Global warming is changing the optimal time of breeding in birds (1), and as a result interest has increased in causes and consequences of variation in time of breeding. Thomas et al. (2) reported that energy expenditure of blue tits, Parus caeruleus, feeding young decreased as their breeding time was closer to the peak in caterpillar food supply, and that “persistence” (number of years individuals breed) is lower in a mismatched population, compared with a matched population breeding at the same time. We do not believe that their data justify these conclusions.

It appears from figure 2c in (2) that the reported seasonal decrease in metabolic effort hinges on only one data point. To verify this, we recalculated the regression after reading the data from the graph. We found that \( r^2 = 0.23 \) (\( P = 0.11 \)), which deviates substantially from the \( r^2 = 0.45 \) (\( P < 0.001 \)) that was reported. (Incidentally, if \( r^2 = 0.45 \), then \( P = 0.01 \), and not \( P < 0.001 \).) In contrast, our recalculation gave very similar results for figures 2a (\( r^2 = 0.30, 0.34 \) reported) and 2b (\( r^2 = 0.53, 0.56 \) reported), and our recalculation closely matched the regression line in figure 2c, which is much shallower then the regression line mentioned in the text. Furthermore, when the most extreme data point was removed, \( r^2 \) dropped to 0.08 (\( P = 0.4 \)), a pattern that confirmed our first impression. Thus, it appears that the evidence for an effect of time of breeding on metabolic effort is weak at best.

That is not to say that we should not perhaps expect such a relationship and, indeed, this could be important in understanding the effects of global warming and the consequences of the resulting mismatching of time of breeding. We therefore investigated whether such a trend is present in our own data set (3, 4) on a closely related species, the great tit, Parus major, where reproductive success also decreases with increased mismatching (5). We did not correct for night-time expenditure, because metabolic rate during day and night may not be independent (6). We found no effect of degree of matching between breeding time and caterpillar peak on energy expenditure (Fig. 1). Thus, we were unable to replicate the pattern reported by Thomas et al., despite having a much larger sample size (104 versus 13).

Furthermore, even if we did find the pattern reported by Thomas et al., why could this not be caused by some other reason than the degree of mismatching? Could this not also be, for example, attributable to inherent differences between early and late breeding individuals or their territories, or to a seasonal increase in ambient temperature? The problem of interpretation also applies when comparing “persistence” between populations, since populations are likely to differ in other factors besides the degree of mismatching. For example, it is possible that only low-quality individuals, with a short lifespan, breed in the low-quality habitat on the continent, or that the likelihood of dispersal out of the study area may differ. Only experiments can demonstrate a causal relationship between timing of breeding and parental energy expenditure, persistence or any other parameter (7). Such experiments can lead to very different conclusions (8).

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References

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Response: Verhulst and Tinbergen begin by criticizing our statistics and our figure 2c (1). We have checked our analyses and find no errors apart from the \( P \) value for metabolic effort in table 1, which should read \( P < 0.05 \). Three different tests (studentized residuals, leverage, and Cook’s \( D \)) detected no outliers, so we find no statistical justification for excluding any data points. The confusion over our regression analyses appears to stem from our graphs in (1), in which we introduced a slight random jitter to separate overlapping points. Thus, scanning the graphs does not permit an accurate reconstruction of raw data or regression analyses, leading Verhulst and Tinbergen to incorrectly conclude that we had erred in our analyses. We agree that graphs should accurately reflect the data, and we present a jitter-free version here (Fig. 1).

Verhulst and Tinbergen find no correlation between energetic cost and the degree of mismatching between nesting demand and caterpillar peak for their two study populations, Vlieland and Hoge Velleu. The contrast between their data and ours raises an important point concerning the effect of varying environmental productivity on the optimal size of a reproductive effort and the energetic cost of provisioning nestlings. In our evergreen Holm oak (Quercus ilex) habitat in Corsica, mean brood mass for blue tits was 57 g [6.3 chicks \( \times 9.0 \) g] and peak caterpillar biomass was \( \leq 0.78 \) g caterpillars day\(^{-1}\) m\(^{-2}\) (2, 3). Mean brood mass for great tits

Fig. 1. Parental daily energy expenditure (DEE, in kJ/24h) plotted against the day relative to the peak in caterpillar abundance. Measurements from two study areas, Vlieland and Hoge Velleu. Symbols were grouped as shown, because previous analyses showed that females rearing reduced broods on the Hoge Velleu and males (measured only on Vlieland) had lower DEE (2, 3). We tested for the effect of date relative to the caterpillar peak (RELDATE), while statistically controlling for sex and brood size manipulation (manipulation = 1 for females rearing reduced broods on the Hoge Velleu, and manipulation = 0 for all other measurements). We also tested RELDATE\(^2\), because under the hypothesis of Thomas et al., birds that are relatively late or early are both expected to have an elevated DEE. Neither RELDATE nor RELDATE\(^2\) were significantly correlated with DEE in this model (RELDATE: \( F_{1,100} = 0.50, P = 0.5 \); RELDATE\(^2\): \( F_{1,99} = 0.04, P = 0.8 \); sex: \( F_{1,101} = 19.8, P < 0.001 \); manipulation: \( F_{1,101} = 5.8, P < 0.02 \)).

Controlling for year, study area, or ambient temperature did not change this result.
increased to 162 g (9.0 chicks × 18.0 g) in their mixed deciduous forest populations (4), but peak caterpillar biomass increased to 5.2 g day⁻¹ m⁻² at these same sites (5). Although demand increased 2.9-fold, supply increased by 6.7-fold, shifting the average supply-demand ratio from 14 mg caterpillars day⁻¹ m⁻² g chick⁻¹ in Holm oak habitats to 32 mg caterpillars day⁻¹ m⁻² g chick⁻¹ in mixed deciduous forest. This 2.3-fold increase in the supply-demand ratio between poor and rich habitats should reduce, and possibly eliminate, the energetic consequences of mismatching demand with supply; it should also relax the intensity of selection on the timing of reproductive events relative to the peak in food supply. The broad, high-amplitude peak in caterpillar biomass in rich habitats provides a wider temporal window for successful breeding than does the narrow, low-amplitude peak in poor habitats.

Data for our poor evergreen oak habitat and a separate rich deciduous downy oak (Q. pubescens) habitat in Corsica (2) allow us to test for an effect of amplitude in peak caterpillar biomass on fledging success (proportion of hatcheds chicks that fledge). In evergreen oak habitat, a stepwise regression shows that success is strongly affected by amplitude (F = 34.0, P < 0.0001), brood size (F = 18.1, P < 0.001), and breeding date (F = 5.7, P = 0.02), with increasing amplitude weakening the negative effects of brood size and date (n = 395 nests, 10 years). In Corsican deciduous oak forest, where peak caterpillar biomass was 10 times higher (7.4 g d⁻¹-m⁻², similar to Vlieland and Hoge Veluwe), fledging success was independent of amplitude, brood size, or date (P > 0.1 in all cases; n = 179 nests, 7 years). The same pattern has been described for Hoge Veluwe (6). These data suggest that because tits do not closely track increasing environmental productivity (supply) by proportional increases in clutch size (demand), energetic and fitness costs associated with the timing of reproductive events change between years within a habitat and across broad landscapes. We view the data of Verhulst and Tinbergen as a valuable complement to ours, shedding new light on spatial variation in the selection pressures that shape breeding.

Verhulst and Tinbergen stress the importance of experiments in ecological studies, arguing that without experimental manipulations we cannot unambiguously establish a causal relationship between breeding date and energetic cost or metabolic effort and persistence in the breeding population. We heartily agree. We relied on a unique natural experiment whereby gene flow and immigration from adjacent populations created one population in which the timing of breeding was mismatched with peak food availability. Although the pattern of increasing energetic cost and decreasing persistence of adults in the breeding population was consistent with theory predicting trade-offs between current effort and future reproductive prospects (7), other ecological factors could confound this interpretation. Unfortunately, breeding date cannot easily be manipulated independently of other ecological variables, so our natural experiment was the closest thing to a controlled experiment that currently exists. We anxiously await breakthroughs that may one day permit phenotypic engineering (8) and allow for truly controlled experiments in free-ranging populations. In the meantime, our data provide provocative support for the existence of a trade-off between metabolic effort and future reproductive prospects, which in turn shapes breeding patterns when food is limiting.

**References**

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