

Food availability dictates the timing of parturition in insectivorous mouse-eared bats

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Arlettaz, R., Christe, P., Lugon, A., Perrin, N. and Vogel, P. 2001. Food availability dictates the timing of parturition in insectivorous mouse-eared bats. – *Oikos* 95: 105–111.

Which of these two confounding factors, weather or food availability – that largely correlate and interact – controls the timing of parturition in insectivorous bats? To answer this question, we took advantage of a predator-prey system that offers a unique opportunity to perform natural experiments. The phenology of reproduction of two sibling bat species that inhabit the same colonial roosts, but exploit different feeding niches, was investigated. *Myotis myotis* feeds mainly on carabid beetles, a food source available from the end of hibernation onwards, whereas bush crickets, the main prey of *M. blythii*, are not available early in the season due to their successive instars; cockchafers are actually the sole possible alternative prey for *M. blythii* at that time of the year, but they occur every third year only, independently of local weather conditions. By comparing the species responses to the presence/absence of cockchafers, we could test the hypothesis that food availability, rather than climate, influences the timing of bat parturition. Our data show that *M. blythii* gave birth, on average, 10 d later than *M. myotis* in years without cockchafers, whilst parturition (1) was synchronous during cockchafer years, and (2) did not show much among-year time variation in *M. myotis*. This suggests that food availability is the chief factor regulating the timing of parturition in mouse-eared bats.

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All biomes are marked by the seasonality of climate and, its corollary, that of food resources. Accordingly, for any animal population, natural selection usually promotes synchronization of breeding events with the period of maximum resource availability (Lack 1950, 1968, Nager and van Noordwijk 1995), so that breeding adults eventually tend to optimize both survival of their offspring and their own life-time reproductive success (Klomp 1970, Korpimäki 1992). The timing of reproduction is therefore a very important life history trait of species (Drent and Daan 1980, Price et al. 1988, Daan and Tinbergen 1997). Like most insectivorous vertebrates, bats occurring in the temperate zones give birth when insect food is plentiful, normally in late spring or early summer (Racey et al. 1987, Ransome 1990, Rydell

1992, Ransome and McOwat 1994, Rydell et al. 1994). Yet, before the onset of hibernation, females have not only to lead their offspring to weaning, but they must also mate and deposit enough fat reserves (Barclay 1991, Grindal et al. 1992, Ransome 1995). The latter are crucial to over-winter survival, particularly for yearlings (Ransome 1968, Thomas et al. 1990). Early breeding is thus favoured in temperate-zone insectivorous bats (Ransome 1995) as in other vertebrates (Korpimäki 1987, Daan et al. 1988, Hochachka 1990; but see Nager and van Noordwijk 1995).

Bat parturition seems chiefly influenced by atmospheric conditions, with cool and rainy springs usually provoking a delay in the delivery period (Ransome 1973, Grindal et al. 1992, Ransome and McOwat 1994).

Accepted 29 March 2001

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ISSN 0030-1299

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The mechanism behind this is clear: gestation slows down dramatically when bats enter torpor, which in turn causes a reduction in overall metabolic turnover for both the mother and the embryo (Eisentraut 1937, Racey 1973, Ransome 1973, Racey and Swift 1981, Lewis 1993, McOwat and Andrews 1994–95). The question remains, however, whether the influence of weather on gestation length and bat delivery term is direct or indirect, because bats are presumed to readily enter torpor either when weather is cold, or food is scarce. As food availability correlates with climate, it is difficult to isolate the factor contributing more to reproduction postponement. Although laboratory experi-

ments have established that both factors can indeed interact (Racey 1973), field studies could mainly find correlations between the onset of reproduction and weather conditions (e.g. Ransome 1973, Rydell 1989, Grindal et al. 1992, Ransome and McOwat 1994). Empirical evidence for an independent role of food supply during gestation is thus lacking. We present here comparative data collected over seven years on two sibling species of bats that coexist intimately in their breeding colonies, testing for the food availability hypothesis, against climate, as a major factor determining the timing of bat parturition in nature.

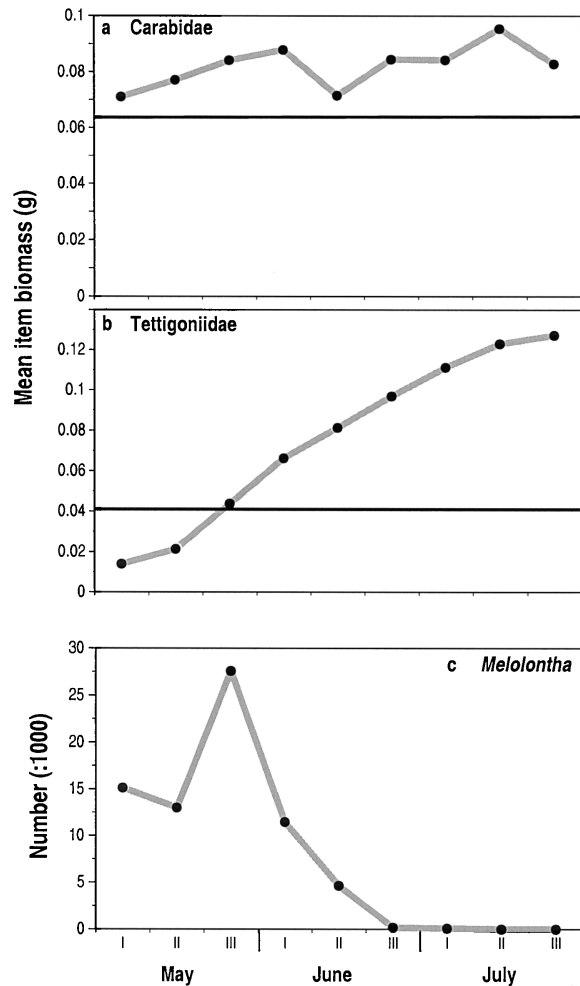


Fig. 1. Mean item biomass (g dry weight) of carabid beetles (a) and bush crickets (b) collected at the study site (redrawn from Arlettaz 1995). The horizontal black line indicates the minimum estimated body mass of prey items found in the diet (faecal analyses) of *M. myotis* and *M. blythii* (from Arlettaz and Perrin 1995). Due to their successive instars, bush crickets are not available until the last 10 d of May, contrary to carabid beetles. (c) Phenology (number of individuals emerging from the ground) of cockchafer at the study site (redrawn from Arlettaz (1995); see that study for more details).

Study species

The greater and lesser mouse-eared bats, *Myotis myotis* (Borkhausen 1797) and *M. blythii* (Tomes 1857), respectively, are two sibling species of bats which have diverged recently (Ruedi et al. 1990, Arlettaz et al. 1991, 1997a). Where sympatric, they coexist intimately in the same nursery colonies but exploit different categories of prey and habitats (Arlettaz et al. 1997b, Arlettaz 1999). *M. myotis* relies principally on terrestrial carabid beetles, whereas the bulk of the diet of *M. blythii* consists of bush crickets typical of grassy habitats. Although carabid beetles present an almost constant food resource throughout the season for *M. myotis* (Arlettaz 1996), bush crickets become available to *M. blythii* only from early June onwards because of their successive instars (Fig. 1a, b). So, while *M. myotis* has access to its primary prey from around the exit of the hibernation period, the basic prey of *M. blythii* is not available before late May or early June. Indeed, Arlettaz and Perrin (1995) have shown that the minimum body mass of bush crickets eaten by *M. blythii* is 0.043 g (dry weight) (vs 0.063 g for carabid beetles, the main prey of *M. myotis*), which corresponds to a body size “threshold” which is not reached before the last 10 d of May in the warmest habitats of southern Switzerland (Fig. 1b). Consequently, *M. blythii* cannot forage optimally early in the season, contrary to *M. myotis* (Fig. 1a), unless alternative prey is available. At the study site, cockchafer *Melolontha melolontha* is actually the only prey that can play this substitutive role (Fig. 1c; Arlettaz and Perrin 1995), making up to 96% of the estimated biomass caught by *M. blythii* in May [in comparison, that prey plays a marginal role for *M. myotis* (Arlettaz et al. 1997b)]. However, cockchafer occur only every third or fourth year, according to geographic area, but independently of climatic conditions within a given area (Arlettaz 1996). Thus, whilst this prey represents an unlimiting food supply in the so-called cockchafer years, due to their phenomenal emergences, it remains almost totally absent in years when no flights of *M. melolontha* are observed. As a

result, in years without cockchafers, *M. blythii* lacks optimal food early in the season, which would theoretically constrain it to spend comparatively more time in torpor, thus inexorably prolonging gestation in pregnant females.

Hypothesis testing

Taking advantage of this predator-prey system, we tested the following hypotheses. If resource availability is the main factor that determines the timing of parturition in insectivorous bats, then we predict that births should take place later in *M. blythii* than in *M. myotis* during years without cockchafers, but synchronously when the two species have access to sufficient food resources, i.e. during cockchafer years. As a corollary, the (absolute) date of parturition should show little variation among years in *M. myotis*, at least when compared to the variation induced by the presence/absence of *M. melolontha* as regards parturition in *M. blythii*. Given that we replicated measures over seven years and used years with and without cockchafers as treatment and control, respectively, our study is a “natural experiment” (Begon et al. 1986). Also, because the two bat species roost in the same church attics in our sympatric populations, they face similar overall environmental conditions, which provides a control for climatic factors.

Methods

This study was conducted in 1991–1992 and 1995–1997 at one roost (Raron, site A), and in 1998–1999 at two roosts (Raron; Naters, site B) in the upper Rhône valley (canton of Valais, southwestern Switzerland, 46°15' N, 7°30' E); no data were collected in 1993 and 1994. Both roosts shelter mixed nursery colonies of *M. myotis* and *M. blythii*.

Every ten days from early May to the first 10 d of July, bats were mist-netted at the entrance to church attics when they returned from nightly foraging. At any visit to a given roost, we attempted to capture at least 15 reproductive females per species. Pregnant females were easily distinguished by the bulk of embryo, perceptible at palpation, whereas lactation was assessed by gently squeezing the nipples to extract some milk (Racey 1989). For every 10-d period, by considering colonies and species separately, we calculated the proportion of captured reproductive females that had already given birth, i.e. that had entered the phase of lactation.

When analysing the results, the question of the independence of data arises, i.e. what constitutes a sampling unit. One option is to consider each reproducing female

as an independent source of information, and thus each colony as a collection of samples. The conservative alternative is to consider individuals within one colony as non-independent (because the decision to initiate reproduction may depend on what conspecifics in the colony are doing), so that each colony would provide only one independent data point per species. We chose this second, conservative option, and used the specific samples from each colony to infer a single parameter on which tests were performed. This parameter was the median of the distribution, corresponding to the date at which 50% of the females of one species within a colony had given birth (i.e. were lactating). It was inferred by fitting a logistic regression to the temporal data for each species and colony:

$$y = \frac{1}{1 + e^{c-rx}} \quad (1)$$

where y is the proportion of females having given birth, and x is time. The parameter r expresses the rate at which the asymptote (unity) is reached, and c fixes the localization of the distribution on the time axis. Both parameters were obtained by non-linear fitting of eq. 1 (least-squares estimate) using the NONLIN procedure of Systat (Wilkinson et al. 1992). The median \bar{x} was then obtained by setting $y = 0.5$, i.e.:

$$\hat{x} = \frac{c}{r} \quad (2)$$

We first tested whether there was a difference in the median date (absolute time; day 0 was arbitrarily set on 1 May) of parturition in both species in relation to the presence-absence of cockchafers over the time series. Then we tested the effect of prey availability on the difference in timing (relative time) between species; this allowed us to get rid of any among-year variance, presumably climatic, affecting both species simultaneously. A non-parametric (Mann-Whitney) test was thus performed on the dependent variable $d_x = \hat{x}_b - \hat{x}_m$, where \hat{x}_m and \hat{x}_b are the median dates for initiating parturition in *M. myotis* and *M. blythii*, respectively, estimated for each year and each colony over the seven years of data collection. The grouping variable was again the presence/absence of *Melolontha*.

Results

In *M. myotis*, parturition took place, on average (\pm s.d.; n), on day 45.8 (± 6 , $n = 4$) (ca 15 June) during cockchafer years, compared to day 48.1 (± 6 ; $n = 5$) (17 June) in years without cockchafers, a non-significant difference (Mann-Whitney, $U = 11$, $n = 4$ and 5 , $p = 0.81$). In contrast, in *M. blythii*, the mean date of

parturition was day 48.2 (± 3 , $n = 4$) (17 June) in cockchafer years, compared to day 57.8 (± 6 ; $n = 5$) (27 June) in years without cockchafers; this difference is statistically significant ($U = 19$, $n = 4$ and 5 , $p = 0.027$). Accordingly, *M. blythii* gave birth, on average, 9.7 (± 1 ; $n = 5$) d later than *M. myotis* in years without cockchafers, whereas this delay was only 2.4 (± 2 ; $n = 4$) d in cockchafer years (Fig. 2), a difference which is significant ($U = 20$, $n = 5$ and 4 , $p = 0.014$).

Discussion

These natural experiments demonstrate that the timing of parturition in free-ranging mouse-eared bats is essentially under the control of seasonal food availability. Compared to *M. myotis* that exploits almost unvarying food sources (Arlettaz 1996), the time of parturition in *M. blythii* – the species relying on cockchafers early in the season when available – was substantially delayed (about 10 d on average) in years when that prey was absent, whereas mean delivery terms were almost synchronous in the two species in years when food supply was sufficient for both of them, i.e. during cockchafer years. It can further be inferred from our data that most of the variation in the period when parturition takes place in mouse-eared bats depends on prey availability rather than on climatic factors, since the cockchafers effect in *M. blythii* was significantly greater than the (non-significant) among-year variation – which chiefly relates to seasonal weather conditions – in the timing of parturition of *M. myotis*. This suggests that food availability, rather than climate, is the prime factor determining the period when temperate-zone insectivorous bats give birth. In other words, the weather would affect delivery term indirectly, through its impact on food availability, instead of acting directly upon the bats' physiological decisions. Studies on birds have led to similar conclusions. Yet, the patterns observed in mouse-eared bats (average time lag of 10 d between species) appear much more contrasted than in any bird study (usually 3–6 d; Källander 1974, Clamens and Isenmann 1989, Källander and Karlsson 1993, Svensson and Nilsson 1995); this is probably due to the heterothermic behaviour of bats that can take instantaneous, daily decisions as regards energy allocation (lethargy vs homeothermy), and this at any stage of their yearly cycle. That physiological option seemingly produces greater time lags in bats than in birds.

As cockchafers are in no case available later than mid-June (Fig. 1), the presence of that prey affects primarily the nutritional state of *M. blythii* females during pregnancy, but would be a priori of marginal importance for lactating females. However, gravid females that have access to sufficient food resources remain largely homeothermic throughout pregnancy

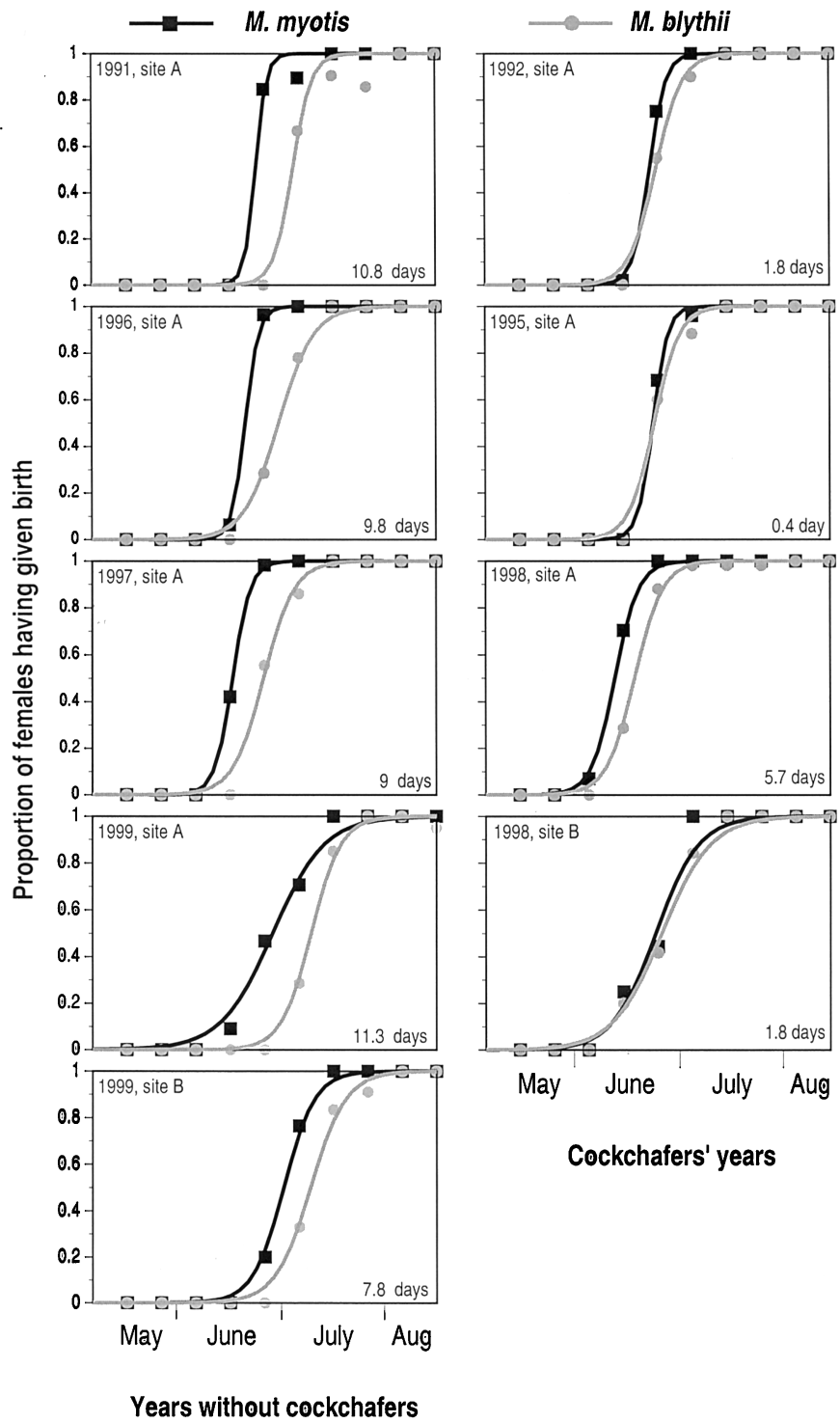
and allocate proportionally more energy to reproduction, i.e. foetus growth, than to maintenance. This means that the advantage of feeding on a temporarily and spatially unlimited food source such as cockchafers early in the season (Arlettaz 1996) further enables females to start lactation, i.e. the energetically most demanding period of the bat reproductive cycle (Kurta et al. 1989, 1990), in excellent physical condition.

The species-specific pattern observed in the reproduction of the two species of mouse-eared bats lets us envisage diverging life history strategies. Early breeding in bats improves both the immediate survival of the new cohort and the long-term survival of mothers (Ransome 1989, 1995). Accordingly, we predict that cohorts of *M. blythii* born in cockchafer years should be overrepresented in the population, whilst no preponderance of a given cohort should be found in *M. myotis* as no such marked inter-annual variation in timing of parturition occurs in the latter species (Fig. 2). Also, the age at first reproduction may differ between the two species, with *M. blythii* being, on average, more inclined to reproduce at an older age; it is indeed unlikely for females born in non-cockchafer years to reproduce during their first year of life as natural selection would impede bats born so late in the season from completing their first-year biological cycle with a first attempt to mate (Arlettaz et al. 1999).

Cockchafers could also play a major role in the context of species distribution and population survival. Their presence might for instance be a decisive prerequisite for the colonization of northern areas by *M. blythii*. As this species relies primarily on bush crickets throughout its range (Arlettaz et al. 1997b), alternative prey are apparently necessary for the establishment of reproductive populations at high latitudes. In Central Europe, there are obviously no other prey than cockchafers which may play that role (Arlettaz 1996). Interestingly, the geographic distribution of *M. blythii* in northern Central Europe seems to coincide with that of *Melolontha* (Arlettaz et al. 1994). The reduction of cockchafer populations in many European countries over the past decades, due mainly to the intensification of farming practices and to the degradation of agricultural habitats, may have had strong effects upon local populations of the lesser mouse-eared bat. This may for instance be the reason for its current absence in areas of Switzerland where the species occurred formerly (Chapuisat and Ruedi 1993). Cockchafers may therefore appear crucial for the long-term survival of *M. blythii* at the northern border of its range.

Acknowledgements – We thank all who took part in field work, in particular G. Carron, Y. Crettenand, B. Posse and A. Sierro. The municipalities and parishes of Raron and Naters provided free access to bat roosts. This research was supported by a credit of the Swiss National Science Foundation (31-52584.97) to P. Vogel, R. Arlettaz and Ph. Christie; additional fundings were provided by the Réseau Chauves-souris Valais (Coordination Suisse pour l'Etude et la Protection des Chauves-souris) and the Fondation Dr Ignace Mariétan.

Fig. 2. Proportion of reproductive females having given birth in two mouse-eared bat populations in 1991–1992, and 1995–1999, with respect to presence/absence of cockchafer. Logistic equations were calculated from the observed distributions indicated by the dots. The interval (in days) between the median time values obtained for the two species is given for each situation.



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