Differential species-specific ectoparasitic mite intensities in two intimately coexisting sibling bat species: resource-mediated host attractiveness or parasite specialization?

PHILIPPE CHRISTE*, MAUD S. GIORGI*, PETER VOGEL* and
RAPHAËL ARLETTAZ†

Institut d'Ecologie, Laboratoire de Zoologie et d'Ecologie Animale, Bâtiment de Biologie, Université de Lausanne, CH-1015 Lausanne, Switzerland, and †Zoological Institute – Conservation Biology, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

Summary

1. The mechanisms underlying host choice strategies by parasites remain poorly understood. We address two main questions: (i) do parasites prefer vulnerable or well-fed hosts, and (ii) to what extent is a parasite species specialized towards a given host species?

2. To answer these questions, we investigated, both in the field and in the lab, a host–parasite system comprising one ectoparasitic mite (*Spinturnix myoti*) and its major hosts, two sibling species of bats (*Myotis myotis* and *M. blythii*), which coexist intimately in colonial nursery roosts. We exploited the close physical associations between host species in colonial roosts as well as naturally occurring annual variation in food abundance to investigate the relationships between parasite intensities and (i) host species and (ii) individual nutritional status.

3. Although horizontal transmission of parasites was facilitated by the intimate aggregation of bats within their colonial clusters, we found significant interspecific differences in degree of infestation throughout the 6 years of the study, with *M. myotis* always more heavily parasitized than *M. blythii*. This pattern was replicated in a laboratory experiment in which any species-specific resistance induced by exploitation of different trophic niches in nature was removed.

4. Within both host species, *S. myoti* showed a clear preference for individuals with higher nutritional status. In years with high resource abundance, both bat hosts harboured more parasites than in low-resource years, although the relative difference in parasite burden across species was maintained. This pattern of host choice was also replicated in the laboratory. When offered a choice, parasites always colonized better-fed individuals.

5. These results show first that host specialization in our study system occurred. Second, immediate parasite choice clearly operated towards the selection of hosts in good nutritional state.

Key-words: host specificity, host–parasite coevolution, *Melolontha melolontha*, *Myotis myotis*, *Myotis blythii*.

Journal of Animal Ecology (2003) **72**, 866–872

Introduction

Reproductive success and survival of free-living animals largely depend on environmental conditions, in

Correspondence: Philippe Christe, Institut d'Ecologie, Laboratoire de Zoologie et d'Ecologie Animale, Bâtiment de Biologie, Université de Lausanne, CH-1015 Lausanne, Switzerland. Tel: +41 21 692 41 82; E-mail: philippe.christe@ie-zea.unil.ch

particular habitat and trophic resources. In parasites, habitat and trophic conditions can both be merged into the notion of 'host status'. Yet, what determines 'host quality' from a parasite viewpoint remains a challenging issue because host traits influencing the parasite's colonization success may differ considerably from those influencing their suitability as a nutritional resource. Hosts that are vulnerable to parasitism are likely to be in a poor nutritional state, and thus may represent a suboptimal source of nutrients. Parasites

seeking out such vulnerable hosts may improve their survival and reproductive success by visiting a greater number of individual hosts; in other words, host quantity can compensate for poor host quality. Alternatively, parasites may favour the exploitation of fewer high-quality hosts, which would provide better single meals (high energetic and nutritive value). However, the efficacy of antiparasite avoidance mechanisms used by the host is expected to correlate positively with general host physiological condition, so high-quality hosts may be particularly difficult to colonize and exploit (Gershwin, Beach & Hurley *et al.* 1985; Lochmiller, Vestey & Boren 1993; Saino, Calza & Møller 1997; González *et al.* 1999; Møller 2000). Since most host–parasite systems are dynamic, with the two parties subjected to continuous reciprocal evolution (coevolution), the relative importance of host accessibility and quality to host-choice strategies may change over time, resulting in an evolutionarily stable mix of individuals preferring vulnerable or high-quality hosts. Alternatively, coevolution could maintain a continuum of host preferences, of which these two strategies represent the extremes.

Some empirical studies of host-choice strategies have demonstrated fixed preferences for vulnerable hosts. In bats, for instance, it has been demonstrated that juveniles, which exhibit low body mass, relatively naive immune systems and nearly no antiparasite behaviour (McLean & Speakman 1997), harbour many more parasites than adults (Christe, Arlettaz & Vogel 2000a). Similarly, within clutches of bird nestlings, it has been hypothesized that parasites aggregate on the chick with the lowest immune defences, with that particular chick usually showing the poorest body condition (Christe, Møller & de Lope 1998). In contrast, other studies have described preference for hosts with good body condition or better development within brood (Blanco, Tella & Potti 1997; Dawson & Bortolotti 1997; Roulin *et al.* 2003). It remains therefore difficult to envision whether mixed strategies actually occur in nature and, if so, under what circumstances they are maintained.

Coevolutionary processes should also affect the diversity of and preference for different potential host species. Broad tolerance to environmental factors, as well as a high mobility, will generally facilitate the exploitation of several host species (Tripet & Richner 1997), while narrow selection pressures and restricted mobility lead to host specialization and to speciation (Futuyama & Moreno 1988; McCoy *et al.* 2001; Johnson *et al.* 2002; Tripet, Christe & Møller 2002). Colonial birds and bats living in social aggregations offer very favourable circumstances for parasite specialization and speciation because such colonies are usually discrete units with restricted exchanges among populations (McCoy *et al.* 1999, 2001; Tella 2002; Tripet *et al.* 2002). They thus represent excellent opportunities for investigating the questions raised by host specialization.

In the present study, we attempted firstly to evaluate the relative importance of alternative host-choice strategies for an ectoparasitic mite (*Spinturnix myoti* Kolenati 1856) infesting bats. For this purpose, we used its two principal hosts, the greater and lesser mouse-eared bats, *Myotis myotis* Borkhausen 1797 and *M. blythii* Tomes 1857, respectively, and looked at patterns of host preference with respect to nutritional condition. Secondly, we investigated the extent of host specialization in *S. myoti* by comparing infestation rates and mite preference for the two host species. This system is ideal for studying the evolution of parasite specialization for three main reasons. First, *M. myotis* and *M. blythii* are two genetically closely related, sibling species, which share a long common evolutionary history since they appear to have diverged recently (Arlettaz *et al.* 1997a). Second, despite their high morphological similarity, *M. myotis* and *M. blythii* exhibit clear-cut partitioning of dietary niches (Arlettaz & Perrin 1995; Arlettaz, Perrin & Hausser 1997b; Arlettaz 1999), exploiting species-specific categories of arthropod prey which differ in abundance among seasons and years, producing some interspecific variation in host nutritional status. Third, when sympatric, these two bat species usually form mixed nursery colonies, which could potentially allow interspecific transmission of ectoparasites. *Spinturnix myoti* is a rather specific parasite, having apparently been recorded on only a few other *Myotis* species in addition to the mouse-eared bats (Uchikawa *et al.* 1994). The mite is clearly detrimental to the bats: when faced with an experimentally increased number of *Spinturnix*, both their grooming rate and respirometry metabolism increase drastically (Giorgi *et al.* 2001). The life cycle of *S. myoti* is restricted to active blood and/or lymph feeding stages that contribute to maturation and reproduction. During its entire life, *S. myoti* never leaves the flight and tail membranes of the bat, i.e. it never colonizes or requires any other secondary hosts or inanimate substrates. Thus, any selection pressures exerted on this mite are exclusively determined by the hosts. Parasite transmission always takes place while individuals are in close contact, i.e. mostly within colonial roosts, and parasites do not themselves disperse actively. Whether both potential host species are equally colonized by *S. myoti* may depend on intrinsic species preferences by the parasite. Even if there are no intrinsic preferences, however, species or individuals could differ in parasite infestation due to differences in the nutritional status of the hosts resulting from differential trophic resources (prey categories, availability, profitability).

We compared the parasite loads of individual *M. myotis* vs. *M. blythii* coexisting within the same nursery roosts over a period of 6 years. In order to detect any potential influence of host's nutritional status on parasite loads, we undertook comparisons of mite intensities in *M. myotis* vs. *M. blythii* across years with different trophic conditions. We took advantage of the occurrence of a cyclic prey, cockchafers *Melolontha*

melolontha Linnaeus 1758, which, when available, represents an unlimited source of food to mouse-eared bats, particularly *M. blythii* (Arlettaz *et al*. 1997b). Cockchafers have massive flights every third year, between which they are absent (this 'natural experimental system' is described in detail in Arlettaz *et al*. 2001). In addition, to equalize nutritional condition and to remove as far as possible hypothetical interspecific resistances that could be mediated by the exploitation of distinct trophic resources, we conducted laboratory choice experiments to investigate species and condition preferences under controlled conditions. Through this combination of observations and experiments, we ought to be able to disentangle the mechanisms underlying host choice in this particular mite species.

Methods

FIELDWORK

From 1995 to 2001 (except in 1999), we mist-netted juvenile bats in two nursery colonies in the upper Rhône valley (Naters and Raron, canton of Valais, SW Switzerland) at the end of the breeding season, during the second half of August. The term 'juvenile' applies here to yearlings that were already weaned at the time of capture. A total of 402 juvenile *M. myotis* and 202 juvenile *M. blythii* were investigated. Parasite intensities were recorded visually (see Christe *et al*. 2000a) on each individual. Visual inspection produced reliable counts of parasite infestation. The repeatability of parasite counts during the same capture was 0·99 ($n = 52$, $P < 0.001$). Forearm lengths were measured to the nearest 0·01 mm with a calliper; this enabled us to calculate a wing area index for each individual (forearm length squared). Bats were released immediately after manipulation. We investigated first whether there was an overall interspecific difference in parasite intensities between *M. myotis* and *M. blythii*. Second, we reanalysed the data using wing area as a covariate to test whether differences could be explained by species differences in infestation area (greater mouse-eared bats have larger wing areas than lesser mouse-eared bats). Third, we looked at the possible effect of food abundance (available to bats) on parasite intensities by comparing parasite loads between years without cockchafers (1996, 1997, 2000) vs. years with cockchafers (1995, 1998, 2001).

LABORATORY EXPERIMENTS

In 2001, 36 individual bats (18 juvenile *M. myotis* and 18 juvenile *M. blythii*) were captured within the same colonies as above and kept at Lausanne University in large semi-outdoor enclosures (under licences). They were fed a mixed diet *ad libitum* consisting of mealworms (*Tenebrio molitor*) and crickets (*Acheta domesticus*). After 1-week acclimatization to captivity, bats were randomly assigned to two experimental groups:

18 individuals (9 per species) in a food-restricted group, where a fixed amount of food was provided individually once a day (5 g for *M. blythii* and 5·5 g for *M. myotis*), and a second group with the remaining 9 individuals to which food was provided *ad libitum*. All bats had unlimited access to water.

After 1 week of this differential feeding regime, 17 *Spinturnix myoti* originating equally from *M. blythii* and *M. myotis*, respectively, were deposited on the wing membranes of each individual bat (day 0 of experiment). This number lies within the range of intensities observed in nature (Christe *et al*. 2000a). During the following 11 days, all bats were kept together in the same aviary. A single roost was offered; this constrained the bats to cluster together during the entire day, allowing complete parasite transmission among individual bats. Every day, each bat was weighed to the nearest 0·1 g and parasite number was recorded. After inspection, a given amount of food was given to each bat according to the experimental group to which it had been attributed (diet restricted vs. well fed). Then, from day 12 to day 18, food was provided *ad libitum* to all bats. On day 18, parasite number was recorded a last time before releasing the bats at the capture site.

At day 11 host immunocompetence was assessed by measuring the ability of the bat to monopolize T lymphocytes (see Christe *et al*. 2000a) against a subcutaneous injection of 0·02 ml of phytohaemagglutinin (PHA-P, Sigma Chemical Co., St Louis) in the middle of the bat footpad. Phytohaemagglutinin has a mitogenic effect on T-lymphocytes and the injection stimulates macrophage infiltration and dense perivascular accumulation of lymphocytes (Stadecker *et al*. 1977); this mimics a cell-mediated *in vivo* immune response. Ten hours after injection, footpad-swelling response at the inoculation site was measured with a calliper micrometer (0·01 mm). The change in thickness of the footpad where PHA was injected was used as a relative measure of immunocompetence (Lochmiller *et al*. 1993; Smits, Bortolotti & Tella 1999; Christe *et al*. 2000a).

STATISTICAL ANALYSIS FOR PARASITE SURVIVAL EXPERIMENT

Data analyses were performed using the program S-PLUS 2000 (MathSoft Inc. 1988–99, Seattle, WA). Every variable was tested for normality (Kolmogorov–Smirnov one-sample test) and heteroscedasticity (one-way ANOVA). No variable deviated from these two assumptions. ANOVAs (with bat species, experimental group and interaction terms as factors) were performed on body mass recorded at the time of capture, at the onset of the experiment and, finally, on body mass and number of parasites at the end of the experiment.

A repeated-measures design was used for the number of parasites recorded during the ongoing experiment because counts of the number of parasites were repeated over successive days. During the experiment,

Table 1. Mean (± SE) body mass of *M. myotis* and *M. blythii* after 11 and 18 days of experiment, respectively. During 1 week before experiment and until day 11, bats were fed individually according to the experimental treatment. From day 11 to day 18, food was given *ad libitum* to the two groups (*n* = 9 in the four experimental groups)

Body mass	*M. myotis*		*M. blythii*	
	Ad libitum	Restricted diet	*Ad libitum*	Restricted diet
Day 11	25·4 ± 0·4	21·1 ± 0·6	21·8 ± 0·7	18·9 ± 0·7
Day 18	27·4 ± 0·4	26·6 ± 0·5	24·7 ± 0·4	23·7 ± 0·3

few parasites were given birth (deuteronymphs). Bat species, experimental group and interaction were used as between-factor terms, and time was used as within-factor term. To compensate for possible lack of compound symmetry in the repeated measures ANOVA, Huynh-Feldt adjustment of the degrees of freedom in the within-factor (time) analysis was used (Glantz & Slinker 1991; Talan *et al.* 1996; Zar 1999). The adjusted degrees of freedom are directly reported in the text. All values reported are means ± SE and all *P*-values are two-tailed.

Results

PARASITE PREVALENCE AND INTENSITIES IN NATURE

Prevalence of *S. myoti* was extremely high: 99·5% of juvenile *M. myotis* and 99·2% of juvenile *M. blythii*, respectively, harboured at least one parasite. Parasite intensity, the number of parasites per infected host, was statistically different between the two host species with juvenile *M. myotis* harbouring more mites than juvenile *M. blythii* (*t*-test on log-transformed data – juveniles: *M. myotis*: 10·7 ± 0·3; *M. blythii*: 7·9 ± 0·4; $t = 6·53$, d.f. = 602, $P < 0·001$). Wing area did not account for the interspecific differences recorded (ANCOVA – species: $F_{1,599} = 8·08$; $P = 0·005$; wing area index: $F_{1,599} = 1·82$, $P = 0·177$). We are therefore definitely not in a presence of a mere between-species scaling effect.

The presence of cockchafers significantly affected the number of parasites recorded on bats. In cockchafer years, juvenile bats of both species had a higher number of parasites compared with years without cockchafers (10·0 ± 0·4 vs. 8·5 ± 0·4); the species factor was still significant, whereas the interaction term was not significant (ANOVA on log-transformed data; species: $F_{1,600} = 46·6$, $P < 0·001$; presence/absence cockchafers: $F_{1,600} = 6·39$, $P = 0·012$; species * cockchafers: $F_{1,600} = 0·013$, $P = 0·909$).

LABORATORY EXPERIMENT

Effect of feeding treatment on body mass

The two experimental groups did not differ in body mass when originally captured (species: $F_{1,32} = 5·12$, $P = 0·030$; experimental group $F_{1,32} = 0·022$, $P = 0·881$;

species * experimental group $F_{1,32} = 0·026$, $P = 0·608$). At the onset of the experiment (i.e. after 7 days of different feeding regimes within the two experimental groups), body mass was significantly higher for both species in the group fed *ad libitum* compared with the group with restricted diet (ANOVA: experimental group: $F_{1,32} = 32·53$, $P < 0·001$; species $F_{1,32} = 19·92$, $P < 0·001$; experimental group * species $F_{1,32} = 1·15$, $P = 0·290$). At the end of the experiment (i.e. after the second experimental phase of 1-week duration with food *ad libitum* for both groups) there was still a significant, although smaller, body mass difference between the two experimental groups (ANOVA: experimental group: $F_{1,32} = 4·8$, $P = 0·035$; species $F_{1,32} = 49·4$, $P < 0·001$; experimental group * species $F_{1,32} = 0·05$, $P = 0·290$) (Table 1).

Effect of experiment on parasite load

Feeding treatment strongly affected the number of parasites present during the 11 days of the experiment within the two feeding groups (ANOVA: experimental group: $F_{1,32} = 7·89$, $P = 0·008$; species $F_{1,32} = 42·42$, $P < 0·001$; experimental group * species: $F_{1,32} = 1·59$; $P = 0·217$; time (Huynh-Feldt correction) $F_{1,35}$, $P = 0·002$). *Myotis myotis* fed *ad libitum* harboured higher numbers of parasites (Fig. 1a). At day 18 (i.e. when both groups had been fed *ad libitum* again during 1 week), there was a highly significant difference in parasite load between species, with *M. myotis* harbouring more mites than *M. blythii*. In contrast, the effect of the feeding treatment had disappeared then (ANOVA: experimental group: $F_{1,32} = 0·009$, $P = 0·923$; species $F_{1,32} = 11·523$, $P = 0·001$; experimental group * species: $F_{1,32} = 0·126$; $P = 0·724$) (Fig. 1b).

Effect of experiment on cellular immune response

At day 11, T-cell response was significantly affected both by experimental treatment and by species. *Myotis myotis* fed *ad libitum* had higher PHA responses whereas *M. blythii* belonging to the food restricted group had the lowest values (ANOVA – experimental group: $F_{1,32} = 4·29$, $P = 0·046$; species $F_{1,32} = 8·56$, $P = 0·006$, experimental group * species: $F_{1,32} = 0·807$; $P = 0·376$). The immune response levels were as follows: *M. myotis ad libitum*: 1·23 ± 0·1 mm; *M. myotis* restricted diet: 0·93 ± 0·1 mm; *M. blythii ad libitum*: 0·85 ± 0·1 mm; *M. blythii* restricted diet: 0·73 ± 0·1 mm.
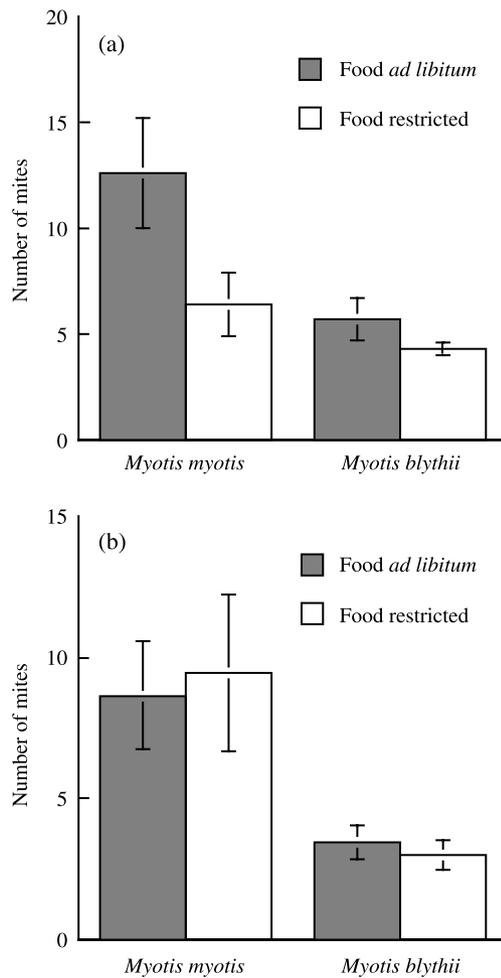
Fig. 1. Mean (± SE) individual number of mites present at day 11 (a) and at the end of the experiment (day 18, b) within the two experimental groups. *Myotis myotis* harboured more parasites than *M. blythii*, whereas individuals fed *ad libitum* furthermore exhibited more mites than bats submitted to restricted food. The effect of feeding treatment was no longer significant after both groups had been fed *ad libitum* during 1 week (b).

Discussion

HOST SPECIALIZATION

Although intimate contact among individual bats within mixed colonial clusters would theoretically enable an equal distribution of parasite burdens across species, we found significant interspecific differences in the degree of infestation by the ectoparasitic mite *Spinturnix myoti*: *M. myotis* was, on average and under all circumstances, more parasitized than *M. blythii*. This actually points to a clear host–parasite specialization within the system under scope, which appears to be, firstly, unrelated to a between-species scaling effect (*M. myotis* has a larger wing area index than *M. blythii*) and, secondly, independent of immediate host nutritional status. Different interspecific induced responses that could affect subsequent intensity of infestation

(Gasparini *et al*. 2002) between the two sibling species cannot be excluded but seems unlikely. Different explanations may hence account for the observed pattern of host species infestation.

First, interspecific differences in parasite loads observed in nature might reflect the exploitation of highly distinct resources by the sibling bat species *M. myotis* and *M. blythii* (Arlettaz *et al*. 1997b; Arlettaz 1999). Although both species are opportunistic predators that glean prey from substrates (Arlettaz 1996), they exhibit strong spatial segregation during foraging, exploiting distinct habitat types (Arlettaz 1999) and, as a result, different trophic niches (Arlettaz & Perrin 1995; Arlettaz *et al*. 1997b). *Myotis myotis* prefers feeding zones with bare ground surfaces offering easy access to ground-dwelling prey, such as ground beetles (Carabidae), which present an almost constant and highly predictable source of food for *M. myotis* throughout the vegetation period (Arlettaz 1996). In contrast, *M. blythii* appears to be associated with dense grass vegetation and feeds predominantly on grass-dwelling arthropods such as bush crickets (Tettigonidae), whose biomass (and hence availability to *M. blythii*) increases steadily from spring to mid-summer because of successive instar stages, making that prey unavailable early the season (Arlettaz *et al* 1997b; Arlettaz 1999). As this species-specific pattern of resource exploitation by the bats is likely to have remained the same for at least several thousands of years (Arlettaz *et al*. 1997a), it is possible that the evolutionary adaptations of the bat hosts to different environmental conditions may ultimately impose differential constraints on the life-history strategies of the mite. If, as discussed below, individuals in better immediate nutritional state are preferred by the parasite, it is more likely that *S. myoti* would evolve a preference for *M. myotis* rather than *M. blythii*. In other words, immediate trophic advantages may have led, over the long term, to the evolutionary fixation of the most profitable strategy within the parasite population.

Secondly, the distinct, species-specific prey exploited by *M. myotis* and *M. blythii* could influence the capacity of the host to deter and/or resist parasites. For instance, ground beetles and bush crickets may differ in their content of some substances (e.g. carotenoids) that might play an important role for acquiring immunocompetence. Although our laboratory experiment indicates that this is probably not the case (in captivity food regime was identical across bat species), the limited duration of the experiment does not really enable us to rule out that the consumption of different food types could influence the general immune system in the long term.

A third explanation that could account for the interspecific difference in parasite intensities is relative host abundance. The evolution of host specialization and specificity is thought to be related to the availability and predictability of hosts, so as to minimize extinction rates (Ward 1992; McCoy *et al*. 2001). Potential selective

pressures could arise from different host phenology or, more globally, from some differences in life-history traits between species. In a comparative analysis of parasitic nematodes, host population density and average parasite abundance were strongly positively correlated within mammalian taxa, and this was also the case when looking for a single parasite species occurring in several host species (Arneberg *et al.* 1998). In our study area, *M. myotis* is more abundant than *M. blythii*, and this could explain the observed difference in parasite intensities. In addition, the sibling mouse-eared bat species appear to differ in various life-history traits which may have some relevance. *Myotis myotis* usually breeds much earlier in the season than *M. blythii*, with a chronological gap in the timing of reproduction of 8–11 days (Arlettaz *et al.* 2001). Yet, every third year, i.e. during cockchafer years, this gap disappears completely as parturition becomes synchronous in both species (Arlettaz *et al.* 2001). This difference in host phenology could strongly influence parasite survival because late breeding may negatively affect bat juvenile survival (Arlettaz *et al.* 1998). Furthermore, *M. blythii* females reach maturity later than *M. myotis*; they begin to reproduce, on average, one year later than *M. myotis* (R. Arlettaz & P. Christe, unpublished data). Since non-reproductive bats visit nursery colonies irregularly, this will correspondingly further reduce the opportunities for parasite transmission between the two host species. Therefore *M. myotis* is a more predictable and more available host for *S. myoti* than *M. blythii*. Consequently, the absence of mobility of *Spinturnix* may have favoured spatial population structuring and promoted local adaptation in this host–parasite system.

Whatever the explanations of the interspecific difference in parasite loads, individual mites would be expected to prefer the host to which they are best adapted, that is *M. myotis* in the present case. Host preference may ultimately favour the formation of host races if not full speciation. Only genetic analyses would permit evaluation of whether formation of host races is occurring or even, alternatively, if *Spinturnix myoti* is a complex of cryptic species as recently discovered in the phytophagous *Botrytis cinerea* infesting different sympatric host plants (Giraud *et al.* 1999). However, it should be noted that the mites involved in our laboratory experiment originated equally from both host species but there was always a strong choice of parasites towards *M. myotis*. The patterns observed are thus very unlikely to originate from a simple cryptic species effect.

STRATEGIC CHOICES: VULNERABLE VS. WELL-FED HOSTS

Independently of parasite preference for a given host species, we could also demonstrate during this study that, irrespective of host species, parasite density was significantly higher on individual hosts in a good nutri-

tional state when compared with poorly fed hosts. This provides support to the 'well-fed host strategy' described in the Introduction. Although immunocompetence (T-cell response) usually correlates positively with body condition and/or nutritional status (review in Alonso-Alvarez & Tella 2001), reports on a direct link between parasite intensities and T-cell response to a phytohaemagglutinin injection remain scarce (Christe *et al.* 2000b; Gwinner *et al.* 2000).

In a previous study on host–parasite relationships with the same species, we found (Christe *et al.* 2000a) that female bats had higher parasite burdens in early pregnancy than later on, a pattern of infestation that we could associate with increasing levels of T-cell response during gestation, probably induced by hormonal changes. However, parasites switched massively towards juvenile bats (up to 200 on a single newborn!) as soon as they became available in the population. We believe that this apparent discrepancy between preference for 'vulnerable hosts' (Christe *et al.* 2000a) and 'well-fed hosts' (this study) merely reflects the circumstances under which the observations and experiments were undertaken. Indeed, in the present investigation differences in host physiological status were not as extreme as in the former study. As a consequence, our 'poorly fed hosts' were possibly not 'vulnerable' enough to be selected by the blood-sucking mites, and thus it was more advantageous to feed on fit individuals. The two strategies described in the Introduction may thus effectively occur in nature, moreover within the same host–parasite system. In that perspective, our host–parasite model offers now a unique opportunity for attempting to model the strategic choices operated by the parasites when confronted to hosts of various conditions and physiological status, in particular to define host condition thresholds which can trigger sudden massive strategic switches in the parasite, as observed earlier in the case of freshly born bat pups (Christe *et al.* 2000a).

References

Alonso-Alvarez, C. & Tella, J.L. (2001) Effects of experimental food restriction and body-mass changes on the avian T-cell-mediated immune response. *Canadian Journal of Zoology*, **79**, 101–105.

Arlettaz, R. (1996) Feeding behaviour and foraging strategy of free-living mouse-eared bats, *Myotis myotis* and *Myotis blythii*. *Animal Behaviour*, **51**, 1–11.

Arlettaz, R. (1999) Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology*, **68**, 460–471.

Arlettaz, R. & Perrin, N. (1995) The trophic niches of sympatric sibling *Myotis myotis* and *Myotis blythii*: do mouse-eared bats select prey? *Symposium of the Zoological Society of London*, **67**, 361–376.

Arlettaz, R., Ruedi, M., Ibañez, C., Palmeirim, J. & Hausser, J. (1997a) A new perspective on the zoogeography of the two sibling bat species *Myotis myotis* and *Myotis blythii*: morphological, genetical and ecological evidence. *Journal of Zoology (London)*, **242**, 45–62.

Arlettaz, R., Perrin, N. & Hausser, J. (1997b) Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology*, **66**, 897–911.

Arlettaz, R., Baeriswyl, P.-A., Christe, P. & Lugon, A. (1998) A female vespertilionid bat (*Myotis blythii*) lactating in October at 460 N latitude. *Le Rhinolophe*, **13**, 17–22.

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

Arneberg, P., Skorping, A., Grenfell, A. & Read, A.F. (1998) Host densities as determinants of abundance in parasite communities. *Proceedings of the Royal Society London B*, **265**, 283–1289.

Blanco, G., Tella, J.L. & Potti, J. (1997) Feather mites on group living red billed choughs: a non-parasitic interaction? *Journal of Avian Biology*, **29**, 197–206.

Christe, P., Møller, A.P. & de Lope, F. (1998) Immunocompetence and nestling survival in the house martin: the tasty chick hypothesis. *Oikos*, **83**, 175–179.

Christe, P., Arlettaz, R. & Vogel, P. (2000a) Variation in intensity of a parasitic mite (*Spinturnix myoti*) in relation to the reproductive cycle and immunocompetence of its bat host (*Myotis myotis*). *Ecology Letters*, **3**, 207–212.

Christe, P., Møller, A.P., Saino, N. & de Lope, F. (2000b) Genetic and environmental components of phenotypic variation in immune response and body size of a colonial bird, *Delichon urbica* (the house martin). *Heredity*, **85**, 75–83.

Dawson, R.D. & Bortolotti, G.R. (1997) Ecology of parasitism of nestling American kestrels by *Carnus hemapterus* (Diptera: Carnidae). *Canadian Journal of Zoology*, **75**, 2021–2026.

Futuyama, D.J. & Moreno, G. (1988) The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, **19**, 207–233.

Gasparini, J., McCoy, K.D., Tveera, T. & Boulinier, T. (2002) Related concentrations of specific immunoglobulins against the Lyme disease agent *Borrelia burgdorferi sensu lato* in eggs, young and adults of the kittiwake (*Rissa tridactyla*). *Ecology Letters*, **5**, 519–524.

Gershwin, M.E., Beach, R.S. & Hurley, L.S. (1985) *Nutrition and Immunity*. Academic Press, Orlando, FL.

Giorgi, M.S., Arlettaz, R., Christe, P. & Vogel, P. (2001) How energetically costly are parasitic mites (*Spinturnix myoti*) for their bat host (*Myotis myotis*)? *Proceedings of the Royal Society London B*, **268**, 2071–2075.

Giraud, T., Fortini, D., Levis, C., Lamarque, C., Leroux, P., Lobuglio, K. & Brygoo, Y. (1999) Two sibling species of the *Botrytis cinirea* complex, transposa and vacuma, are found in sympatry on numerous host plants. *Phytopathology*, **89**, 967–973.

Glantz, S.A. & Slinker, B.K. (1991) *Primer of Applied Regression and Analysis of Variance*. McGraw-Hill, Inc, New York.

González, G., Sorci, G.M., Møller, A.P., Ninni, P., Haussy, C. & de Lope, F. (1999) Immunocompetence and condition-dependent sexual advertisement in male house sparrows (*Passer domesticus*). *Journal of Animal Ecology*, **68**, 1225–1234.

Gwinner, H., Holtrogge, M., Trost, L. & Nienaber, U. (2000) Green plants in starling nests: effects on nestlings. *Animal Behaviour*, **59**, 301–309.

Johnson, K.P., Williams, B.L., Drown, D.M., Adams, R.J. & Clayton, D.H. (2002) The population genetics of host specificity: genetic differentiation in dove lice (Insecta: Phthraptera). *Molecular Ecology*, **11**, 25–38.

Lochmiller, R.L., Vestey, M.R. & Boren, J.C. (1993) Relationships between protein nutritional status and immunocompetence in northern bobwhite chicks. *Auk*, **110**, 503–510.

McCoy, K.D., Boulinier, T., Chardine, J.W., Danchin, E. & Michalakis, Y. (1999) Dispersal and distribution of the tick *Ixodes uriae* within and among seabird host populations: the need for a population genetic approach. *Journal of Parasitology*, **85**, 196–202.

McCoy, K.D., Boulinier, T., Tirard, C. & Michalakis, Y. (2001) Host specificity of a generalist parasite: genetic evidence of sympatric host races in the seabird tick *Ixodes uriae*. *Molecular Ecology*, **14**, 395–405.

McLean, J.A. & Speakman, J.R. (1997) Non-nutritional maternal support in the brown long-eared bat. *Animal Behaviour*, **54**, 1193–1204.

Møller, A.P. (2000) Survival and reproductive rate of mites in relation to resistance of their barn swallow hosts. *Oecologia*, **124**, 351–357.

Roulin, A., Brinkhof, M.W.G., Bize, P., Richner, H., Jungi, T.W., Bavoux, C., Boileau, N. & Burneleau, G. (2003) Which chick is tasty to parasites? The importance of host immunology vs. parasite life history. *Journal of Animal Ecology*, **72**, 75–81.

Saino, N., Calza, S. & Møller, A.P. (1997) Immunocompetence of nestling barn swallow in relation to brood size and parental effort. *Journal of Animal Ecology*, **66**, 827–837.

Smits, J.E., Bortolotti, G.R. & Tella, J.L. (1999) Simplifying the phytohemagglutinin skin testing technique in studies of avian immunocompetence. *Functional Ecology*, **13**, 567–572.

Stadecker, M.J., Lukic, M., Dvorak, A. & Leskowitz, S. (1977) The cutaneous basophil response to phytohemagglutinin in chickens. *Journal of Immunology*, **118**, 1564–1568.

Talan, M.I., Kirov, S.A., Clow, L.A. & Kosheleva, N.A. (1996) Cold acclimation-associated changes in brown adipose tissue do not necessarily indicate an increase of nonshivering thermogenesis in C57BL/6J mice. *Physiology and Behaviour*, **60**, 1285–1289.

Tella, J.L. (2002) The evolutionary transition to coloniality promotes higher blood parasitism in birds. *Journal of Evolutionary Biology*, **15**, 32–41.

Tripet, F. & Richner, H. (1997) The coevolutionary potential of a 'generalist' parasite, the hen flea *Ceratophyllus gallinae*. *Parasitology*, **115**, 419–427.

Tripet, F., Christe, P. & Møller, A.P. (2002) The importance of host sociality for parasite specialization and speciation: a comparative study of avian host and their fleas (Siphonaptera: Ceratophyllidae). *Journal of Animal Ecology*, **71**, 735–748.

Uchikawa, K., Zhang, M.Y., O'Connor, B.M. & Klompen, H. (1994) Contribution to the taxonomy of the genus *Spinturnix* (Acari: Spinturnicidae), with the erection of a new genus, Emballonuria. *Folia Parasitologica*, **41**, 287–304.

Ward, S.A. (1992) Assessing functional explanations of host specificity. *American Naturalist*, **139**, 883–891.

Zar, J.H. (1999) *Biostatistical Analysis*. 4th edn. Prentice Hall, Inc., Upper Saddle River, NJ.