Energetic and Fitness Costs of Mismatching Resource Supply and Demand in Seasonally Breeding Birds

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By advancing spring leaf flush and ensuing food availability, climatic warming results in a mismatch between the timing of peak food supply and nestling demand, shifting the optimal time for reproduction in birds. Two populations of blue tits (*Parus caeruleus*) that breed at different dates in similar, but spatially distinct, habitat types in Corsica and southern France provide a unique opportunity to quantify the energetic and fitness consequences when breeding is mismatched with local productivity. As food supply and demand become progressively mismatched, the increased cost of rearing young pushes the metabolic effort of adults beyond their apparent sustainable limit, drastically reducing the persistence of adults in the breeding population. We provide evidence that the economics of parental foraging and limits to sustainable metabolic effort are key selective forces underlying synchronized seasonal breeding and long-term shifts in breeding date in response to climatic change.

Matching the timing of breeding with the local peak in food abundance is crucial to reproductive success for income breeders such as small passerine birds (*1–3*), which must forage daily to cover breeding costs. Many insectivorous birds show a seasonal decline in nestling growth, condition, and survival that can be attributed to a falloff in prey abundance (*4, 5*), resulting in a progressive mismatching between food supply and nestling demand. By advancing the phenology of budding, leaf production, and food supply, climatic warming exacerbates such mismatching (*6*). Any mismatch between nestling demand and food supply must be mediated by parents, affecting both foraging costs and provisioning rates.

We hypothesize that the economics of parental foraging is a key selection pressure shaping the evolution of highly seasonal breeding in birds and underlying the tracking of climate change. Energetic and fitness consequences of mismatching cannot easily be measured in wild populations because strong stabilizing selection drives the frequency of early- and late-breeding phenotypes to low levels, making it impossible to quantify the performance of "maladapted" phenotypes. However, two populations of blue tits (*Parus caeruleus*) that breed at different dates relative to the local peak in prey abundance, due to differences in gene flow from adjacent habitats (*7, 8*), offer a unique opportunity to expose energetic and fitness costs when breeding is mismatched with food supply. Here, we show that parental foraging costs increase and that adult survival and nestling condition decrease with the degree of mismatching.

In the Mediterranean region, blue tits exhibit extreme variation in breeding date (*9*) mediated by interpopulation differences in photoperiod response (*10–12*). Differences in the timing of breeding between populations appear to be genetic and adaptive, acting to match the period of peak nestling food demand with the brief spring peak in caterpillar abundance in the forest type that dominates the local landscape (*7, 8*). Because the spring flush in new foliage supports caterpillar production, the phenology of prey abundance changes between forest types as a function of interspecific differences in the timing of leaf growth (*13*). In Corsica, the local landscape is dominated by forests of evergreen Holm oak (*Quercus ilex*), which renew about 30% of leaves in early June. Here, blue tits time breeding such that peak nestling demand coincides with the early June peak in caterpillar abundance (*14*). At the same latitude and altitude in continental southern France, the local landscape is dominated by deciduous Downy oak (*Q. pubescens*) forest where the spring leaf flush occurs in early May. Here, blue tits breed nearly 4 weeks earlier than in Corsica, again matching peak nestling demand with food supply (*7, 8*).

In continental southern France, however, the May-breeding phenotype of blue tits overflows from deciduous oak forest into less common patches of evergreen oak, where pairs breed about 3 weeks too early relative to the local peak in caterpillar abundance (*8*). This phenotype overflow creates two blue tit populations that occupy the same evergreen oak habitat, yet differ in the degree of matching between nestling food demand and the local peak in caterpillar abundance. These two populations, which we refer to as matched (Corsican evergreen oak population) and mismatched (continental evergreen oak population), allow us to test for energetic and fitness costs when breeding is mismatched with food supply.

For selection to act on the timing of breeding via parental energy budgets, two conditions must be met. First, the degree of matching between peak nestling demand and the local peak in caterpillar abundance must affect the field metabolic rate (FMR) of breeding adults, with the most mismatched individuals making the greatest metabolic effort. Second, mismatched individuals must have lower lifetime reproductive output (measured either directly as survival or indirectly as persistence in the breeding population) than matched individuals. We show that Mediterranean blue tits meet both conditions.

Caterpillar abundance (*15*) showed a repeatable seasonal peak with similar timing and amplitude in both Corsican and continental evergreen oak habitats (Fig. 1) (Julian dates, i.e., days since 1 January: Corsica peak, 156.8 ± 8.0; continent peak, 157.9 ± 6.1). In Corsica, breeding dates for our study nests were well matched with caterpillar abundance (*16*), with all nesting dates falling within the 13-year range in peak caterpillar abundance (Julian dates: nesting, 163 to 172; caterpillar peak, 151 to 172). In the continental population, most birds bred before the 10-year range in caterpillar peak (nesting, 132 to 149; caterpillar peak, 148 to 172). Brood size was not significantly correlated with breeding date in either the matched Corsican population or the mismatched continental population (Table 1). However, in the continental population, total brood mass declined and daytime FMR for adults (FMR_{day}) (*17*) rose as the offset between breeding date and caterpillar peak increased (Table 1 and Fig. 2). The daily unit cost for rearing young (per gram of nestling) rose from a mean of 1.01 ± 0.49 kJ day^{-1} $adult^{-1}$ in Corsica and 1.27 ± 0.16 kJ day^{-1} $adult^{-1}$ in the three most matched continental nests to 2.59 ± 0.59 kJ day^{-1} $adult^{-1}$ in the four least matched continental nests, an increase of more than 100%. Metabolic effort of adults, measured as $FMR_{24\text{-}h}/BMR$ (24-hour FMR divided by basal metabolic rate), rose from

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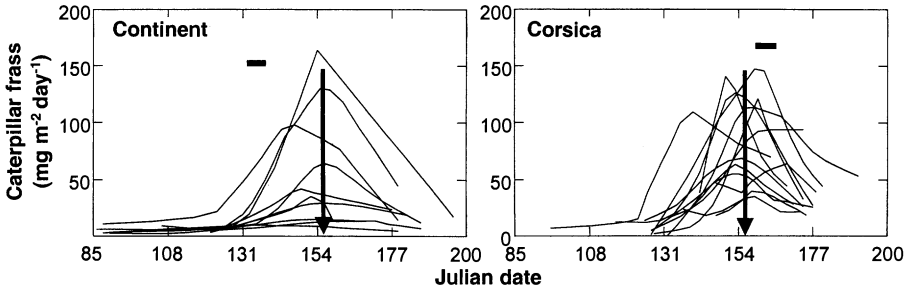

Fig. 1. Caterpillar prey abundance in continental and Corsican evergreen oak (*Q. ilex*) forests. The vertical arrow indicates the interannual mean in peak caterpillar abundance; the horizontal bar indicates the timing of breeding for study pairs.

Table 1. Contrasts in brood parameters and parental energetics between matched and mismatched populations of breeding blue tits. Results are for regressions of parameters against breeding date. Response direction indicates the direction of response for the mismatched population as breeding date approaches the peak in caterpillar prey abundance.

Parameter	r^2		Response direction
	Matched (Corsica; n = 13)	Mismatched (continent; n = 13)	
Brood size	0.01	0.18	0
Brood mass	0.02	0.34*	+
FMR_{day} (kJ day^{-1})	0.04	0.39*	−
Rearing cost per gram of nestling (kJ day^{-1} adult^{-1})	0.00	0.56**	−
Metabolic effort ($FMR_{24\text{-}h}$/BMR)	0.01	0.45**	−

*P < 0.05, **P < 0.001. Other values are not significant.

4.91 ± 0.54 × BMR in the three most matched to 6.96 ± 1.27 × BMR in the four most mismatched continental nests, but averaged only 3.45 ± 0.88 in Corsica. The metabolic effort exhibited by the most mismatched pairs is among the highest reported to date for breeding birds (*18–20*). The relation between metabolic effort and breeding date (effort = 27.96 − 0.16 · date) was such that effort in the continental population would fall to the Corsican level of 3.45 × BMR at Julian date 156—exactly when the breeding date is matched with the interannual peak in food supply (Fig. 1).

If there is a tradeoff between current metabolic effort and future survival and reproductive prospects, as postulated by the prudent parent hypothesis (*21*), then one would expect lower persistence of breeding pairs in mismatched populations compared with matched populations, reflecting a difference in survival. Mean persistence (*22*) was significantly lower for both males and females in mismatched continental evergreen oak compared with matched Corsican evergreen oak forest [females: continent, 1.35 ± 0.66 years; Corsica, 2.16 ± 1.44 years; analysis of variance (ANOVA): F = 18.71, P < 0.001; males: continent, 1.35 ± 0.75 years; Corsica, 2.23 ± 1.62 years; ANOVA: F = 15.29, P < 0.001]. The proportion of females that bred more than 1 year in the local population fell from 52.7% in the matched population to only 25.0% in the mismatched population, and for males it fell from 49.6% to 22.2% (females: χ^2 = 13.2, P < 0.001; males: χ^2 = 14.9, P < 0.001).

The following pattern emerges: When breeding date is matched with the peak in food supply, blue tits work at levels typical of other breeding birds when provisioning their young (*18–20*). Brood size and nestling demand appear to be adjusted to the level of prey abundance such that parental metabolic effort lies at 3 to 4 × BMR, which the prudent parent hypothesis associates with the highest metabolic effort that does not compromise survival and future reproductive success (*21*). Individuals who fail to match breeding date with local food supply, as a result of either gene flow from habitats with a different resource phenology or insufficient phenotypic plasticity, face low prey densities. The consequent mismatching between nestling demand and prey abundance forces parents to increase foraging effort beyond their sustainable limit, resulting in a tradeoff between immediate metabolic effort and persistence in the breeding population. The reduction in adult persistence and the decline in nestling size that result from mismatching act together to constitute stabilizing selection, setting photoperiod response and the chronology of the ensuing reproductive events.

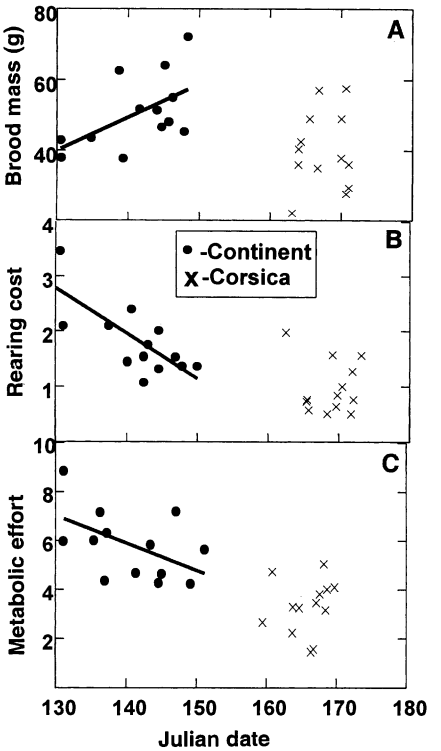

Fig. 2. Brood mass and energetic costs for blue tit parents as a function of breeding date. (**A**) Summed mass of all nestlings at 14 days of age. (**B**) Cost to individual parents rearing nestlings, in terms of kJ day^{-1} adult^{-1} per gram of nestling (calculated from FMR_{day}/brood mass). (**C**) Metabolic effort for adults, measured as $FMR_{24\text{-}h}$/BMR. Slight variations in date between panels are due to random jitter induced so as to separate overlapping data points.

The combination of lower metabolic effort and higher persistence in the matched Corsican population and higher metabolic effort and lower persistence in the mismatched continental population supports the prudent parent hypothesis. By interacting with nestling number and quality, the tradeoff between foraging cost and persistence sets the optimal level for metabolic effort at 3 to 4 × BMR, beyond which individuals face a decline in fitness. The fitness cost of excessive metabolic effort also provides the physiological mechanism by which a broad spectrum of terrestrial birds have responded to global warming by advancing their breeding date (*23*).

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15. This study was conducted in 1998 at Pirio in the Fango Valley, Corsica, and near Vic-le-Fesq, 40 km north of Montpellier, France. Caterpillar abundance was monitored at 3-day intervals with 15 frass collectors, each 0.5 m^2, placed under the tree canopy at five stations in each study site (Corsica, 13 years; continent, 10 years).
16. Blue tits bred in nestboxes at densities of 0.5 to 2 pairs per hectare. First egg and hatching dates and clutch and brood size were determined by routine nest inspections. When nestlings were 13 to 14 days of age (here used to define breeding date), adults were captured in mist nets, then weighed to ±0.1 g, banded, and injected with 60 μl of doubly labeled water ($^2H_2{}^{18}O$). After a 30-min equilibration period, an initial blood sample (20 to 30 μl) was drawn from the brachial vein and sealed in a capillary tube. We then released adults and weighed nestlings. We recaptured adults in the nest after 24 ± 0.5 hours and drew a second blood sample. Blood samples were later microdistilled, and ^2H and ^{18}O abundances in the water were determined by isotope ratio mass spectrometry at the University of Aberdeen. See (*24*) for detailed descriptions of doubly labeled water applications and methodology.
17. We calculated $FMR_{24\text{-}h}$ for 13 Corsican and 13 continental adults using the single pool equation (equation 7.17) from Speakman (*24*). $FMR_{24\text{-}h}$ did not differ significantly between males and females in either population, so sexes were pooled. Because only daytime (sunrise to sunset) FMR is directly related to nest provisioning, we subtracted nighttime metabolic rates from $FMR_{24\text{-}h}$ to leave FMR_{day}. We estimated nighttime metabolic rate (mW) as $609.64 - 17.41 \cdot T_a$, where T_a is average ambient temperature recorded during the measurement night (*21*). BMR was 15.5 mW/g and 17.5 mW/g for birds from the continental and Corsican populations, respectively (D. W. Thomas, J. Blondel, P. Perret, *Zoology*, in press).
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22. We used mean interannual residency time to estimate survival for breeding individuals in the two populations (Corsica: 383 females, 387 males; continent: 60 females, 54 males).
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Sterility of *Drosophila* with Mutations in the Bloom Syndrome Gene—Complementation by *Ku70*

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The *Drosophila Dmblm* locus is a homolog of the human Bloom syndrome gene, which encodes a helicase of the RECQ family. We show that *Dmblm* is identical to *mus309*, a locus originally identified in a mutagen-sensitivity screen. One *mus309* allele, which carries a stop codon between two of the helicase motifs, causes partial male sterility and complete female sterility. Mutant males produce an excess of XY sperm and nullo sperm, consistent with a high frequency of nondisjunction and/or chromosome loss. These phenotypes of *mus309* suggest that *Dmblm* functions in DNA double-strand break repair. The mutant *Dmblm* phenotypes were partially rescued by an extra copy of the DNA repair gene *Ku70*, indicating that the two genes functionally interact in vivo.

The human recessive disorder, Bloom syndrome, is characterized by an elevated risk for a wide variety of cancers, as well as immunodeficiency, slow growth, and partial sterility (*1*). Cells from Bloom syndrome patients exhibit greatly enhanced rates of sister chromatid exchange. The causative mutations are in *BLM* (*2*), which encodes a RECQ helicase. Mutations in two other RECQ helicase genes, *WRN* and *RecQ4*, are responsible for Werner syndrome and Rothmund-Thomson syndrome, which are both associated with cancer predisposition and premature aging (*3*, *4*).

In mice, one *BLM* mutant line is viable and exhibits Bloom syndrome phenotypes (*5*). Our previous work showed that the *Drosophila Dmblm* gene is closely related to *BLM* (*6*). Here, we show that *Dmblm* corresponds to *mus309*, which had been originally identified in a mutagen-sensitivity screen (*7*).

In an earlier study, Beall and Rio (*8*) reported that *mus309* corresponds to a *Drosophila* homolog of *Ku70*, whose gene product binds to the ends of double-stranded DNA breaks. Their conclusion was based on low-resolution mapping information and a preliminary indication of partial complementation by a *Ku70* transgene of the mutagen sensitivity of *mus309*. However, Szabad (*9*) found that deficiency *Df(3R)T–7*, abbreviated *Df T7*, failed to complement the sterility of *mus309* mutations. This deficiency lies in polytene chromosome region 86F1-2 (*10*, *11*) as opposed to 86E2-3 where *DmKu70* had been placed (*11*). These considerations suggested that *Dmblm*, which maps to 86F1-4 (*6*), is a better candidate for *mus309* than *DmKu70*.

To test this possibility, we used P element–induced male recombination (*12–14*) to create a series of deletions in the 86E-F region. These deletions, along with *Df T7*, were tested against the mutant allele $mus309^{D2}$, and four P element–insertion mutations in the area, to generate a more detailed deletion map of 86E-F (Fig. 1A). The *mus309* phenotypes tested were mutagen sensitivity and female sterility. The results ruled out the reported identity between *DmKu70* and *mus309*, but were consistent with identity between *Dmblm* and *mus309*.

We next sequenced the *Dmblm* genes from the two existing mutant alleles of *mus309*, and found that both carry mutational changes that could potentially impair or abolish the function of *Dmblm* (Fig. 1B). The less severe allele, $mus309^{D3}$, encodes lysine instead of glutamic acid within a conserved region of helicase motif II, plus another amino acid substitution near the COOH-terminus. The more severe allele, $mus309^{D2}$, has a stop codon between helicase motifs III and IV, and is expected to yield a severely truncated polypeptide. Both *mus309* alleles were induced by ethylmethane sulfonate (*7*), which generates predominantly G → A transitions (*15*), and notably, the two suspect changes in the helicase region are both G → A transitions (Fig. 1B).

We constructed a P element–borne transgene carrying the *Dmblm* cDNA driven by an *hsp70* heat shock promoter (*16*), and we tested its ability to rescue *mus309* phenotypes. The methylmethane sulfonate (MMS) sensitivity was rescued, at least partially, by each of two transgene insertions tested (Fig. 1C). Position effects normally preclude complete rescue by transgenes of this kind. Both mutant *mus309* alleles were rescued by the *hsp-Dmblm* transgene, and the degree of complementation was enhanced by heat shock for both transgene insertions (Fig. 1C). The sterility phenotype of *mus309* males and females was also complemented by the *Dmblm* transgene (Fig. 2) (*17*).

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