Host sex and ectoparasites choice: preference for, and higher survival on female hosts

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Summary

1. Sex differences in levels of parasite infection are a common rule in a wide range of mammals, with males usually more susceptible than females. Sex-specific exposure to parasites, e.g. mediated through distinct modes of social aggregation between and within genders, as well as negative relationships between androgen levels and immune defences are thought to play a major role in this pattern.

2. Reproductive female bats live in close association within clusters at maternity roosts, whereas nonbreeding females and males generally occupy solitary roosts. Bats represent therefore an ideal model to study the consequences of sex-specific social and spatial aggregation on parasites' infection strategies.

3. We first compared prevalence and parasite intensities in a host–parasite system comprising closely related species of ectoparasitic mites (*Spinturnix* spp.) and their hosts, five European bat species. We then compared the level of parasitism between juvenile males and females in mixed colonies of greater and lesser mouse-eared bats *Myotis myotis* and *M. blythii*. Prevalence was higher in adult females than in adult males stemming from colonial aggregations in all five studied species. Parasite intensity was significantly higher in females in three of the five species studied. No difference in prevalence and mite numbers was found between male and female juveniles in colonial roosts.

4. To assess whether observed sex-biased parasitism results from differences in host exposure only, or, alternatively, from an active, selected choice made by the parasite, we performed lab experiments on short-term preferences and long-term survival of parasites on male and female *Myotis daubentoni*. When confronted with adult males and females, parasites preferentially selected female hosts, whereas no choice differences were observed between adult females and subadult males. Finally, we found significantly higher parasite survival on adult females compared with adult males.

5. Our study shows that social and spatial aggregation favours sex-biased parasitism that could be a mere consequence of an active and adaptive parasite choice for the more profitable host.

Key-words: bats, mites, parasite survival, sex-biased parasitism, *Spinturnix*.

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Introduction

Parasitism is a key factor influencing fitness and shaping the life-history traits of most organisms (Clayton & Moore 1997; Fredensborg & Poulin 2006). Although parasites are ubiquitous, individuals within host populations often show a strong variation in the probability

and in the magnitude of infestation depending on both the level of exposure and the ability to mount efficient immune defence mechanisms. For example, sex-specific parasitism may be mediated by gender differences in susceptibility to parasitism. Most studies found that males are more parasitized than females (Zuk 1990; Poulin 1996; Schalk & Forbes 1997; Klein 2000; Moore & Wilson 2002; Morand *et al.* 2004; Amo, Lopez & Martin 2005), with some exceptions (Poulin 1996; Schalk & Forbes 1997; McCurdy *et al.* 1998; Morales-Montor *et al.* 2004).

Fundamental biological differences between genders may explain why susceptibility to parasites often differs between females and males. First, sex-specific behaviour may affect exposure to parasites, one sex being more vulnerable than the other (Reimchen & Nosil 2001; Krasnov *et al.* 2005a). Such behaviours that increase the likelihood of becoming infected may be, for instance, aggressions between males for mating opportunities, decreased male grooming rate during the mating season (Mooring & Hart 1995; Mooring *et al.* 2006) or spatial aggregation within the members of one sex (Zuk & McKean 1996). Secondly, negative association between steroid hormones, particularly testosterone, and immune responses are thought to play a major role in this difference (Grossman 1985; Zuk 1990; Folstad & Karter 1992; Roberts, Buchanan & Evans 2004).

In this study, we take advantage of the particular social habit of bats to investigate whether spatial aggregation within the members of one sex favours differential susceptibility to parasites, eventually leading to preference for a given host sex in parasites. Females of most temperate zone bat species usually aggregate during the breeding season in nursery colonies, whereas males are mainly solitary and occupy satellite roosts (Lewis 1995). Colonial habits of female bats during reproduction favour vertical and horizontal parasite transmission (Christe, Arlettaz & Vogel 2000). Moreover high temperature of nursery roost sites, including the heat generated by tight associations among individuals in a colonial cluster, may favour parasites' reproductive output (Marshall 1981). These two factors could lead to a strong sex-linked difference in the opportunity to become infested. Two recent studies have shown that under natural conditions, females of some temperate zone bat species have higher prevalence and intensity of parasitism than males and that these differences vary with season (Zahn & Rupp 2004; Lucan 2006). It remains unknown, however, whether differential encounter probability due to spatial aggregation selects for an active choice on more profitable hosts by the parasite.

Ectoparasitic mites of the genus *Spinturnix* represent a good model to investigate the effect of sex on host susceptibility to parasites. These parasites complete their entire life cycle on their hosts and are thus strictly dependent on close contact between individuals to disperse and infect new hosts (Rudnick 1960). Individual bats cannot be infected by *Spinturnix* while visiting empty roosts, contrary to other parasite taxa that undergo developmental stage irrespective of host presence (Lewis 1995; Reckardt & Kerth 2006). Randomly choosing a male as host could lead to a drastic reduction in reproductive success in an individual *Spinturnix* because, once installed on a male, dispersal opportunities are much lower than on a female. One would therefore expect a strong selection for female hosts in these parasites.

To assess whether parasites are able to actively select one, more profitable gender, we performed dual choice experiments with wild-caught bats kept for a while in captivity. Males and females *Myotis daubentoni* and the mite *Spinturnix andegavinus* were used as a model system. Host's nutritional status was standardized so as to remove any confounding factors as far as possible (Christe *et al.* 2003; Krasnov *et al.* 2005b).

Because temperate zone bats typically mate during the fall, testosterone reaches its highest level during an entire year cycle between mid summer and early autumn. One could therefore expect seasonal variation in parasite preference because parasites could take advantage of the immunosuppressor effect of testosterone for infecting males during mating when opportunities for parasite transmission between sexes are high.

Among juveniles prior to weaning, equal parasite loads should be observed in males and females due to similar behaviours and hormone profiles at that early life stage in the two genders. However, if mites have other cues than hormones to identify host sex at that young bat age, they should preferentially settle on females if exploiting female hosts increases their future survival prospect.

The aims of the present paper are thus manifold. We tested: (1) whether there is a natural bias in parasite prevalence and intensity between male and female hosts in five bat species; (2) whether juveniles within colonies harbour different parasite loads according to host sex; (3) if the patterns of parasite choice observed in natural conditions, with respect to host sex and/or sexual maturity, can be replicated under experimental laboratory conditions with captive bats; (4) if parasite choice fluctuates seasonally in laboratory conditions; and (5) if the mid-term survival functions of parasites differ with respect to host gender, this under experimental conditions where mites cannot switch between female and male hosts.

Materials and methods

STUDY SPECIES

Data were collected from 1995 to 2006 in different areas of Switzerland. Juvenile greater and lesser mouse-eared bats *Myotis myotis* (Borkhausen, 1797) and *M. blythii* (Tomes, 1857), respectively, were captured at the end of August in two mixed colonies located in church attics, between 1995 and 2001 (except 2000). Each individual was sexed, and the number of

parasites recorded. Adult lesser mouse-eared bats were captured between June and August in the same breeding colonies where some isolated males can occasionally roost apart from females. Male and female greater mouse-eared bats *M. myotis* and brown long-eared bats *Plecotus auritus* (L., 1758) were caught between September and October at the entrance of caves in the Swiss Jura mountains. Daubenton's bats *Myotis daubentoni* (Kuhl, 1819) were mist-netted above the Chamberonne River, next to the University of Lausanne, Switzerland, or hand-netted while night roosting at the same site, between May and September. Male and female noctule bats *Nyctalus noctula* (Schreber, 1774) were collected while roosting together in nestboxes, from March to May and from September to November in the forest close to the University of Lausanne.

The present study focuses on mites of the genus *Spinturnix*. Our parasite model species are *Spinturnix* spp. (Acari, Mesostigmata, Spinturnicidae). These are mobile ectoparasites completing their entire life cycle on bat wings and tail membranes (Rudnick 1960). All developmental stages are haematophagous. These mites are specific to their host species with *Spinturnix myoti* (Kolenati, 1856) infesting *M. myotis* and *M. blythii*, *S. andegavinus* (Deunff, 1977) infesting *M. daubentoni*, *S. acuminata* (Koch, 1836) infesting *Nyctalus noctula* and, finally, *S. plecotina* (Koch, 1839) infesting *Plecotus auritus*. Prevalence of *Spinturnix* spp. is expressed as the percentage of parasitized individuals, and intensity of parasitism as the mean number of parasites found on parasitized individuals.

Because mites live exclusively on bat wings and tail membranes, which are entirely bare in these species, and have never been found in fur, parasites have no place to hide and visual inspection produces reliable counts of parasite infestation. The repeatability of parasite counts during the same capture is high (Christe *et al.* 2003). Mites *S. andegavinus* used in experiments with *M. daubentoni* were collected from bats originating from the same population. As *S. andegavinus* cannot survive off the host for more than 3 h at ambient temperature (Giorgi *et al.* 2004), parasites were collected at most 30 min before experiments.

HOST CHOICE BY PARASITES: *MYOTIS DAUBENTONI* AND *SPINTURNIX ANDEGAVINUS*

Dual host choice experiments were designed as follows. A pair of deparasitized bats was exposed to *S. andegavinus* (n = 91 trials). Deparasitized bats were obtained by gently removing all mites with soft forceps after visual inspection of bats' unfolded wings and tail membranes. These preference experiments were performed between adult females presented alongside adult males (n = 50 trials) or subadult males (n = 41 trials). In addition, because levels of testosterone and degree of association between males and females could vary throughout seasons in natural conditions, host choice experiments were performed over the reproductive period with

about 20 tests per month (May–September). For the 91 trials, 20 *S. andegavinus* (seven males, seven females and six unsexed deuteronymphs) were deposited in an open receptacle (Petri dish) glued at the centre of a small wooden box (10 × 5·5 × 3 cm). The experiment began when every mite was immobile and waiting for a host either inside or at the apex of the Petri dish. Then, a pair of freshly deparasitized bats was placed into the box, which was small enough to force close bat body contact and, consequently, direct parasite transfer from the receptacle to the bats and from bat to bat. Parasites and bats were able to move inside the box. After a 3-h run, the number of parasites present on each bat was counted. After trial runs, bats were released at their place of capture or re-allocated to survival experiments (see below). For analyses, the percentage of mites on a given host was calculated from the final number of parasites found instead of the initial 20 mites, because in some replicates a few parasites appeared (birth) or disappeared (death) during runs [mean (± SE) number of parasites variation per run: –0·32 ± 0·08]. Death of parasites is assumed to be the result of forceps manipulation as well as, to a lesser extent, grooming behaviour of bats.

PARASITE SURVIVAL EXPERIMENTS

Twenty nonbreeding adult *M. daubentoni* (10 females and 10 males) were captured in August as described above and kept in *c*.4 m^3 semioutdoor aviaries. Bats were fed *ad libitum* a mixed diet consisting of mealworms *Tenebrio molitor* and crickets *Acheta domesticus*. All bats had unlimited access to water.

After 1-week acclimatization, two replicates of two groups of five bats each (two groups of males and two groups of females) were formed and assigned to different aviaries (day 0 of experiment). In each aviary, only one roost was provided to constrain bats to sleep together, allowing complete horizontal parasite transmission among bats. Because density-dependent intraspecific competition among parasites may affect their fitness, initial intensity of infection was manipulated to mimic the mean number of parasites observed in the free-ranging populations from which parasites and bats stemmed from. In *M. daubentoni*, mite burden was (average ± SE) 6·11 ± 0·28 mites. Consequently, we placed seven *S. andegavinus* mites on each deparasitized individual bat (i.e. in total 35 parasites per aviary). Once the experiment was launched, parasite numbers were counted daily on every bat during 10 days. In addition, the percentage of remaining mites (with respect to the initial deposited number at day 0) was calculated at the end of the 10-day experiment in order to obtain demographic growth. Parasites not recovered from bats were assumed to have died in between as *S. andegavinus* cannot survive long off the host (Giorgi *et al.* 2004). Demographic growth functions were averaged over the two replicate trials. A 100% growth function represents a constant mite population while a

growth function lower or higher than 100% represents a decreasing or increasing mite population, respectively.

All females kept in captivity for laboratory experiments were non-reproductive. Bats were captured under licence (Conservation de la Faune du canton de Vaud and Service de la Conservation de la Nature du canton du Valais, Switzerland).

STATISTICAL ANALYSES

All statistical tests were computed with R 1·7·1 (R Development Core Team 2003) and S-PLUS 2000 (MathSoft Inc. © 1988–99, Seattle, WA, USA). Nonparametric tests were used when data were not normally distributed. To test for differences in parasite prevalence and intensity between sexes, we used Chi square and Mann–Whitney tests, respectively. For juveniles *M. myotis* and *M. blythii*, a two-way ANOVA was used to investigate intensity as a function of sex and year.

For host choice experiments, Wilcoxon signed rank tests were performed on the percentage of mites on both genders. To compare survival of mites, repeated-measure ANOVAS were applied to the number of parasites recorded daily (repeated measure) over the whole duration of experiments. Sex and replicates were assigned as between-factors terms while time was used

as within-factor term. To compensate for a possible lack of compound symmetry in repeated measure ANOVAS, Huynh–Feldt adjustments of the degrees of freedom in the within-factor (time) analyses were accounted for (Gurevitch & Chester 1986; Zar 1999). The adjusted degrees of freedom are directly reported in the text. All values reported are mean ± SE and all *P*-values are two-tailed.

Results

PREVALENCE AND PARASITE INTENSITIES IN NATURE

Prevalence of *Spinturnix* spp. observed on the five bat host species was significantly higher for females (range 63–100%) than for males (range 9·2–45·7%; Table 1). Three species (*M. blythii, M. daubentoni, N. noctula*) had significantly higher parasite intensity in females (average range 2·8–10·9) than in males (averages range 1·8–3·7). For *M. myotis* there was a marginally significant trend, whereas intensities did not differ between males and females in *P. auritus* (Table 1).

Nonweaned male and female juvenile mouse-eared bats had similar intensities and prevalence of *S. myoti* (Table 2).

Table 1. Differences between sexes in parasite prevalence (%) and average intensity in five European bat species. The host species is mentioned first (with parasite species in brackets). Differences between male and female estimates were tested with χ^2 or Mann–Whitney *U*-tests

Host *Spinturnix* spp.	Prevalence %			Average intensity (SE)		
	Males	Females	Test	Males	Females	Test
Myotis myotis	23·9	82·4	$\chi^2 = 15·4$	2·3 (0·54)	3·5 (0·43)	$U = 47$
(*S. myoti*)	$n = 46$	$n = 17$	$P < 0·001$	$n = 11$	$n = 14$	$P = 0·091$
Myotis blythii	40·7	100	$\chi^2 = 94·6$	3·7 (1·04)	10·9 (0·76)	$U = 334$
(*S. myoti*)	$n = 27$	$n = 157$	$P < 0·001$	$n = 11$	$n = 157$	$P < 0·001$
Myotis daubentoni	45·7	91·2	$\chi^2 = 117·3$	2·7 (0·42)	8·6 (0·33)	$U = 2765$
(*S. andegavinus*)	$n = 129$	$n = 364$	$P < 0·001$	$n = 59$	$n = 332$	$P < 0·001$
Plecotus auritus	9·2	63	$\chi^2 = 35·7$	2·9 (0·96)	2·8 (0·43)	$U = 85$
(*S. plecotina*)	$n = 130$	$n = 27$	$P < 0·001$	$n = 12$	$n = 17$	$P = 0·432$
Nyctalus noctula (spring)	20·5	64	$\chi^2 = 34·8$	1·8 (0·137)	2·9 (0·30)	$U = 742$
(*S. acuminata*)	$n = 83$	$n = 100$	$P < 0·001$	$n = 17$	$n = 64$	$P = 0·016$
Nyctalus noctula (fall)	45·2	84·6	$\chi^2 = 18·6$	2·3 (0·35)	4·7 (0·4)	$U = 804$
(*S. acuminata*)	$n = 42$	$n = 65$	$P < 0·001$	$n = 19$	$n = 55$	$P < 0·001$

Table 2. Differences between sexes in parasite *S. myoti* prevalence (%) and average intensity in juvenile mouse-eared bats *M. myotis* and *M. blythii* within colonies. Differences between male and female estimates were tested with χ^2. Interactions (sex × year) in ANOVA were nonsignificant

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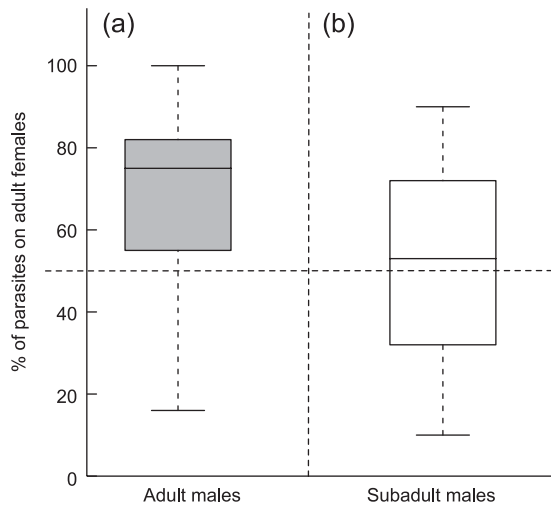| Host	Prevalence %			Average intensity (SE)		ANOVA	
	Males	Females	Test	Males	Females	Sex	Year
Myotis myotis	82·5	84·3	$\chi^2 = 0·1$	10·7 (0·6)	10·1 (0·5)	$F = 0·58$	$F = 10·79$
	$n = 200$	$n = 261$	$P = 0·70$	$n = 165$	$n = 220$	$P = 0·45$	$P < 0·001$
Myotis blythii	89·1	83·8	$\chi^2 = 1·0$	7·6 (0·6)	8·1 (0·7)	$F = 0·28$	$F = 4·55$
	$n = 129$	$n = 105$	$P = 0·32$	$n = 115$	$n = 88$	$P = 0·57$	$P = 0·001$

Fig. 1. Box plots of percentage of mites (*S. andegavinus*) counted on each individual female bat after running a 3-h dual host choice experiment in a closed box where a pair of bats was placed in close contact. Twenty mites were placed in a small cup between the two bats at the onset of the experiment. There was a clear parasite preference for adult females when confronted with adult males throughout the season (a), whereas mites settled at random when the choice was given between adult females and subadult males (b).
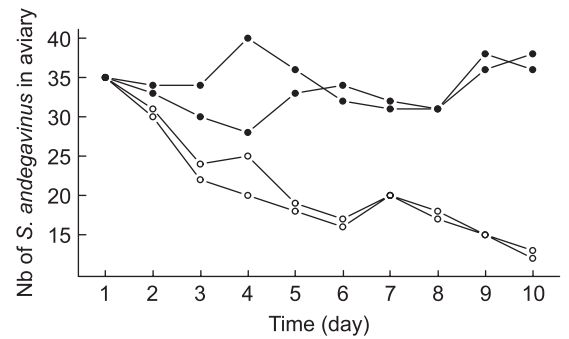

Fig. 2. Survival of ectoparasitic mites deposited either on male or female Daubenton's bats during a 10-day experiment (two replicates). Dots show results for female hosts, whereas circles depict survival on male hosts. Mites survived significantly better on females than on males.

EXPERIMENTAL HOST SEX CHOICE BY PARASITES WITH *S. ANDEGAVINUS* ON *M. DAUBENTONI*

Over the whole season, *S. andegavinus* exhibited a clear instantaneous preference for adult females, as parasites were mostly found on that sex and age class at the end of the experiment (Wilcoxon signed rank test: whole summer: $V = 1074·5$, $n = 50$, $P < 0·001$; Fig. 1a). However, this varied among months with a significant directional gender preference in early summer (Wilcoxon signed rank test: May: $V = 77$, $n = 12$, $P < 0·01$; June: $V = 42$, $n = 9$, $P < 0·01$ and July: $V = 57$, $n = 11$, $P < 0·05$), whereas in late summer both hosts were colonized at random (August: $V = 34$, $n = 10$, $P = 0·54$; September: $V = 25$, $n = 8$, $P = 0·36$). In contrast, over the whole summer, mites showed no apparent host choice between adult females and subadult males (Wilcoxon signed rank test; whole summer: $V = 426·5$, $n = 41$, $P = 0·83$; Fig. 1b), pointing out to a random distribution between these categories of host.

PARASITE SURVIVAL EXPERIMENTS WITH *S. ANDEGAVINUS* ON *M. DAUBENTONI*

The temporal pattern of survival of *S. andegavinus* was explained by a single significant term, namely sex of host, whereas neither replicates nor time accounted significantly for the observed variation (repeated-measure ANOVA: $r^2 = 0·49$; sex: $F_{1,17} = 43·9$, $P < 0·001$; replica: $F_{1,17} = 2·2$, $P = 0·15$; time: $F_{1,17} = 2·4$, $P = 0·14$; Fig. 2). Over the 10-day experimental period, the demographic stability of *S. andegavinus* on adult females was clear, with a mean demographic growth function of $106 \pm 3\%$, while the demographic decline over time on adult males was quite important (demographic drop of $36 \pm 1\%$).

Discussion

The sex-biased parasitic load observed in this study is in accordance with previous results obtained from various ectoparasite species infesting European vespertilionid bats (Zahn & Rupp 2004; Lucan 2006). The present study adds data for two new, so far noninvestigated species, *P. auritus* and *M. blythii*. Female bats have thus higher ectoparasite prevalence than males, which strikingly contrasts with the pattern observed in other vertebrate taxa (Poulin 1996; Klein 2004; Morand *et al.* 2004; Amo *et al.* 2005; Krasnov *et al.* 2005b). We could further experimentally demonstrate that parasites contribute to this bias by actively selecting female host. Therefore, if differences in host's exposure to parasitism remain a key factor for explaining sex-biased parasitic load, strong selection for sex recognition within *Spinturnix* species has evolved as evidenced here by our survival experiments, which established that settling on females strongly increases parasite survival prospect.

Sex bias in parasite rate most likely stems from sex-specific differences in host social behaviour, with female aggregation during the reproductive period being likely to play a central role for the evolution of this pattern. In a previous study (Christe *et al.* 2000), we have demonstrated that *Spinturnix myoti* show a strong preference for hosts with either low behavioural antiparasite defences (juveniles), or lowered cell-mediated immunity (reproductive females over non-reproductive females). Thus, a combination of immunosuppression during reproduction and aggregation in nursery colonies facilitates both horizontal and vertical parasite transmission among favourable hosts. Male solitary lifestyle decreases transmission probability of *Spinturnix*, which in turn may result in

adaptive parasite choice. Moreover, sex-specific thermal roosting conditions in most temperate-zone bat species may be an additional important factor, with the high temperature prevailing in nursery roosts potentially boosting parasite transmission and reproduction (Solick & Barclay 2006). However, in the case of *Spinturnix* spp., which complete their entire life cycle on the host, abiotic factors are likely to play a minor role, contrary to biotic factors. Biotic factors concern mainly bats' peculiar physiology. In effect, bats aggregating in reproductive clusters remain the whole day homeothermic. This enables them to sustain a high metabolism, thereby maximizing embryo growth and lactation. In contrast, non-reproductive females and males, especially when roosting solitarily, enter regular phases of torpor, even during the summer (Kurta & Kunz 1988). These phases of lethargy would correspondingly slow down the metabolism of ectothermic ectoparasites such as mites.

The difference in parasitism could be attributed to differences in grooming rate between males and females. Because grooming activity is energetically costly (Giorgi *et al.* 2001), mothers may reduce grooming activity, which is traded-off against other components of maternal care (McLean & Speakman 1997). Consistent with this hypothesis, it has been shown that reproductive female bats groom less than non-reproductive females (McLean & Speakman 1997). Similarly, rutting male impalas and bisons engage in much less grooming than females, presumably to increase vigilance towards herding females and bachelor males (Mooring & Hart 1995; Mooring *et al.* 2006). Although we cannot exclude differential, sex-specific grooming rate in most situations in this study, grooming ability – or at least its efficiency – was certainly hampered if not totally suppressed in the flat, small-sized boxes we used for our dual choice experiments. Overall, if males would be more inclined than females to perform grooming, this would further bias parasite adaptive preference for females; the pattern observed would thus in no case be reversed but reinforced.

Gender differences in parasite infestation have also been attributed to possible resource-based trade-offs between growth and immunity in species with sexual dimorphism (Sheldon & Verhulst 1996; Møller, Sorci & Erritzøe 1998; Zuk & Stoehr 2002; Tschirren, Fitze & Richner 2003) and/or to the immunosuppressive effect of androgens, particularly in species with a high level of sexual selection (Alexander & Stimson 1988; Zuk 1990). The five bats species studied here all exhibited sexual size dimorphism in favour of females. Our findings thus conform to the pattern observed in a comparative analysis, which revealed that mammal species in which the female is the larger sex exhibit female-biased parasitism, whereas the opposite trend is found when males are the larger sex (Moore & Wilson 2002). We could thus not exclude the possibility that during growth, females allocate resources differently than males. This difference in resource allocation would lead to difference in future sex-specific defences against parasites.

Mites survived better and reproduced significantly better on females than on males. As suggested by the outcome of our experiments, sex-biased parasitism observed in free-ranging bats would be a mere consequence of both parasite preference and differential survival according to host status. Male and female bats seem to represent different types of hosts and thus parasites may evolve 'habitat' choice strategies to infect better quality hosts (Gandon 2004; Hawlena, Abramsky & Krasnov 2005). Male and female noctule bats spend the winter in common hibernation roosts. Despite close body contact during this long period of inactivity, we found a significant difference in prevalence and intensity of parasites already soon after the end of the hibernating period (Table 1). This suggests a permanently readjusted, active choice on the side of the parasites. Previous experiments had demonstrated that *Spinturnix* are able to precisely detect, and select almost immediately, the 'right' host, i.e. their native host species (Giorgi *et al.* 2004). In addition, individual hosts with an excellent nutritional status were at once recognized and chosen (Christe *et al.* 2003). As there is no clear sexual dimorphism (e.g. partial fur coverage on the wings of one sex only), i.e. no external recognition signal usable by the parasite, steroid level is the most probable candidate as regards host selection cues. In this respect, we speculate that hormone concentrations could indirectly translate into differential (e.g. sex specific) metabolic rates that might theoretically be detected by body temperature or other biochemicals (Osterkamp *et al.* 1999). In the absence of appropriate tests, however, the stimuli involved in host sex recognition remain unknown.

In our choice experiments, we first found marked seasonal effects in host selection, with strong female preference at the beginning of the season and random choice during the mating period. During mating, testosterone levels are high in males, and this period also corresponds to a high probability of transmission of parasites between males and females due to the constitution of pairs in the mating alcoves. Second, we could document a random choice between adult females and sexually immature, subadult males. These results support the hypothesis of subtle cues used by *Spinturnix* for host selection. In natural populations of *M. daubentoni*, prevalence in adult females (94·5%) was significantly higher than in subadult females (83·4%). The inverse was true for males with a prevalence of 60·8% on subadults, vs. 35·4% on adults.

There was no difference in parasite intensities between juveniles of either sex within colonies, probably due to similar parasite exposure and identical hormone profiles at this early stage of life. A similar result has been shown for juvenile *M. daubentoni* (Lucan 2006). These two studies are thus in accordance with two studies on juvenile birds (Møller *et al.* 1998; Bize *et al.* 2005) but contrast with a study on great tit

nestlings in which males showed a reduced cellular immunity (Tschirren *et al*. 2003).

In conclusion, this study adds to the exceptions to the female host supremacy paradigm in parasitic infections of mammals (Morales-Montor *et al*. 2004) as it reveals distinct female-biased parasitism in five different bat species. The particular social life of bats, compared with other mammals on which most host–parasite studies have been carried out so far, is likely to imply different selective pressures leading to a largely female-biased parasite preference. For hosts, this difference in parasite susceptibility is expected to select for different life-history traits according to sex. For parasites, our results suggest first that male and female hosts represent different types of 'habitats', and, second, that parasites have evolved subtle cues to detect and infest better quality hosts under most circumstances.

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