Oecologia (1997) 111:183–188

Gabriele Sorci · Michelle de Fraipont · Jean Clobert

Host density and ectoparasite avoidance in the common lizard (*Lacerta vivipara*)

Received: 18 August 1996 / Accepted: 7 February 1997

Abstract Increased transmission of parasites and diseases is generally considered as a major cost of social life. In this study we tested the hypothesis regarding ectoparasites as a cost of living in crowded habitats in the common lizard (*Lacerta vivipara*). We used two approaches to explore this question. First, we tested if ectoparasite load and prevalence are positively correlated with host density in the field. Second, we experimentally tested if lizards avoid parasitized conspecifics. Contrary to expectation, we found that (1) ectoparasite load is negatively correlated with lizard density; (2) prevalence does not significantly increase with density; (3) unparasitized lizards do not avoid parasitized conspecifics but are attracted by them whatever their parasite load. These findings suggest that ectoparasites cannot be considered as a cost of living at high density in the common lizard, in spite of the potential negative impact mites may have on lizard fitness.

Key words Ectoparasites · Host density · Lizards · Parasite transmission

Introduction

Increased probability of parasite transmission is generally considered as one of the principal costs of group living (Alexander 1974). Living in crowded habitats can dramatically increase the transmission rate of those parasites that need close proximity among hosts (contagious parasites, Côté and Poulin 1995). Moreover, crowded habitats, favouring parasite transmission, may also favour parasite virulence, thus resulting in negative impact on individual host fitness (Levin and Svanborg Edén 1990). Both the increased transmission of contagious parasites and their negative impact on organisms living in groups have been documented (Brown and Brown 1986; Møller 1987; Hochberg 1991; Poulin 1991). However, for some mobile parasites, which actively seek hosts (e.g., dipterans, leeches), hosts aggregating in groups may benefit from a selective advantage. For these mobile parasites, the same phenomenon that reduces predation in grouped prey may be effective in reducing parasitism in grouped hosts (see Mooring and Hart 1992; Côté and Poulin 1995 for recent reviews).

If contagious parasites represent a cost for host social life we should expect that there would be selection pressure to minimize such a cost. Although individuals living in large groups may experience higher risks of infection than isolated individuals, they could minimize these risks by avoiding contact with parasitized conspecifics. This implies that hosts are able to detect the parasite load of conspecifics. There is some evidence that individuals may indeed discriminate between infected and uninfected conspecifics, and, for instance, prefer to mate with healthy individuals (Johnson and Boyce 1991).

We used the host-parasite association between the lizard *Lacerta vivipara* and a mite belonging to the genus *Ophionyssus* (Mesostigmata) to test if these contagious mites are a cost of living in crowded conditions in the common lizard and if hosts exhibit any mechanisms to reduce this cost (e.g., avoidance of parasitized conspecifics). This model system was particularly convenient for several reasons:

1. The common lizard may live in very dense populations (higher than 1000 individuals/ha; Massot et al. 1992; Clobert et al. 1994).
2. It has been shown, in other lizard species, that individuals tend to be attracted by conspecifics (Stamps 1987, 1988).
3. Mites may negatively affect lizard fitness (Sorci and Clobert 1995).
4. Mites may potentially affect lizard behaviour (Sorci et al. 1994).

G. Sorci (✉) · M. de Fraipont · J. Clobert
Laboratoire d'Ecologie, CNRS URA 258,
Université Pierre et Marie Curie, Bât. A., 7ème étage,
7 quai St. Bernard, Case 237, F-75252 Paris Cedex 05, France
Fax: (33)-1–44273516; e-mail: gsorci@snv.jussieu.fr

To test the hypothesis that parasites are a cost of living in crowded habitats we correlated both parasite load and prevalence with lizard density in the field. To test the hypothesis of parasite avoidance, we set up two different experiments. In the first one, we tested lizard choice between two patches, one of which had been previously occupied by a parasitized or an unparasitized lizard. This experiment reproduced the natural situation in which a lizard must make a decision where to settle on the basis of odour cues. In the second experiment we tested lizard choice between sharing a refuge with a parasitized or an unparasitized conspecific based on both visual and odour cues.

Methods

Study organisms, study site, and lizard collection

The common lizard (*Lacerta vivipara*) is a live-bearing lacertid living in peatbogs and heathland in northern Europe and Asia. Three age classes can be easily recognized because of differences in body size: juveniles (lizards born in the year, snout-vent length 20–30 mm); yearlings (1-year-old lizards, snout-vent length 30–45 mm); adults (snout-vent length >45 mm). The common lizard is strictly diurnal and spends the night in refuges (repeated observations have shown that several lizards may share the same refuge; personal observations). In the common lizard, as in most species of reptiles (Schoener 1985), population density remains stable through years and can reach very high levels (>1000 individuals/ha; Massot et al. 1992).

Lacerta vivipara is the host of haematophagous mites belonging to the genus *Ophionyssus* (Mesostigmata). These are temporary parasites of several species of reptiles, living on the ground and climbing on the host to take a blood meal (Cooper and Jackson 1981). Several lines of evidence support the hypothesis that mites have a negative effect on host fitness. In a previous study we found that: (1) parasite load was negatively correlated with host body condition in yearlings (Sorci and Clobert 1995); and (2) mites were negatively correlated with adult female host survival under laboratory conditions (Sorci and Clobert 1995). Finally, mites can transmit blood parasites (Cooper and Jackson 1981) which have been observed in this population (Sorci 1995, 1996; Sorci et al. 1996).

The lizards used in this study were collected in June during three consecutive years (1992–1994) at a study site in southern France (Mont Lozère, 44°30′ N, 3°45′ E). At the time of capture, we recorded sex, parasite load, and the location where each individual was captured using a grid of coordinates with an accuracy of 3 m. To compute host density, we divided the field site into 405 squares of 36 m^2 (6×6 m) and we counted the number of lizards caught per patch each year.

Parasite scoring

We scored parasite load by counting the number of mites present per lizard. Because of the relatively small size of the parasites (<1 mm), we needed to assess the validity of our estimate. To do this, we captured 14 yearlings, scored their parasite load (mean ± SE = 11.0 ± 2.20, range 1–31), housed them individually in plastic terraria and treated them with a 0.1% solution of tricholfon which killed all the mites. We collected the dead mites at the bottom of the terraria and we counted them. As expected, the number of mites counted in the field and the number of mites counted in the laboratory were highly correlated ($r = 0.922$, slope $= 0.988, P < 0.001, n = 14$), confirming that our field estimate of parasite load was reliable.

Testing parasitized conspecific avoidance

If mites are a cost of social life we should expect selection pressure for hosts to discriminate between parasitized and unparasitized conspecifics, so as to avoid the former. In 1994 we conducted two experiments, using yearlings, to test this hypothesis. We used individuals showing high differences in parasite load: unparasitized lizards (UP) and parasitized lizards (P) carrying more than 15 mites (15 mites represent the 95% percentile of the distribution of parasites in field-caught yearlings). All yearlings were individually housed in plastic terraria ($15 \times 20 \times 15$ cm high), and were used for the experiments within 24 h of their capture.

Experiment 1: patch choice

To test if lizards were attracted toward patches which had been previously occupied by P or UP conspecifics we used a PVC enclosure ($75 \times 75 \times 15$ cm high) divided in two compartments by a wall. The bottom of the enclosure was covered by soil. Two light bulbs (100 W) were symmetrically suspended 60 cm over the two longest enclosure walls and a heat source was placed in front of the enclosure. A symmetrical temperature gradient was thus obtained in the two compartments, ranging from 35 to 27°C. The temperature gradient was identical for all trials conducted (the mean field body temperature of the common lizard is within this range, Van Damme et al. 1990). A video camera was placed on the ceiling and recorded all trials. One lizard (L1) was placed in one compartment for 3 h. At the end of this period, we removed the lizard and the wall dividing the enclosure in two compartments. A second individual (L2) was introduced, and we recorded the time it spent in each compartment. L2 was introduced by placing it in the middle of the enclosure under a dark plastic cup and removing the cup after 1 min. We monitored L2 behavior during two consecutive periods of 20 min. During these periods L2 displayed three types of behaviour: exploration, thermoregulation, and resting (Lecomte 1993; Lecomte et al. 1993, 1994). We did not, however, quantitatively score the time L2 spent performing any particular behaviour. Since we were primarily interested in the behaviour of UP individuals when facing the choice between a patch previously occupied by P or UP individuals, L2 was always a UP individual. The control was made up of UP-UP pairs. We run 18 UP-UP and 17 P-UP pairs. In few cases ($n = 5$), we performed trials with P-P pairs. These trials were included only in the overall test on patch choice irrespective of the parasite group (see Results). For each trial, we randomized the L1 compartment (left $= 16$, right $= 24$), the sex of the individuals, and the trial sequence (UP-P; UP-UP; P-P). We also used individuals of approximately the same size. Between two trials, we replaced the enclosure soil and washed the enclosure bottom to prevent that odors from previous individuals could bias the following trial. We conducted one or two trials per day. No pair was tested more than once, thus we cannot estimate the repeatability of individual choice between trials. However, as each trial was composed of two 20-min periods, we tested the consistency of individual choice between periods.

Experiment 2: shelter choice

To test if lizards preferred to share a shelter with a P or a UP conspecific, we used six identical outdoor PVC enclosures ($100 \times 100 \times 25$ cm high). In each enclosure were placed two identical hollowed out bricks ($25 \times 10 \times 10$ cm high), thus providing two shelters. To eliminate a possible brick effect, we randomized the combination of brick pair for each trial. At 5 p.m., we placed two yearlings (A and B) in each enclosure, after having scored their parasite load. The following day at 8.30 a.m., before individuals became active, we recorded whether they were sharing the same shelter or not. We also recorded parasite load, which allowed us to estimate repeatability over night of this character, and parasite transmission. Between trials, we washed the enclosure and the bricks. We tested 83 different pairs. As for the experiment on patch choice, there were three parasite groups: UP-P ($n = 44$), UP-UP

($n = 32$), and P-P ($n = 7$). The few trials involving P-P pairs were only used for the overall test on shelter choice. We never tested one pair more than once, thus we cannot estimate the repeatability of shelter choice.

Statistical analyses

We used Pearson's correlation coefficient (r) to test the stability of lizard density over time. To test if lizards were randomly distributed in the field we computed the variance over mean ratio of the number of lizards per patch. A random distribution has an expected variance over mean ratio equal to 1. We tested if the observed ratios were significantly higher than 1 using Student's t-tests (Randolph 1975 provides the formula to compute standard errors of the variance over mean ratio). Kruskal-Wallis tests and χ^2 were used to test among-year variability in parasite load and prevalence. We used Spearman's correlation coefficient (r_s) and logistic regression to test correlation between ectoparasite load, prevalence and host density in the field (ectoparasite load was log-log transformed to reduce skewness). To test lizard patch and refuge choice we used Student's t-tests and χ^2 respectively (Sokal and Rohlf 1981). As we did not find any significant effect of sex or any significant interactions between sex and parasite load (all $P > 0.3$) we pooled data for males and females.

All analyses were performed using SAS (SAS Release 6.4, SAS Institute 1990).

Results

Lizard aggregation and density stability over time

Lizards were not uniformly distributed in the field. In each year, most of the patches contained only one individual and only a few squares were occupied by more than five or six individuals. The variance over mean ratio (β) significantly differed from 1 in each year (1992: $\beta = 1.30$, $n = 144$, $t = 2.47$, $P < 0.02$; 1993: $\beta = 2.10$, $n = 140$, $t = 9.2$, $P < 0.01$; 1994: $\beta = 1.35$, $n = 138$, $t = 2.92$, $P < 0.01$).

Lizard density was relatively consistent over time. We found a positive correlation between the number of lizard captures per patch from one year to another, and even when the time lag was 2 years (Pearson's correlation coefficient, 1992–1993: $r = 0.515$, $n = 122$, $P < 0.001$; 1993–1994: $r = 0.630$, $n = 119$, $P < 0.001$; 1992–1994: $r = 0.452$, $n = 116$, $P < 0.001$; Fig. 1 refers to the 1993–1994 correlation). When we considered the number of different lizards caught per square, we still found positive correlations, although significant only for the 1992–1993 comparison (Pearson's correlation coefficient, 1992–1993: $r = 0.324$, $n = 80$, $P = 0.003$; 1993–1994: $r = 0.204$, $n = 66$, $P = 0.101$; 1992–1994: $r = 0.136$, $n = 74$, $P = 0.247$). Using Fisher's method to combine probabilities yields an overall significant correlation between the number of different lizards caught per square across time ($\chi^2_6 = 19.00, P < 0.01$).

Parasite load, prevalence, and host density

Ectoparasite load slightly increased among years (mean ± SD, min–max: 1992, 2.77 ± 3.92, 0–26, $n = 268$; 1993, 2.64 ± 4.84, 0–45, $n = 299$; 1994, 4.29 ± 7.07, 0–59, $n = 236$; Kruskal-Wallis test $\chi^2_2 = 8.933, P = 0.012$). Prevalence was stable among years (1992: 57.8%, $n = 268$; 1993: 56.5%, $n = 299$; 1994: 64.4%, $n = 236$; $\chi^2_2 = 3.744$, $P = 0.154$). The number of lizards per patch varied from 1 to 7 in 1992, from 1 to 9 in 1993, and from 1 to 6 in 1994. In all three years ectoparasite load was weakly negatively correlated with host density per patch, although not significant in 1993 (Spearman's correlation coefficient, 1992: $r_s = -0.197$, $P = 0.021$, $n = 138$; 1993: $r_s = -0.019$, $P = 0.837$, $n = 123$; 1994: $r_s = -0.207$, $P = 0.020$, $n = 127$). Using Fisher's method to combine probabilities yields an overall significant correlation between ectoparasite load and host density per patch ($\chi^2_6 = 15.91$, $P < 0.02$). Prevalence was not correlated with density in any of the three years (1992: Wald $\chi^2 = 0.584$, $P = 0.445$, $n = 268$; 1993: $\chi^2 = 0.011$, $P = 0.918$, $n = 299$; 1994: $\chi^2 = 0.420$, $P = 0.517$, $n = 236$; Fig. 2).

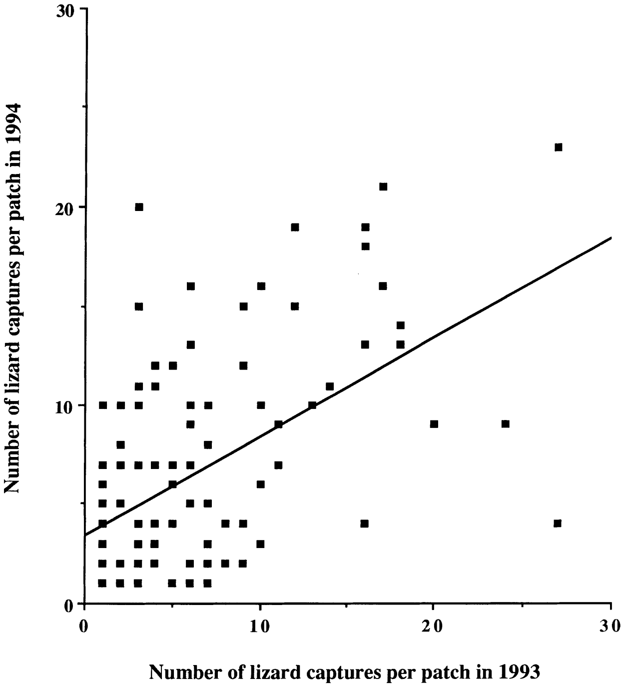

Fig. 1 Correlation between the number of different captures per patch in 1993–1994

Experiment 1: patch choice

Individual patch choice, expressed as the time spent in each compartment, was repeatable between time periods. The correlation between the time spent in one compartment during the two 20-min periods was significant ($r = 0.563, n = 40, P < 0.001$).

Overall, lizards tended to prefer previously occupied patches (mean time spent in the previously occupied patch ± SD = 1346.78 ± 370.84(s), $n = 40$; t-test comparing the observed to the expected mean, $t = 2.50$,

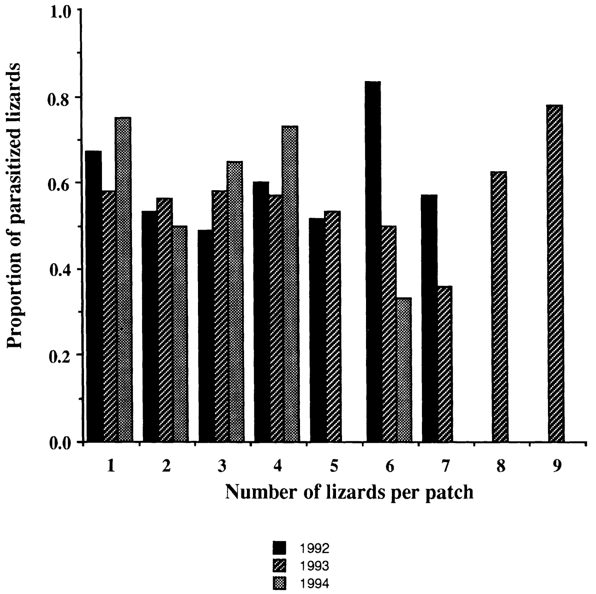

Fig. 2 Proportion of parasitized individuals (prevalence) as a function of host number per patch during 1992–1994

$df = 38$, $P < 0.02$). Lizards spent 12.2% more time in the previously occupied patch.

Ectoparasite load did not affect individual patch choice. UP individuals did not avoid patches that had been previously occupied by P lizards (mean time spent in the patch previously occupied by a UP lizard $\pm$SD $= 1416.44 \pm 402.60, n = 18$; mean time spent in the patch previously occupied by a P lizard $\pm$ SD $=$ 1228.88 ± 357.84, $n = 17$; $t = 1.45$, $df = 33$, $P = 0.156$).

Experiment 2: refuge choice

Parasite load remained constant between the time when we introduced the lizards into the enclosure and the moment when we scored their position the morning after ($r = 0.985$ for a randomly chosen lizard per pair, $n = 44$, P $<$ 0.001). Although most of the individuals kept the number of mites they had the previous evening, some of them (9 out of 44) showed an increase or a decrease in parasite load. This could reflect parasite transmission between individuals. To test this hypothesis we recorded, for each lizard belonging to the P-UP group, the difference in parasite load between the evening and the subsequent morning, and we correlated these values for each pair. As expected, the change in parasite load was negatively correlated for pairs of lizards ($r_s = -0.455$, $P = 0.002$, $n = 44$). This indicates that when A lost some parasites, B's parasite load increased.

In 47% ($n = 39$) of the trials both individuals entered a shelter. Lizards did not tend to share the same shelter (24 trials where individuals shared the same shelter vs. 15 where they chose different shelters; χ^2 comparing observed vs. expected frequencies due to chance, $\chi^2_1 = 2.08$, $P = 0.150$).

UP lizards did not avoid sharing a shelter with P individuals: 63.6% of the individuals in the UP-P pairs ($n = 22$) and 62.5% in the control ($n = 16$) shared the same refuge ($\chi^2_1 = 0.005, P = 0.944$).

Discussion

One of the principal costs of social life and of living in crowded habitats is generally recognized as the increased probability of acquiring parasites and diseases (Alexander 1974). According to this hypothesis parasite load should increase with host group size and/or density for those parasites which need close proximity among hosts (Côté and Poulin 1995). Indeed, positive correlations between parasite load and host group size have been reported for different groups of contagious parasites (Freeland 1979; Brown and Brown 1986; Møller 1987; Hochberg 1991; Poulin 1991). Our findings are not in agreement with the hypothesis that ectoparasites are a cost of living in crowded habitats, as we did not find a positive correlation between mite load and lizard density. Rather, we found weak negative correlations between parasite load and host density, and no correlation between prevalence and host density.

A negative correlation between mite load and host density may arise from several reasons. For instance, lizards could aggregate on areas with reduced number of parasites, or alternatively, lizards in good microhabitats can be in better conditions than other individuals and therefore suffer less from mite infections.

A more ultimate explanation of a negative correlation between ectoparasite load and host density may be that hosts lower the risk of ectoparasite infection by aggregating. The mechanism underlying the decrease of parasite load with host density may involve a sort of parasite dilution (Mooring and Hart 1992; Hart 1994), each host being just one of several potential targets. The result of our experiment on shelter choice, showing that parasitized hosts confined with another individual in a small area experience a decrease in their parasite load, can account for the observed pattern of parasite dilution. However, if parasitized lizards benefit from a decrease in their parasite load by sharing the same shelter with other lizards, uninfected lizards paid a cost as some of them became infested. Thus, why did uninfected lizards not avoid parasitized conspecifics? First, as previously noted, we found that prevalence is not correlated with host density in the field, therefore there is no clear evidence that the probability to be infected increases with host density in the field. Moreover, even in the case where the prevalence was positively correlated with density (as suggested by experiment 2), living at high densities could be beneficial to lizards if the probability of encountering parasites is overall high and if parasite load decreases with host density. Both of these conditions seem to be fulfilled, as we found that prevalence was high (ranging from 56.5% to 64.4% during the 3 years of the study for the whole sample, and reaching

80% for yearlings), and that individuals living at high density had fewer mites per capita than individuals living in isolated patches.

Host aggregation as an antiparasite defence has already been reported in primates (Freeland 1977), feral horses (Duncan and Vigne 1979; Rubenstein and Hohmann 1989), and sticklebacks (Poulin and FitzGerald 1989). However, all of these studies did not involve contagious parasites, but rather mobile parasites which actively seek for their hosts. Recently, Côté and Poulin (1995) reviewed the published studies on the correlations between prevalence, intensity of parasitism and host group size. They found a very consistent pattern of association between these variables depending on the mode of parasite transmission, that is positive correlations between intensity of parasitism and host group size for contagious parasites, and negative correlations for mobile parasites. In the present case, mites should be considered as contagious parasites, since their movement capacities do not allow them to cover long distances to search for potential hosts. Thus, if the hosts are resident at high densities in a area, it is difficult to understand why the parasites should not build up in proportion to host abundance. One possible explanation for these findings is that the most infected individuals regularly leave the patches at high density, possibly because they have lower competitive capacities than other individuals. This might be particularly true for yearlings for whom a negative correlation between mite load and body mass has been shown (Sorci and Clobert 1995). Another possible explanation could be that individuals of high phenotypic quality aggregate in good environments, and this may result in lower mite loads. Interestingly, Arnold and Lichtenstein (1993) also reported a negative correlation between mite load and number of neighbouring groups in marmots.

If lizards living in crowded habitats do not suffer from increased parasite load, we should not expect any avoidance of parasitized conspecifics; moreover if host aggregation is an antiparasite defence we should expect lizards to be attracted by conspecifics independently of their parasite load. The results of the experiments we carried out on avoidance of parasitized conspecifics are in agreement with these predictions. Unparasitized lizards did not show any avoidance of parasitized individuals. Moreover, in the experiment on patch choice, lizards were significantly attracted towards the patch that had been previously occupied. The finding of an attraction towards occupied patches of habitat is consistent with those reported by Stamps (1987, 1988) who found that the lizard *Anolis aeneus* prefers to settle in habitats previously occupied by other lizards.

A major problem one can face when investigating the behaviour of wild animals in the laboratory is that the observed behaviours may be artefacts due to the experimental conditions. Therefore, one could wonder if the responses we observed in our enclosures could apply to natural conditions. For instance, we could have added some environmental heterogeneity to our enclosures to make them more realistic (Avery et al. 1982). However this would have limited the possibility of repeatedly using the same enclosure as we needed to wash it carefully between each trial to eliminate the odour tracks of previous individuals. Several factors support the idea that the lizards' behaviour was not altered by the experimental protocol. First of all, lizards displayed three types of behaviour during the trials (exploring, thermoregulation, resting) which correspond to those observed under natural conditions (Lecomte 1993; Lecomte et al. 1993, 1994). Secondly, patch choice was repeatable for a given lizard, showing that the observed behaviours corresponded to an individual characteristic.

An alternative explanation for the lack of avoidance of parasitized lizards is that lizards might not be able to assess the level of parasite infection of other individuals, especially when they can only rely on odour cues, as for the experiment on patch choice. However, in natural conditions it is likely that lizards mostly base their choice of settling in a given patch by using odour signals, and this should be particularly true for *Lacerta vivipara* which lives in densely covered habitats. Previous studies have shown that *L. vivipara* may recognize both conspecific and predator odors (Thoen et al. 1986; M. de Fraipont and Lena, personal communication). Moreover, Kavaliers and Colwell (1995) recently showed that female mice can discriminate between the odours of parasitized and non-parasitized males, and prefer the odours of non-parasitized males. Finally, the argument that lizards are unable to assess parasitized conspecifics through odours does not apply for the experiment on shelter choice, when the two lizards were in visual contact. Indeed, it has been shown that some visual cues can be used to detect parasite infection (e.g., Clayton 1990), even when parasites are not directly visible, as in the case of mites.

In spite of possible alternative explanations for the negative correlation between parasite load and host density and for the lack of parasitized conspecific avoidance, this study clearly showed that host density does not necessarily result in increased risks of ectoparasite transmission in the common lizard. Nevertheless, to what extent aggregating represents a defence against contagious mites definitely requires further investigations.

Acknowledgements We are grateful to T. Boulinier, Y. Michalakis, S. Plesner-Jenssen who critically revised a previous draft of the paper, and provided many constructive suggestions and comments. We are grateful to E. Danchin who kindly provided the video equipment to record lizard behaviors. We also thank the Parc National des Cévennes and the Office National des Forêts for providing facilities during our field work. This research has been supported by the Centre National de la Recherche Scientifique (CNRS-PIREN), and by the Ministère de l'Environnement (SRETIE).

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