.

Although linear mixed models can identify significant correlations, path analyses are better equipped to determine the causal nature of the relation of laying date, phenology, and temperature. Table 2 summarizes the tests of the path models. Models 1 and 2 are rejected ($P < 0.05$) at both Muro and at Pirio. Model 3 is not rejected at Muro but is rejected at Pirio. Given that all possible models except model 4 are rejected at Pirio, model 4 is the only remaining model. Because model 3 is not rejected at Muro, model 4 cannot be rejected either. Thus, the data are consistent with two possibilities: (1) model 4 applies at both sites, but the strength of the causal relationships differs and the temperature→laying date path at Muro is sufficiently weak that it is not significantly different from zero; or (2) the temperature→laying date path at Muro really is zero (i.e., no causal connection) and so the underlying causal structure of birds' response to the cues differs at the two sites.

Model 4 is not statistically rejected at either site, using the d-separation test; however, it can still be rejected if there are no significant differences in the strength of the path coefficients between the two sites. Therefore, to test for such differences, we ran a mixed-effects model with laying date as the dependent variable, site (Muro–Pirio) as a categorical covariate, temperature and phenology as independent variables, and year and female as random effects and included the site*temperature and site*phenology interactions. The significant interactions site*temperature ($P < 0.01$)

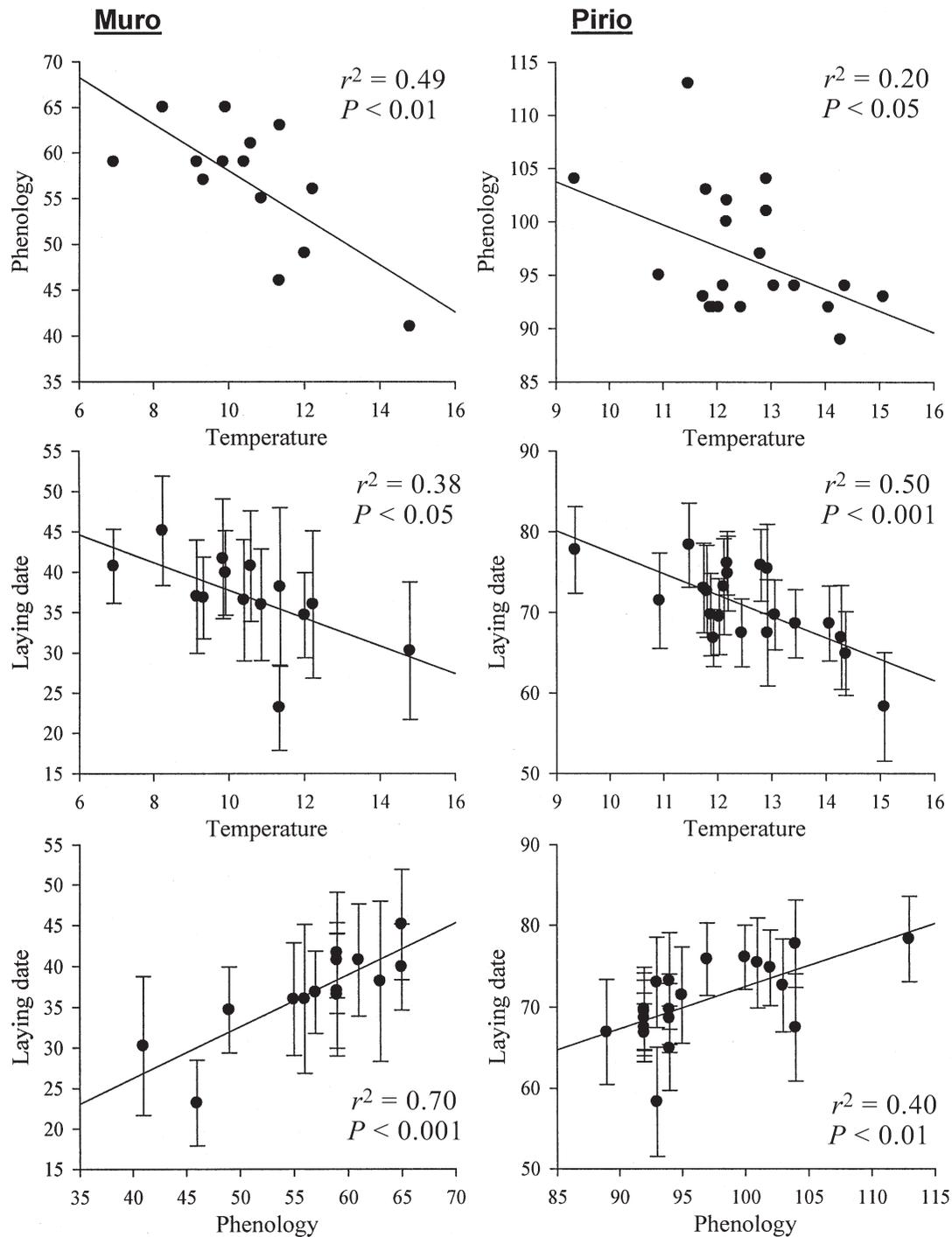


FIG. 4. Relations between mean laying date in Blue Tits, spring phenology, and mean daily temperature during the month preceding egg laying at Muro and Pirio.

and site*phenology ($P < 0.001$) confirm that the relative contributions of temperature and phenology in setting laying date change between forest types and as the season progresses.

Figure 2 shows the path coefficients for model 4 at each site. At Muro (the early-laying population), the direct effect of temperature

on laying date is at best modest, in that a 1°C increase in spring temperature advances laying date by between 0 and 0.126 days. By contrast, the indirect effect of temperature was substantial and advanced the laying date by 1.55 days; this indirect effect is the product of the temperature→phenology and phenology→laying

TABLE 2. Results of path models of the relationship between laying date and two environmental cues, spring phenology and temperature, in Blue Tits breeding in deciduous oak forest (Muro) and evergreen oak forest (Pirio). Models 1–4 (Fig. 2) are the only logically possible models, given the three variables, that do not contradict known causal orderings. Variables: temp = mean daily air temperature prior to egg laying, phenology = March date of caterpillar peak, and laying date = March date of egg laying. The basis set of d-separation claims lists the statistically testable predictions of independence made by each model. Also given is the overall test of the model for the two sites; *P* values of rejected models are in bold.

	Model 1	Model 2	Model 3	Model 4
Basis set of d-separation claims	temp_ _laying date phenology_ _laying date/temp	phenology_ _laying date/temp	temp_ _laying date/phenology	None
Muro	<i>C</i> = 87.13, <i>df</i> = 4, <i>P</i> < 10⁻¹⁶	<i>C</i> = 9.00, <i>df</i> = 2, <i>P</i> = 0.011	<i>C</i> = 3.84, <i>df</i> = 2, <i>P</i> = 0.179	
Pirio	<i>C</i> = 81.30, <i>df</i> = 4, <i>P</i> < 10⁻¹⁶	<i>C</i> = 14.84, <i>df</i> = 2, <i>P</i> = 0.0006	<i>C</i> = 14.53, <i>df</i> = 2, <i>P</i> = 0.0007	

date path coefficients. At Pirio (the late-laying population), the direct effect of temperature on laying date was 16× greater: a 1°C increase advanced laying date by 2.026 days. Therefore, the indirect effect of temperature on laying date at Pirio (an advance of 0.66 days) was only half as important as that at Muro. At Muro, an advance in spring phenology by 1 day at a fixed temperature advanced the laying date by 0.604 days. At Pirio, phenology at a fixed temperature advanced the laying date by only 0.328 days.

DISCUSSION

The relative roles of temperature and of tree and insect phenology in setting laying date of forest-breeding, temperate passerines have received considerable attention in the avian literature as researchers have sought to explain variation in breeding dates over local landscapes (e.g., Järvinen 1993, Nilsson and Källander 2006) and to understand and predict the responses of bird populations to climate change (Brommer et al. 2005, Nussey et al. 2005). Most attention, however, has focused on temperature, leading to efforts to refine post-hoc empirical models to better “explain” the effect of temperature on laying date (e.g., Gienapp et al. 2005, Visser et al. 2006). This focus on temperature has been justified primarily by concern over global warming (a temperature effect) and indications of an increasing mismatch between the optimal time of breeding and prey abundance (thought to be a temperature effect; Sanz 2003, Visser and Both 2005). It is important to note, however, that no studies have actually confronted phenology-based and temperature-based models of the timing of avian reproduction and partitioned effects between the two. This can most probably be explained by the lack of an appropriate study system that provides sufficient variation in breeding date to allow us to juxtapose the two models and so partition the effects of temperature and phenology. The heterogeneous Corsican landscape where Blue Tits breed over a time window of 1 to 2 months provides an exceptional study system.

Our analyses indicate that the relative weighting of temperature and phenology varies between habitats or as the season advances. In deciduous oak forest, where Blue Tits lay early, the timing of egg laying is primarily determined by spring phenology and temperature acts principally as an indirect cause through its effect on phenology. In evergreen oak forest, where Blue Tits lay

roughly 1 month later, the direct effect of phenology declines by about half and temperature becomes an important additional cue for egg laying. We cannot determine whether the variation in the weighting of the direct effects of phenology and temperature on laying date can be attributed to season or to habitat, because our study relied on long-term data that are available for only two populations and study sites. However, one can view habitat and season as an ensemble to which birds must respond when fine-tuning the breeding decision, because evergreen oak forests are consistently later than deciduous oak forests in their spring phenology and peak caterpillar dates and because Blue Tits always breed later in evergreen oak habitats than in deciduous oak habitats (Lambrechts et al. 1997, Blondel et al. 2006). Our results show that the relative contributions of the main environmental cues that set laying date are context dependent and change across the breeding landscape of habitat and season.

The reason that birds shift the emphasis from phenology to temperature in evergreen oak habitats where they breed late in the season may be related to the reliability of the two cues and the penalty of mismatching breeding to the optimal breeding date. During the laying period in deciduous oak forest, temperatures are usually relatively low, with mean (± SD) daily temperatures of 10.5 ± 1.9°C and minimum night-time temperatures often approaching 0°C. Low temperatures result in high thermoregulatory costs, and the absence of foliage coupled with low ambient temperatures results in low overall insect abundance. If birds responded to transient high temperatures by initiating egg laying, we would expect the fitness penalty to be high in terms of egg size or quality (Nager and van Noordwijk 1992, Stevenson and Bryant 2000), incubation costs (Bryan and Bryant 1999), hatching success, and nestling survival once temperatures return to the lower seasonal norms. Tree phenology, however, integrates temperatures over a longer period, so phenology should provide a more reliable cue for breeding, or at least one that is less affected by transient high temperatures early in spring. In addition, there is a direct and causal link between spring tree phenology and caterpillar prey abundance, because caterpillars only develop to the size fed to nestlings once tender young leaves begin to develop. Thus, females may increase the probability that eggs will hatch and nestlings develop when caterpillar prey are most abundant if they use spring phenology as a cue for egg laying.

Of course, we cannot identify whether it is vegetation phenology per se or any of a suite of other factors that accompany the spring development of buds that stimulate birds to lay eggs. So many features of the spring environment in which females develop gonads and begin to lay eggs are tied to the development of the dominant vegetation that it will be difficult to tease apart their effects. However, it appears that some aspects of spring phenology, and not temperature, set laying date in deciduous oak forest.

If phenology is a reliable indicator of the optimal timing for egg laying in deciduous oak forest, why is this not the case in evergreen oak forest? Here, our results show that females integrate both temperature and phenology cues to initiate egg laying. Although our data do not allow us to address this question with certainty, there may be two reasons. First, bud burst in a deciduous forest is easily perceived because it represents an abrupt transition from total absence to presence of foliage. Bud burst in evergreen oak forest is less conspicuous because only 30% of foliage is renewed in a given year and buds are hidden among the existing foliage. Second, the speed of bud burst, leaf development, and caterpillar growth at higher ambient temperatures may not allow birds to rely solely on phenology. It takes ~19 days to lay and incubate a 6-egg clutch (1 egg day⁻¹ and 13 days incubation), which results in a 19-day lag between the time when females could initiate egg laying on the basis of their perception of phenology and when they finally begin feeding nestlings. In May, when females lay clutches in evergreen oak forest (e.g., Pirio), mean daily temperatures are 2–3°C higher than at Muro, where females breed a month earlier (see Fig. 4, middle panel). Because bud burst, leaf development, and caterpillar growth are all temperature-dependent processes, higher ambient temperatures will necessarily accelerate growth and reduce the time between bud development (possibly the earliest phenology signal available to females) and the presence of leaves and caterpillars (the critical period determining nestling growth and survival; van Asch et al. 2007). Even though females may be able to fine-tune breeding schedules to some degree by adjusting clutch size and the start of incubation (Cresswell and McCleery 2003), the time constraint imposed by egg production and incubation may force females to integrate additional cues, such as temperature, in order to anticipate the appropriate breeding date sufficiently early to allow them to synchronize breeding with food availability. The penalty for laying eggs and hatching young even a few days too late is particularly large in evergreen oak because of the brief low-amplitude peak of caterpillar abundance (Tremblay et al. 2003), high nest loads of ectoparasites (*Protophthora* spp.; Simon et al. 2004), and the combined effects of low food abundance and high parasite loads on nestling performance and recruitment (Thomas et al. 2007).

Our results indicate that Blue Tits use a cue system that is context specific to fine-tune laying dates to match local conditions both on a spatial (habitat) scale and on a temporal (interannual) scale. Reliance on both temperature and phenology when breeding late in the season, as occurs in most populations where tits have been intensively studied north of the Mediterranean region, satisfactorily explains how these populations can advance breeding in response to rising spring temperatures while maintaining a relatively large variation in the onset of breeding on a local spatial scale (Nager and van Noordwijk 1995, Massa et al. 2004, Nilsson and Källander 2006). Visser et al. (2009) experimentally

confirmed that rising spring temperatures at a regional scale drive earlier breeding. However, the 22-day offset in that study between laying dates in captivity and in the wild shows that other environmental features may have an even greater effect on laying date than temperature. Differences in the phenology of the dominant tree or shrub species that constitute the local plant community introduce variation in breeding date that can be expressed at an extremely fine local scale. For example, tits breeding in residential garden habitats initiate laying earlier than their counterparts breeding in adjacent forest landscapes (Perrins 1979, Dhondt et al. 1984), and these difference in breeding date can be manifested across a scale measured in hundreds of meters, a scale much finer than that normally found for local temperatures.

Our analyses offer some hope that breeding populations will respond well to global warming. Visser et al. (2005) showed that in some tit populations, breeding date may not accurately track the advance in peak prey availability, which results in an increasing mismatch between nestlings and their prey and a decline in fledging success over time. If a single environmental feature were responsible for the timing of breeding, climate change could cause a severe decline in breeding success, with negative demographic consequences. However, females that combine phenological and temperature cues in the decision process that governs the timing of reproduction may maintain higher reproductive success and fitness in the face of global warming. Although birds and their prey may not respond in concert to increasing spring temperatures, which would result in an asynchrony between nestlings and their preferred prey (see van Asch et al. 2007), the vegetation phenology cue would oppose this mismatch and draw breeding date toward the optimal time window. This view assumes that vegetation phenology and the peak in insect prey abundance are causally linked. We believe this to be the case, at least for Blue Tits feeding on caterpillars, because folivorous insects develop best on young, tender leaves with low levels of constitutive defenses, which results in a very tight correlation between vegetation phenology and caterpillar abundance (see Fig. 3). Also, we have not detected any consistent mismatch between Blue Tit breeding dates and caterpillar peak dates over the 14 and 21 years for which we have data for Muro and Pirio, respectively (P. Bourgault unpubl. data).

Although our results indicate that temperature and phenology both participate in control of breeding date, they tell us little about the relative contribution of these two paths and how they are set. We expect that selection can change the relative weighting of the two cues and, hence, the slope of the relation between temperature or phenology and breeding date. Just as climate change can select for increased or decreased phenotypic plasticity in breeding date (Brommer et al. 2005, Nussey et al. 2005, Bradshaw and Holzapfel 2006), it can modify the weighting of the two primary variables in the breeding control mechanism. The existence of higher phenotypic plasticity in insular than in continental populations (Charmanier et al. 2008) suggests that populations evolve different responses to local conditions. Examining how the relative weighting of these control mechanisms varies between individuals and over time will require experiments in controlled-environment chambers (e.g., Visser 2006, Visser et al. 2009). Our finding that the weighting changes over the season or between habitat types provides the framework for making testable predictions.

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