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Animal behaviour

Does allopreening control avian ectoparasites?

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For birds, the first line of defence against ectoparasites is preening. The effectiveness of self-preening for ectoparasite control is well known. By contrast, the ectoparasite control function of allopreening—in which one birds preens another—has not been rigorously tested. We infested captive pigeons with identical numbers of parasitic lice, and then compared rates of allopreening to the abundance of lice on the birds over time. We documented a negative relationship between rates of allopreening and the number of lice on birds. Moreover, we found that allopreening was a better predictor of louse abundance than self-preening. Our data suggest that allopreening may be a more important means of ectoparasite defence than self-preening when birds live in groups. Our results have important implications for the evolution of social behaviour.

1. Introduction

Behaviour is the first line of defence against parasites [1]. For example, mammals and birds engage in regular grooming behaviour to combat ectoparasites [1,2]. The main form of grooming by birds is preening with the bill, which provides an effective defence against lice, ticks, flies and other ectoparasites [2,3]. Allopreening, in which one birds preens another, may also help control ectoparasites, particularly on regions of the body that cannot be self-preened, such as the head and neck. Nevertheless, most research on allopreening has focused on its role in reducing stress levels in birds, reinforcing pair bonds and other social functions [4–6].

The importance of allopreening for ectoparasite control was suggested by Brooke's [7] field study of tick-infested eudyptid penguins. Unmated penguins, which could only self-preen, had two to three times more ticks on their heads and necks than mated penguins, which engaged in regular allopreening. However, other factors could have influenced the negative correlation between allopreening and ticks. For example, more immunocompetent birds may have been better at attracting mates, and better at resisting blood-feeding ticks with immune responses [8,9].

A more recent study by Radford & Du Plessis [10] showed that dominant green woodhoopoes (*Phoeniculus purpureus*) receive more allopreening than subordinates. Ectoparasites were observed less frequently on dominant birds than subordinate birds, consistent with a role of allopreening in controlling ectoparasites. However, much of the excess allopreening received by dominant birds was directed at body regions that they could already self-preen. Moreover, allopreening was strongly correlated with group size and social status, suggesting that the behaviour serves important social functions.

We explored covariation between allopreening and parasite abundance in captive Rock pigeons (*Columba livia*) experimentally infested with feather-feeding lice (*Columbicola columbae*). *Columbicola columbae* is a permanent ectoparasite that completes all stages of its 24-day life cycle on the body of the host [11]. Adult lice are typically found on the abdomen, wings and tail

of their hosts, while immature lice congregate in larger numbers on the head and neck [12,13]. Because *C. columbae* does not feed on blood, nor living tissues, it is 'invisible' to the immune system. Feral pigeons control *C. columbae* primarily, if not exclusively, by preening [14]. Feral pigeons also allopreen regularly [15]. The goal of our study was to test whether allopreening helps to control feather lice. We monitored *C. columbae* populations on captive pigeons over the course of the study using non-invasive methods, and we assessed host behaviour using instantaneous scan sampling [16].

2. Methods

Rock pigeons were housed in groups of four (two males and two females) in $6 \times 5 \times 3.5$ feet aviaries, each with two nestboxes, on a 12 L : 12 D cycle. Food, grit and water were provided *ad libitum*. Three breeds of rock pigeons were used, with each aviary containing a single breed.

(a) Experimental infestation

At the start of the study, birds were cleared of lice by housing them in low-humidity rooms (less than 25% relative humidity) for several months, which kills lice and their eggs by desiccation [17]. Following the low-humidity treatment, we carefully examined each bird to confirm that it was free of lice or other ectoparasites. Next, we infested each of the four birds per aviary with 25 *C. columbae* taken from 'donor' pigeons. We waited at least six months before collecting data on host behaviour and louse abundance. Two birds died during the course of the study. Lice from each of these birds were removed (see below) and transferred to new parasite-free birds of the same breed and sex. Few, if any, lice were lost because, although *C. columbae* can survive for several days on a dead host, it cannot leave the body of the host under its own power [18].

(b) Parasite abundance

The numbers of lice on birds in each aviary were counted on two occasions, and the mean of the two counts taken as a measure of louse abundance. To estimate the abundance of lice without harming them, each bird was placed in a fumigation chamber and exposed to a stream of CO₂ for 15 min, which anaesthetizes the lice [19]. Anaesthetized lice were removed by gently ruffling the feathers of each bird over a collection surface until the point of diminishing returns [20,21]. Once the lice were counted, they were put back on the same bird unharmed. Each bird was then returned to its aviary.

(c) Host behaviour

Birds within an aviary were given unique colour band combinations. Behavioural data were collected over the course of seven observation sessions, which included at least one of each of the following time windows: 9.00–10.30, 11.30–13.00, 14.00–15.30 and 16.30–18.00. Each session began with a 15 min acclimation period, during which the observer sat motionless within full view of birds in the aviary. Behavioural data were collected using instantaneous scan sampling, with 15 s intervals between birds [16]. Each bird was observed at least 200 times over the seven observation periods. Occasionally, an observation was missed, e.g. because a bird blocked the observer's view of another bird.

(d) Data analysis

Louse abundance was modelled using a generalized linear mixed-effects model (GLMM) with a Poisson distribution and

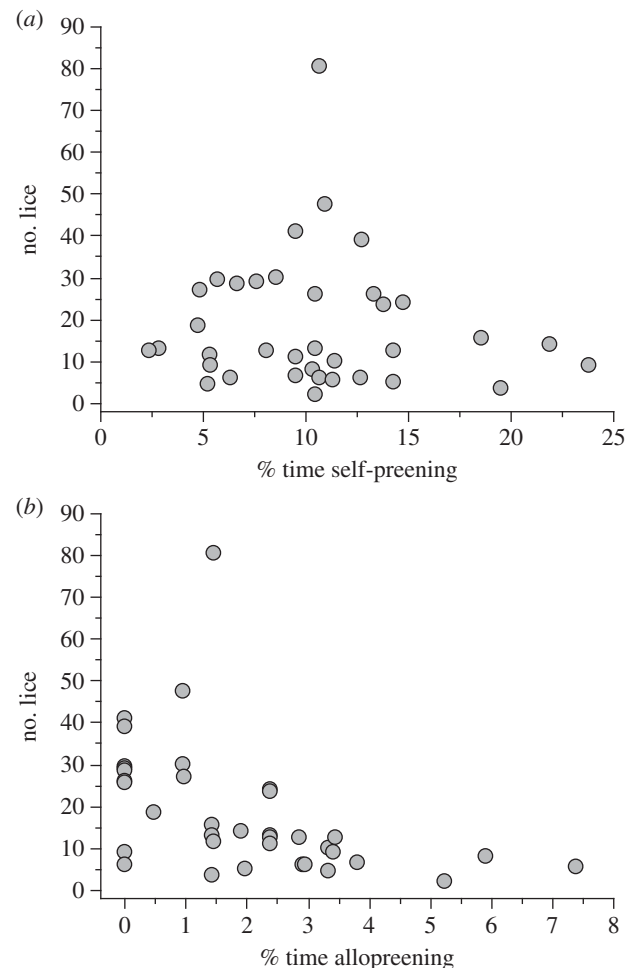


Figure 1. Relationship between the total number of lice per bird and (a) % time spent self-preening and (b) % time spent allopreening.

logarithmic link. We predicted individual-level louse abundance across aviaries by modelling the fixed effects of per cent time allopreening and per cent time self-preening, while breed and aviary were included as random effects with breed 'nested' within aviary. The model had 36 observations from three breeds nested in nine aviaries, and the model intercept was set at the mean level of both allopreening and self-preening. The GLMM was fit in R using the 'lme4' library [22,23]. A linear regression was used to compare the relationship between self-preening and allopreening. All data were made available on the Dryad Digital Repository [24].

3. Results

Birds across the nine aviaries spent a mean (\pm s.d.) of $10.5 \pm 5.0\%$ of their time self-preening, ranging from a low of 2.4% to a high of 23.8% (figure 1a). Birds spent a mean of $2.0 \pm 1.8\%$ of their time allopreening, ranging from a low of 0.0% to a high of 7.4% (figure 1b). The mean louse abundance across all birds was 18.5 ± 15.7 , ranging from a low of 2 to a high of 81.

There was a marginally significant relationship between per cent time self-preening and louse abundance (figure 1a and table 1; GLMM; $Z = -1.79$; $p = 0.074$). By contrast, there was a strong negative correlation between per cent time allopreening and louse abundance (figure 1b and table 1; GLMM; $Z = -8.24$, $p < 0.001$). There was no significant relationship between rates of self-preening and allopreening (Linear regression; $r = -0.07$; $p = 0.67$).

Table 1. GLMM summary of the influence of self-preening and allopreening on louse abundance. Statistical significance in probability tests is indicated by asterisks.

GLMM with Poisson distribution and logarithmic link (intercept at mean preening levels) with 36 observations of three breeds nested in nine aviaries				
random effects	variance	standard deviation		
aviary	0.029	0.171		
breed	0.021	0.144		
fixed effects	estimate	standard error	Z-value	Pr(> z)
intercept	2.780	0.087	31.84	<0.001***
% time self-preening	-0.017	0.009	-1.79	0.0736
% time allopreening	-0.339	0.041	-8.24	<0.001***

*** $p < 0.001$.

4. Discussion

Our results show a strong negative correlation between allopreening and louse abundance, consistent with the hypothesis that allopreening controls ectoparasites. Birds in our study spent an average of 2% of their time allopreening, similar to the 3% rate of allopreening reported for penguins [7]. Our GLMM analysis indicates that this level of allopreening reduces the abundance of lice on birds by more than 40%. Moreover, allopreening was about 17-fold more effective than self-preening. There was no significant relationship between self-preening and allopreening; thus, the effectiveness of allopreening was not an artefact of covariation with self-preening.

There was a marginally significant relationship between self-preening and louse abundance (table 1). This result was heavily influenced by a single, atypical bird with 81 lice (figure 1a). Although this bird is a statistical outlier ($Z > 3.0$), we had no *a priori* reason to exclude it from our main analysis. Temporarily excluding it reveals a significant negative correlation between self-preening and lice (GLMM; $Z = -2.80$, $p = 0.005$), in addition to the significant negative correlation of allopreening and lice (GLMM; $Z = -8.01$, $p < 0.001$). However, allopreening remains 10-fold more effective than self-preening. In summary, our results indicate that self-preening did not play as important a role in controlling lice as allopreening.

Our results show that birds with access to allopreening have fewer lice. But how can so little allopreening be effective? One possibility is that allopreening targets immature lice, which congregate on the head and neck of pigeons [12]. Allopreening in most birds, including pigeons, is directed mainly at the head and neck [4,15]. Unlike adult lice, nymphs lack a fully chitinized exoskeleton [25], making them relatively soft and easy to damage. When birds have opportunities to allopreen, many of these nymphs may be killed, with disproportionate consequences for population recruitment.

Our data further suggest that allopreening is a more important means of ectoparasite control than self-preening when birds live in groups. This benefit of allopreening may

be important for birds that live in larger groups, given that the transmission and abundance of parasites often increase with group size [26]. All else being equal, larger groups of birds should spend more time allopreening [27]. Radford & Du Plessis [10] documented a positive relationship between group size and allopreening in green woodhoopoes.

While allopreening appears to have important social functions [5,10], these functions may be a consequence of the evolution of allopreening as a means of ectoparasite control. Allopreening may enhance the ability of birds to live in large social groups, not primarily by reinforcing social hierarchies and bonds among group members, but by helping to control the increased transmission of parasites that takes place in larger groups [11,26]. Virtually all groups of birds have lice and other ectoparasites [11]. Allopreening has been observed in more than 40 families of birds, including cormorants, finches, herons and parrots. Indeed, most species of birds that live in groups probably engage in at least some level of allopreening [4]. It is conceivable that the ectoparasite control function of allopreening was the main adaptive function of this behaviour in the evolution of social groups, with allopreening only secondarily serving to moderate interactions between the members of such groups.

Ethics. The study was performed with permission from the University of Utah Institutional Animal Care and Use Committee (protocol #14-06010).

Data accessibility. Raw data are available via Dryad (<http://dx.doi.org/10.5061/dryad.gj7sn>) and assigned to the title of this article.

Authors' contributions. S.M.V., G.B.G. and D.H.C. designed the experiment. S.M.V. and G.B.G. collected the data. J.S.R. analysed the data. S.M.V., G.B.G. and J.S.R. wrote the paper with input from D.H.C. All authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Competing interests. We declare we have no competing interests.

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