REPORT

Variation in intensity of a parasitic mite (*Spinturnix myoti*) in relation to the reproductive cycle and immunocompetence of its bat host (*Myotis myotis*)

Philippe Christe, Raphaël Arlettaz and Peter Vogel
Institut d'Ecologie – Laboratoire de Zoologie et Ecologie Animale, Bâtiment de Biologie, Université de Lausanne, CH-1015 Lausanne, Suisse
E-mail:
philippe.christe@ie-zea.unil.ch

Abstract

Given the intimate association in host–parasite systems, parasites are expected to initiate their own reproduction when vulnerable hosts become abundant and/or when adult hosts are less resistant. In this study, we examined the variation in the intensities of a blood-sucking mite (*Spinturnix myoti*, Acarina) with respect to the reproductive cycle and immunocompetence of its host, the greater mouse-eared bat *Myotis myotis*. Reproductive, pregnant females were less immunocompetent and harboured more parasites than nonreproductive females, whilst, during lactation, immunocompetence was positively associated with female body mass. There was a dramatic increase in the T-cell response of gravid females with the advancement of gestation, which coincided with a diminution of individual parasite loads and a progressive switch of parasites from adults to juveniles. The latter not only harboured greater numbers of mites than adult female bats, but they also exhibited gravid parasites in higher proportions, indicating that juvenile hosts are more attractive for parasite reproduction than adult females.

Keywords

Bats, immunocompetence, mites, reproduction.

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INTRODUCTION

Reproduction of ectoparasites is usually assumed to coincide with the reproductive event of their host (Foster 1969). This may be due to an increasing number of hosts suddenly available when births take place, or to a lower defence against parasites at that time of the year (Nelson & Demas 1996). The behavioural defence of juveniles may be reduced as compared with adults. For instance, their ability to perform self-grooming, an efficient mechanism for reducing parasite load (Clayton 1991; Mooring *et al.* 1996), has been shown to be reduced in the early stages of development in bats (McLean & Speakman 1997). Moreover, the naive immune system of offspring may render them particularly attractive to attacks by parasites. Also, reproducing adults have been shown to have a lower immune defence compared with immature (Moshkin *et al.* 1998). Decreased immunocompetence may result from endocrine changes associated with reproduction (Grossman 1985; Zuk 1996), or could be mediated by physiological trade-offs between allocation of resources to current reproduction and to immune function (Wedekind & Folstad 1994). Ultimately, mammalian immune func-

tion has been hypothesized to be compromised during pregnancy so as to avoid spontaneous abortions (Hogarth 1982; Golub & Green 1991; Haig 1993).

In this study, we investigated the temporal variation in mite intensities (*Spinturnix myoti*, Acarina) during the reproductive cycle of its host, the greater mouse-eared bat *Myotis myotis*. The greater mouse-eared bat, *Myotis myotis,* is a large palearctic species that feeds heavily on carabid beetles gleaned from the ground (Arlettaz 1996; Arlettaz *et al.* 1997). Females give birth to a single pup each year in nursery roosts that consist exclusively of female aggregations. During the breeding season, the study colonies contain approximately 25% of nonreproductive female subadults. The juveniles roost beneath the mother's wings during the first 10 days following birth, then separately from their mother among the clustering bats, although they are still suckling.

Mites of the genus *Spinturnix* (Spinturnicidae, Acari) are exclusive ectoparasites of Microchiroptera (Rudnik 1960). They occur on the wing membranes and, less frequently, on the tail membrane (uropatagium) of bats. They complete their entire life cycle on their hosts. The development of eggs and larvae occur in the genital tract of female mites

which give birth to deuteronymphs which already have an adult appearance (Radovsky 1994). All stages are haematophagous, feeding on blood and lymph. Prevalence of *Spinturnix myoti* in the study colonies was 93%.

We made the following predictions. First, if ectoparasites are able to detect the reproductive status of their host and if pregnancy is associated with a decrease in immunocompetence (Grossman 1985), one would predict pregnant females to harbour a higher parasite load than nonreproductive females. Second, at the time of parturition, newborns may represent an attractive target for parasites because of their low behavioural and immunological defences; one would then expect higher parasite intensities on offspring than on adult females. Third, as body condition usually correlates with immune defence (Saino *et al.* 1997; Sorci *et al.* 1997a; Møller *et al.* 1998; Christe *et al.* 1998; Brinkhof *et al.* 1999), we predicted a positive correlation between immunocompetence and female body mass during lactation (i.e. when embryos no longer influence body mass).

METHODS

This study was carried out in the upper Rhône valley, Switzerland, at two bat colonies located in church attics. The colonies are nursery roosts that consist exclusively of female aggregations.

Every 10 days throughout the breeding season in 1998 and 1999 (May to August), bats were mist-netted at the entrance to the colony when returning from their night feedings, between 2 and 6 a.m. In 1998, 140 females were captured and 76 in 1990. Pregnant females were classified with respect to the bulk of embryo (estimated through palpation) into three categories: early, middle and late pregnancy. Lactation was assessed by gently pressing the nipples to extract some milk. Bats were weighed to the nearest 0.1 g and their forearms were measured with a digital calliper (accuracy 0.01 mm). Body mass corrected for structural body size (forearm length) could be used as a body condition index. However, the ratio body mass on forearm length was not significant (linear regression: $r^2 = 0.001$, $N = 47$, $F = 0.028$, $P = 0.865$) and therefore not further used in the analyses.

A blood sample (< 50 μL) was taken from the wing membrane using microcapillary tubes. Haematocrit value, which is the proportion of total blood volume occupied by erythrocytes after centrifugation (15 min at 12800 r.p.m.), was measured using a digital calliper (accuracy 0.01 mm). Mites were counted in the field and classified in three categories according to their external morphology: males, females and deuteronymphs (Uchikawa *et al.* 1994). The repeatability of sex determination in mites was 0.99 ($n = 48$, $P < 0.001$), as determined after binocular

inspection in the laboratory. During the night of 22 June 1998, 11 pairs of mothers plus young were captured for comparison of their respective parasite loads. In order to assess the number of mites on older juveniles roosting independent of their mothers, a random sample of individuals was captured among the clustering bats during the night of 30 June 1998.

Immunocompetence was assessed by the intensity of T-lymphocytes, a cell-mediated *in vivo* immune response to a 0.02-mL subcutaneous injection of phytohaemagglutinin (PHA-P, Sigma, St Louis) in the middle of the 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). In the other footpad, we injected the same volume of a phosphate saline buffer as a control. Ten hours later, footpad swelling responses at the two inoculation sites were measured with a calliper micrometer. The change in thickness of the footpad where PHA was injected minus the change in the control footpad was used as a measure of immunocompetence (Lochmiller *et al.* 1993). Injection of PHA does not increase the level of stress, as shown recently in nestling house martins (Merino *et al.* 1999).

In 1999, we reduced experimentally parasite intensities in the colony by applying an insecticide treatment in late June. As a consequence, results concerning lactation refer to data collected in 1998 only, whereas all other data concern both 1998 and 1999.

These manipulations were performed under licence from the veterinary service of the state of Valais. A given individual was investigated only once during the study. Data analyses were performed using Systat (Wilkinson 1992). Before statistical analyses, percentages were transformed into square root arcsinus values, and absolute numbers of parasites into square root values. All *P*-values reported are two tailed.

RESULTS

Parasite loads

Overall, pregnant females had more parasites (14.8 ± 1.2; mean $\pm$ SE) than nonpregnant females (11.5 ± 1.4), and year did not affect the outcome (ANOVA: $F = 4.11$, d.f. = 1, 152; $P = 0.044$; year effect: $F = 0.202$, d.f. = 1, 152; $P = 0.653$). The difference appeared even greater if only data from early pregnancy were considered (22.5 ± 2.2 *versus* 11.5 ± 1.4 mites). There was a strong negative relationship between parasite number and the three successive stages of pregnancy (comparison of the three stages: $F = 12.41$, d.f. = 2, 92, $P < 0.001$; year: $F = 0.68$, d.f. = 1, 92, $P = 0.41$) (Fig. 1a). As the date of
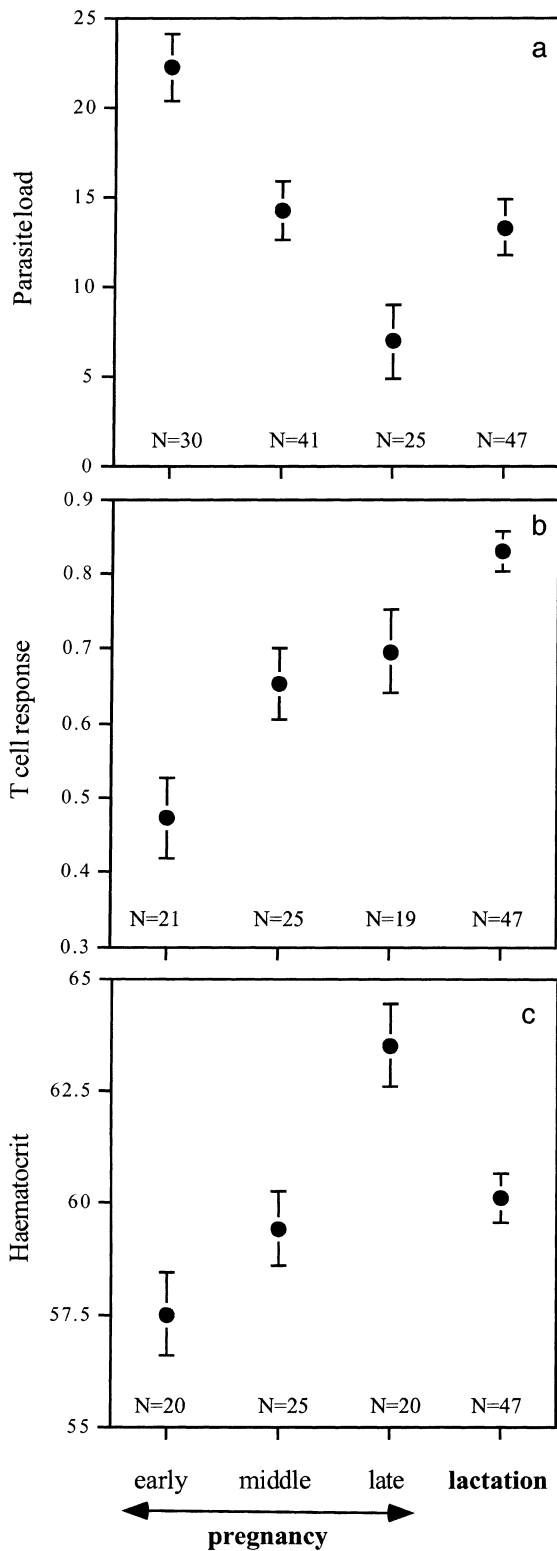
Figure 1 (a) Mean number ($\pm$ SE) of mites found on the membranes of females bats; (b) T-cell response (mm); and (c) haematocrit level (%) with respect to the various stages of reproduction: early, middle, late pregnancy and lactation.

capture correlates with advancement of gestation, we introduced it as a covariate into the model, but the results were not altered (ANCOVA: $F = 11.01$, d.f. $= 1$, 92, $P < 0.001$; date: $F = 0.51$, d.f. $= 1$, 92, $P = 0.475$; year: $F = 0.94$, d.f. $= 1$, 92, $P = 0.334$).

Later on in the season, during lactation, we could evidence a positive relationship between the number of parasites found on a given mother and her young (linear regression: $r^2 = 0.473$, $N = 11$, $F = 8.07$, $P = 0.019$, slope $\pm$ SE $= 0.482 \pm 0.169$), but no difference in parasite loads between newborns and their mothers (Wilcoxon signed ranks test: $z = 1.17$, $N = 11$, $P = 0.241$).

Juveniles that had just begun to roost independently of their mothers (at an age of $\approx$ 8–12 days) harboured, on average, many more parasites (87.8 ± 14 mites) than newborns still attached to their mother (18.0 ± 3.1 mites) (t-test: $t = 5.58$, d.f. $= 25$, $P < 0.001$). At the same period, we also found many fewer mites on lactating females (12.6 ± 2.8 mites) than on independent juveniles (87.8 ± 14.2) (t-test: $t = -6.382$, d.f. $= 25$, $P < 0.001$). The proportion of gravid mite females was $0.05\% \pm 0.02\%$ on adult bat females *versus* $26.3\% \pm 0.03\%$ on juveniles ($t = 5.30$, d.f. $= 25$, $P < 0.001$). While mites were found exclusively on wing membranes in adult bats, some naked newborns were literally covered by parasites, with some mites even present in the ear canal.

During lactation there was a negative relationship between female body mass and parasite load (linear regression: $r^2 = 0.123$, $N = 47$, $F = 6.42$, $P = 0.014$), but no relationship between forearm length and parasite load (linear regression: $r^2 = 0.054$, $N = 47$, $F = 2.69$, $P = 0.107$).

T-cell response

The T-cell response was stronger in nonreproductive females (0.78 ± 0.04) than in pregnant females (0.64 ± 0.04), and year appeared as a significant factor (ANOVA: $F = 11.08$, d.f. $= 1$, 90, $P = 0.001$; year: $F = 5.63$, d.f. $= 1$, 90, $P = 0.02$). As there was a difference in body mass between reproductive and nonreproductive females ($t = 11.07$, $P < 0.001$), body mass was included as a covariate in the model; this did not change the results (nonreproductive *versus* reproductive females: $F = 19.01$, d.f. $= 1$, 87, $P < 0.001$; year: $F = 3.60$, d.f. $= 1$, 87, $P = 0.06$; body mass: $F = 7.18$, d.f. $= 1$, 87, $P = 0.008$).

The T-cell response was positively associated with the advancement of gestation, and the effect of year was again significant (comparison of the three stages: $F = 6.31$, d.f. $= 2$, 60, $P = 0.003$; year: $F = 8.09$, d.f. $= 1$, 60, $P = 0.006$) (Fig. 1b). As there was also an obvious positive relationship between body mass and the advance-

ment of gestation ($F = 29.31$, d.f. = 2, 96; $P < 0.001$), body mass was then included into the model; this did not affect the outcome (stage of pregnancy: $F = 3.87$, d.f. = 2, 57, $P = 0.026$; body mass: $F = 0.099$, d.f. = 1, 57, $P = 0.753$; year: $F = 6.90$, d.f. = 1, 57, $P = 0.011$). Immunocompetence was also significantly lower in early pregnancy than at later stages of gravidity (Scheffé *post hoc* comparison: early middle $P = 0.017$; early late $P = 0.006$; middle-late $P = 0.847$).

Lactating females had similar immune responses to nonreproductive females ($t = 0.467$, d.f. = 76, $P = 0.641$). In lactating females, there was a positive correlation between T-cell response and body mass (Pearson $r = 0.298$, $N = 49$, $P = 0.037$; Fig. 2). Also, there was a negative relationship between parasite load and immune response during that phase of reproduction (Pearson $r = -0.378$, $N = 50$, $P = 0.006$).

Haematocrit level

Nonreproductive females had a lower haematocrit level than pregnant females (t-test, $t = 2.58$, d.f. = 91, $P = 0.011$), and haematocrit level strongly increased during the course of gestation (comparison of the three stages: $F = 9.55$, d.f. = 2, 61, $P < 0.001$; year: $F = 1.23$, d.f. = 1, 61, $P = 0.272$, Fig. 1c). Also, there was a negative relationship between mite number and haematocrit level (Pearson $r = -0.419$, $N = 47$, $P = 0.003$) during lactation.

DISCUSSION

Our results show that the parasitic mite *S. myoti* adjusts its reproductive cycle on that of its host by massively
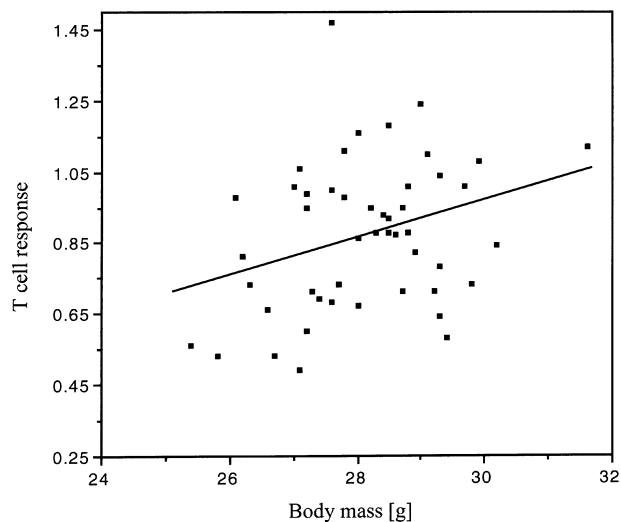

Figure 2 Positive relationship between T-cell response and body mass in lactating *Myotis myotis* females.

infesting newborns, a very vulnerable host. As lactating females harboured more parasites than late pregnant females (Fig. 1a), the decrease in mite number with the progress of gestation cannot be explained by a drop in the absolute mite population as the season progresses, but rather by a transfer of mites from adult to juvenile hosts. Increased level of parasites during lactation may be provoked by the intimate contact between offspring and mother during lactation. Also, newborns harboured a much higher proportion of gravid female mites than adult hosts. Either finding indicates that juvenile hosts are more attractive for parasite reproduction than adults: newborns are actually less proficient in performing self-grooming at the early stages of development (McLean & Speakman 1997), and/or may have a lower immune defence.

Nonreproductive females were less infested than pregnant females, which, in early pregnancy, had a particularly low immune response to antigenic phytohaemagglutinin. A low immunocompetence in early pregnancy is presumably an adaptation to prevent the maternal-rejection response due to genetic conflicts between pups and mothers (Grossman 1985; Haig 1993; Xu *et al.* 2000). Later on, during lactation, females with higher body mass were also less parasitized and more immunocompetent than lighter females. This result is consistent with findings in bird studies where body condition has been demonstrated to be positively correlated with immunocompetence (Saino *et al.* 1997; Sorci *et al.* 1997a; Christe *et al.* 1998; Brinkhof *et al.* 1999).

Several studies have demonstrated a positive correlation between parasite prevalence and reproductive investment (Norris *et al.* 1994; Richner *et al.* 1995; Oppliger *et al.* 1996), probably as a consequence of a diminished immune response elicited by reproductive effort (Deerenberg *et al.* 1997). As the cost of reproduction is assumed to cause a reduction in either survival or fecundity – due to current reproductive activities (Williams 1966; Stearns 1992) – such costs could be mediated by physiological trade-offs between allocation of resources to current reproduction and immune function (Wedekind & Folstad 1994). Our observation that nonreproductive individuals had a higher T-cell response and a lower parasite load than reproductive females actually suggests that gestation may adversely affect resistance to parasitic infections. This result would be consistent with findings in humans where a lower response to phythohaemagglutinin has been reported in pregnant compared with nonpregnant women (Matthiesen *et al.* 1996). Similar trends have been observed as regards humoral immune response (i.e. antibodies) in red (*Clethrionomys rutilus*) and bank voles (*C. glareolus*) (Moshkin *et al.* 1998). Because nonreproductive and lactating female bats had similar immune responses, the

difference observed in T-cell responses between non-reproductive and pregnant females is probably not due to age differences between subadults and adults but rather to immuno-suppression by sex-hormones during gestation (Grossman 1985).

As haematocrit has been shown to be reduced when nestling birds are infested by ectoparasites (Chapman & George 1991; Richner *et al.* 1993; Hurtrez-Boussës *et al.* 1998), the negative relationship observed between mite intensities and haematocrit level suggests that *Spinturnix myoti* may impose some costs to its host. In fact, because of a dilution effect caused by an increase in total circulating blood volume, typical in pregnant female mammals, we expected haematocrit level to decrease during pregnancy. Surprisingly, we found the contrary. This may be explained, in part, by a relatively small blood volume increase found in pregnant bats (17%) compared with human females (40%) (Kallen & Wimsatt 1962). On the other hand, in pregnant female bats, the bulk of embryo implies much higher energetic costs during flight (e.g. Ransome 1973), which may be coupled with a higher production of red blood cells.

To our knowledge, there is no study that has been investigating the possible costs imposed by ectoparasites on bat fitness. Close aggregations typical of bat roosts enable horizontal (among individuals) as opposed to vertical (between mother and infant) transmission of parasites, which may cause increased level of virulence (Clayton & Tompkins 1994). This may be particularly true for *Spinturnix myoti* in colonies of *M. myotis*, as, for saving energy, bats roost in close body contact, thus increasing opportunities for parasitic transmission. This mite therefore represents a good model of a bivalent mode of transfer, which could be useful to study the evolution of virulence.

There seems to be a strong effect of year upon immunocompetence. This probably mirrors the overall nutritional state of bats, which may be chiefly dependent on interannual fluctuations in prey availability. For instance, cockchafers *Melolontha melolontha*, a basic prey of mouse-eared bats, show massive occurrences every third year, whereas they are virtually absent inbetween (Arlettaz 1996; Arlettaz *et al.* 1997). A study of a possible resistance mediated by food resources is in progress (Arlettaz *et al.*, unpublished).

The timing of reproduction is one important life-history trait (Daan & Tinbergen 1997), particularly for bats living in temperate zones, as females have not only to lead their offspring to weaning but also to mate and to deposit enough fat reserves before the onset of hibernation. It has thus been suggested that early breeding must be favoured in temperate zone bats (Ransome 1995). On the other hand, highly host-specific parasites are generally involved in refined coevolutionary processes with their hosts (Foster 1969; Sorci *et al.* 1997b), in which parasites often impose strong selection pressures on various host life history traits (Hochberg *et al.* 1992; Forbes 1993; Perrin *et al.* 1996; Møller *et al.* 1997). As in colonial birds, parasitism might therefore impose another constraint on the timing of parturition within a bat colony (Brown & Bomberger Brown 1996): young born close to the median date of births would benefit from a dilution effect of parasites. Ultimately, natural selection would thus favour synchronization of parturition among colonial species so as to counteract the possible detrimental effect of parasites upon a given individual.

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BIOSKETCH

Philippe Christe's research interests are mainly bird–parasite and bat–parasite interactions.