Of great tits and fleas: sleep baby sleep . . .

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Abstract. Many bird parasites reduce their hosts' fitness and, as a consequence, anti-parasite behaviour such as preening and nest sanitation has evolved. These activities are time consuming and, during the day, compete directly with time devoted to foraging and food provisioning to nestlings. Moreover, infested hosts may have to allocate extra time to foraging in order to compensate for the energy loss that ectoparasites impose on the nestlings and parents. Alternatively, brooding females could, at the expense of sleeping, allocate more time to preening and nest sanitation at night. If sleeping has a short-term restoring function, one may then expect a reduction in feeding efficiency of sleep-deprived females. In this study, the effect of a haematophagous ectoparasite, the hen flea, on the activity budgets of breeding female great tits during the day and at night was investigated experimentally. Time allocated to nest sanitation increased only slightly from 0.6 % of daytime in ectoparasite-free nests to 2.8% of daytime in infested nests, thus demonstrating the higher priority given to food provisioning than parasite control. Females in infested nests reduced their sleeping time significantly (73.5% of night-time in parasite-free nests versus 48.1% in infested nests). The time freed from the reduction of sleeping time was mainly used for nest sanitation (8.3% of night-time in parasite-free nests versus 27.1% in infested nests). Despite this strong decrease in sleeping time, there was no effect of ectoparasites on the females' rate of food provisioning to nestlings. © 1996 The Association for the Study of Animal Behaviour

By definition, parasites reduce the fitness of their hosts (Price 1980). Ectoparasites impair nestling growth and survival (e.g. Møller 1990; Møller et al. 1990; Richner et al. 1993), and anti-parasite behaviour that reduces the parasites' impact must therefore be favoured by natural selection (Keymer & Read 1991; Hart 1992). Clayton (1991) has demonstrated experimentally that feather preening significantly reduces the load of feather lice on non-breeding adult rock doves, *Columba livia*. For nesting birds, parents might be expected to allocate time to nest sanitation in order to control the load of harmful ectoparasites of the nest and the nestlings. Such anti-parasite behaviour is time-consuming (e.g. Cotgreave & Clayton 1995) and will therefore reduce the time that a parent bird can devote to foraging. In

nidicolous birds food provisioning is the most time-consuming activity during the rearing period (Winkler & Wilkinson 1988). Alternatively, since females commonly brood their young at night until they can fully thermoregulate (O'Connor 1984), they could, at the expense of sleeping, postpone nest sanitation until the night hours. Great tits, *Parus major*, for example, brood their offspring for at least 2 weeks after hatching (Berndt & Winkel 1972). Sleep deprivation of females that engage in nocturnal sanitation activities, however, may carry short-term costs such as a reduced foraging efficiency during the day, or longer-term costs such as reduced survival. These potential costs will largely depend on the function of sleep in birds, a subject that is poorly understood.

In this study, we controlled experimentally the load of a common haematophagous ectoparasite, the hen flea, *Ceratophyllus gallinae*, in nests of the great tit, and measured the females' pattern of time allocation to foraging behaviour, and to anti-parasite behaviour in the nest both during the

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day and at night. The main analysis concerns the trade-off between sleeping and nest sanitation, and the potential trade-off between sleeping at night and foraging during the day.

METHODS

We carried out the study during the breeding seasons of 1991–1992 in a beech-dominated forest adjacent to the campus of the University of Lausanne, Switzerland. Nestboxes were installed in 1989 and have been used since by great tits and blue tits, *P. caeruleus*. The hen flea is a common ectoparasite of both species (Harper et al. 1992), and affects components of reproduction in this study population (Richner et al. 1993; Oppliger et al. 1994). For the present experiment, we infested half of the nests of the study population three times between laying of the first egg and hatching of the nestlings with 20 fleas each time. We kept the other half of the nests parasite-free by regularly heat-treating them with a microwave appliance. This treatment produces a highly significant difference in flea numbers in the two experimental nest types (for details see Richner et al. 1993; Heeb et al. 1996). A total of 60 fleas is less than we usually find in naturally infested nestboxes, but more than the number that immigrate naturally over one breeding season into previously cleaned nestboxes (Heeb et al. 1996). We recorded the behaviour of female parents 12 days after hatching. Mean filming date was 4 June ($\pm$ 14 days SD) with sunrise at 0545 hours and sunset at 2120 hours. The hen fleas' generation cycle lasts from 20 to 40 days, and therefore at least the fleas that were introduced at the egg-laying stage had produced a new generation by the time we filmed the females' behaviour. Presence of adult fleas 12 days after hatching was verified both from the films and from nestbox inspections during the day.

For filming, an infra-red light source and an infra-red sensitive video camera were mounted inside the nestbox. A timer switched the camera on at midnight and off at 0300 hours. We recorded 15 females in parasite-free boxes and 14 females in infested ones. From the films, we monitored four types of behaviour, termed sleeping, resting, nest sanitation and grooming. These categories sum up to 100% of time. Following Amlaner & Ball (1983) sleeping is defined here as the time when the beak is pointed backwards and

tucked under the scapulars (classical sleep posture), resting is defined as the time when the beak is pointed forward and the eyes opened. Only rarely do females close the eyes in this position. This position is generally followed by the sleep position described above. Nest sanitation is defined as a period of active search with the head dug into the nest material. Grooming is defined as the combined time when the female is preening her feathers or scratching her body with the legs (Clayton & Cotgreave 1994).

We calculated the total duration of each activity by summing the length of each behaviour bout that occurred during the 3 h of filming. The following morning, between 0900 hours and noon, we filmed each nest for a further 3 h and monitored nest sanitation activities and the female's feeding rate. Of the video recordings taken during the day, 25 films were of sufficient quality to be viewed, giving a sample size of 13 parasite-free nests and 12 infested nests. The percentage of an hour taken up by each activity and mean bout length of each activity were then calculated for each nest. For the statistical analysis, the percentages were arcsine transformed and 95% confidence limits calculated. Among the activities performed at night, only sleeping and nest sanitation were tested for significance. The two percentages for these activities do not sum to 100, and a possible non-independence of the two activities is therefore not considered as a particular problem. For the graphical presentation, the arcsine values were re-transformed into percentages. If the transformed data were not normally distributed, we used non-parametric tests. For the statistical comparison of bout lengths of sleeping, nest sanitation, resting and grooming in infested and parasite-free nests, we applied a Bonferroni correction by setting the alpha-level for significant differences to 0.0125.

RESULTS

Nest Sanitation During the Day

Females in infested nests allocated more time to nest sanitation (Fig. 1) than females in parasite-free nests. The difference is statistically significant ($U=32.5$, $N_1=14$, $N_2=15$, $P=0.013$) but small. In both infested and parasite-free nests the males did not perform nest sanitation activities.
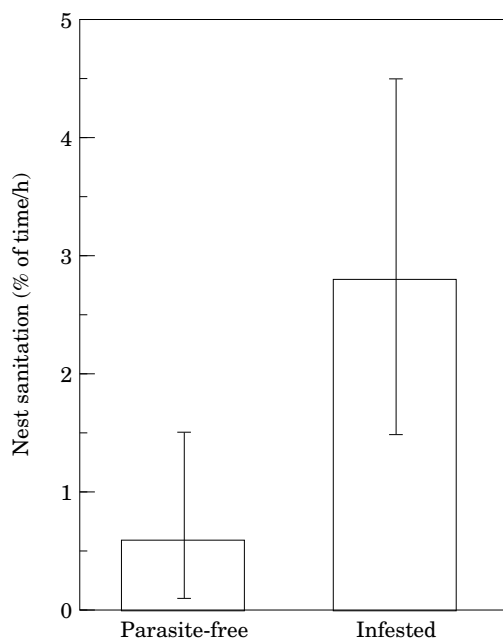
Figure 1. Mean (± 95% CI) percentage of an hour taken up by nest sanitation during the day for females in parasite-free (*N*=12) and infested (*N*=13) nests.

Behaviour at Night

Sleeping

The mean percentage of time that females spent in the sleeping position was 73.5% in parasite-free nests (Fig. 2a), but 48.1% in infested nests. This ectoparasite-induced reduction of 25% is statistically significant (t=2.55, df=27, P=0.017). Mean bout length of a sleeping period (Fig. 2b) was also significantly reduced in infested nests (t=4.26, df=27, P<0.001). On average, the females of infested nests woke up after sleeping for 150 s, and females in parasite-free nests after 360 s.

Nest sanitation

Nest sanitation (Fig. 2c) increased significantly from 8.3% of total time in parasite-free nests to 27.1% in infested nests (t=4.76, df=27, P<0.001). Mean duration of a nest sanitation bout (Fig. 2d) was significantly longer (t=2.82, df=27, P=0.009) when ectoparasites were present (28.4 ± 2.7 s) than if they were absent (41.3 ± 3.7 s).

Resting and grooming

The mean percentage of time that females spent in the resting position was similar for infested (15.1%, range=0–59%) and parasite-free (14.6%, range=0–54%) nests. Mean resting bout length (± 1 SE) did not differ significantly between the two groups (72.9 ± 14.3 s in parasite-free nests versus 49.3 ± 7.0 s in infested nests; t=1.47, df=27, P=0.16, power for detecting a significant difference at alpha of 0.05=29.3% (see Cohen 1988)).

Compared with the other activities, the percentage of time that females groomed themselves was small for both parasite-free (mean=0.9%, range=0–4.6%) and infested birds (mean=1.5%, range=0–9.8%). Grooming bout length did not differ between the two groups (14.2 ± 2.4 s in parasite-free nests versus 11.4 ± 2.4 s in infested nests; t=0.74, df=27, P=0.47, power=12.5%).

Females' Rates of Food Provisioning

The mean number of feeding trips per h (± 1 SE) was not significantly different between females of infested (17.6 ± 2.7) and parasite-free (18.4 ± 2.8) nests (t=0.21, df=23, P=0.83, power=5.5%). Within each treatment group, there was also no correlation between the percentage of time that a female spent in sleeping position and her subsequent rate of food provisioning the following morning (infested nests: r=0.17, N=12, P=0.57; parasite-free nests: r=0.23, N=13, P=0.47).

DISCUSSION

The study shows that ectoparasites affected the pattern of time allocation of brooding females. The most marked changes occurred at night when infested females increased the time spent on nest sanitation more than three-fold. This increase occurred at the expense of sleeping time, and therefore begs the question of the consequences of this considerable reduction in sleeping. The answer depends largely on the supposed function of sleep, which is often considered as a 'non-behaviour'. As Toates (1980) pointed out, the function of sleep in birds is poorly understood, although a relatively large part of a bird's life is devoted to this behaviour. It is interesting to note that for females in infested nests the length of sleeping bouts was considerably shortened. Thus,
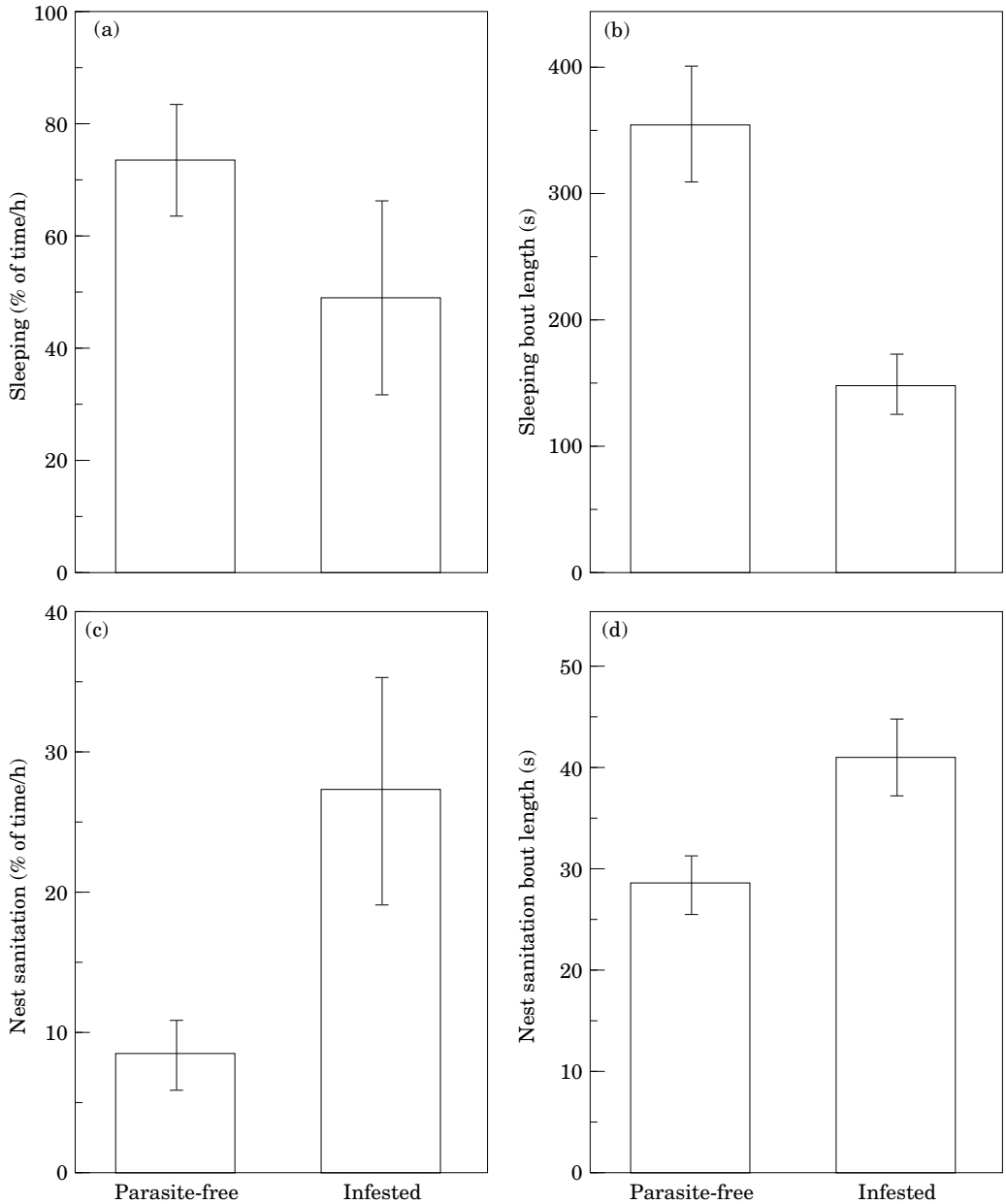
Figure 2. Mean (± 95% CI) percentage of a night hour taken up by sleeping (a), or nest sanitation behaviour (c), for females in parasite-free ($N=15$) and in infested ($N=14$) nests. Mean bout length (± 1 SE) of sleeping (b) and nest sanitation (d) activities during the night inside the nestboxes in parasite-free ($N=15$) and in infested ($N=14$) nests.

ectoparasites do not only affect the quantity of sleeping activity, but may also reduce its quality if one considers that the duration of a sleeping bout may be important for progressing into the subse-

quent phases of sleep. Again, this is a subject where little is known.

Several controversial hypotheses have been proposed for the function of sleep (for reviews see

Toates 1980; and Amlaner & Ball 1983). The three more common ones hold that sleep (1) serves to conserve energy (during sleep body temperature is lowered and energy is thereby saved), (2) has a restoring function (sleep restores physiological properties of some tissues, e.g. through degradation of toxic compounds that accumulated in the body during physical or mental activities), (3) is a state of immobilization that increases safety against predators during times that are unprofitable for the performance of other activities (Meddis 1975). Whatever the function may be, it is generally accepted that sleep provides some benefits to the organism. This also implies that a lack of sleep would carry some costs, which, in the case of a breeding bird, would increase the cost of reproduction.

These costs could manifest themselves over shorter or longer periods and could therefore affect current or future reproduction, or both. If the costs arise during the period of caring for the current brood, one would expect that nest sanitation would also be substantially increased during the day, unless foraging gives a much larger benefit than nest sanitation. The fact that infested birds increased nest sanitation during the day only marginally, but maintained a rate of food provisioning that was similar to that of non-infested birds, supports the above suggestion that the benefits arising from foraging are substantially larger than the benefits arising from nest sanitation.

If the costs arise only after the period of parental care, it would imply that the birds trade off future reproduction against investment in the current brood. As one possibility, the costs of reduced sleeping could be mediated by a reduction in immunocompetence with, as a consequence, a reduced survival after the period of current investment. We did not assess return rates of females in the subsequent year in our study.

Interestingly, females of nests in the heat-treated group also showed some nest sanitation behaviours, although much less than females of infested nests. This may be due to a few fleas that immigrate into the nestboxes during the breeding cycle, as shown elsewhere (Heeb et al. 1996). There is also a striking difference between males and females, for which we cannot, at present, offer a satisfying explanation. Males of infested nests never engage in the typical nest sanitation behaviour shown by females but, in contrast to the

females, increase their rate of food provisioning by nearly 50% compared with males of non-infested nests (Christe et al. 1996). A proximate explanation may be that the sexes differ in bill shape (Gosler 1987) which makes females more efficient than males in finding fleas in the nest and killing them. From a life-history point of view, a major difference between males and females in the underlying trade-offs that govern these activities would be predicted. Sleep deprivation in infested females may well influence such trade-offs. Most of the findings of the present study therefore argue for a need of a better understanding of the function of sleep in birds.

REFERENCES

Amlaner, C. J. Jr. & Ball, N. J. 1983. A synthesis of sleep in wild birds. *Behaviour*, **87**, 85–119.

Berndt, R. & Winkel, W. 1972. Ueber das Nächtigen weiblicher Meisen (*Parus*) während der Jungenaufzucht. *J. Ornithol.*, **113**, 357–365.

Christe, P., Richner, H. & Oppliger, A. 1996. Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. *Behav. Ecol.*, **7**, 127–131.

Clayton, D. H. 1991. Coevolution of avian grooming and ectoparasite avoidance. In: *Bird–Parasite Interactions: Ecology Evolution and Behaviour* (Ed. by J. E. Loye & M. Zuk), pp. 258–289. Oxford University Press.

Clayton, D. H. & Cotgreave, P. 1994. Relationship of bill morphology to grooming behaviour in birds. *Anim. Behav.*, **47**, 195–201.

Cohen J, 1988. *Statistical Power Analysis for the Behavioral Sciences*. Hillsdale, New Jersey: Lawrence Erlbaum.

Cotgreave, P. & Clayton, D. H. 1995. Comparative analysis of time spent grooming by birds in relation to parasite load. *Behaviour*, **131**, 171–187.

Gosler, A. G. 1987. Patterns and process in the bill morphology of the great tit *Parus major*. *Ibis*, **129**, 451–476.

Harper, G. H., Marchant, A. & Boddington, D. G. 1992. The ecology of the hen flea *Ceratophyllus gallinae* and the moorhen flea *Dasypsyllus gallinae* in nestboxes. *J. Anim. Ecol.*, **61**, 317–327.

Hart, B. L. 1992. Behavioral adaptations to parasites: an ethological approach. *J. Parasitol.*, **78**, 256–265.

Heeb, P., Werner, I., Richner, H. & Kölliker, M. 1996. Horizontal transmission and reproductive rates of hen fleas in great tit nests. *J. Anim. Ecol.*, **65**, 474–484.

Keymer, A. & Read, A.F. 1991. Behavioural ecology: the impact of parasitism. In: *Parasite–Host Associations: Coexistence or Conflict?* (Ed. by C. A. Toft, A. Aeschlimann & L. Bolis), pp. 37–61. Oxford: Oxford University Press.

Meddis, R. 1975. On the function of sleep. *Anim. Behav.*, **23,** 676–691.

Møller, A. P. 1990. Effects of a haematophagous mite on the barn swallow (*Hirundo rustica*): a test of the Hamilton Zuk hypothesis. *Evolution*, **44,** 771–884.

Møller, A. P. Allander, K. & Dufva, R. 1990. Fitness effects of parasites on passerine birds: a review. In: *Population Biology of Passerine Birds: An Integrated Approach* (Ed. by J. Blondel, A. Gosler, J.-D. Lebreton & R. H. McCleery), pp. 269–280. Berlin: Springer-Verlag.

O'Connor, R. J. 1984. *The Growth and Development of Birds.* Chichester: John Wiley.

Oppliger, A., Richner, H. & Christe, P. 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the great tit (*Parus major*). *Behav. Ecol.*, **5,** 130–134.

Price, P. W. 1980. *Evolutionary Biology of Parasites.* Princeton, New Jersey: Princeton University Press.

Richner, H. Oppliger, A. & Christe, P. 1993. Effect of an ectoparasite on reproduction in great tits. *J. Anim. Ecol.*, **62,** 703–710.

Toates, F. 1980. *Animal Behaviour. A Systems Approach.* Chichester: John Wiley.

Winkler, D. W. & Wilkinson, G. S. 1988. Parental effort in birds and mammals: theory and measurement. *Oxf. Surv. evol. Biol.*, **5,** 185–214.