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IS ALLOPREENING A STIMULUS-DRIVEN DEFENSE AGAINST ECTOPARASITES?

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KEY WORDS ABSTRACT

Anti-Parasite Behavior
Feather Lice
Pigeon
Columbicola columbae

Allopreening occurs when 1 bird preens another bird. The behavior is normally directed at the head and neck of the recipient, i.e., regions that the bird cannot self-preen. Studies of penguins, pigeons, and other groups of birds suggest that allopreening plays a role in the control of ectoparasites, such as ticks and feather lice. However, it is not known whether allopreening increases in response to increases in parasite load, or whether it is a programmed response that occurs independently of parasite load. We conducted a laboratory experiment using wild-caught rock pigeons (*Columba livia*) to test the relationship between ectoparasite load and allopreening rate. We added feather lice (*Columbicola columbae*) to captive pigeons and tested for changes in allopreening rates compared to control birds with no lice added. Allopreening rates did not change in response to the addition of lice. Interestingly, however, our data revealed a negative correlation between allopreening and self-preening rates.

Self-preening by birds, which is important for controlling feather lice and other ectoparasites, is the most common avian grooming behavior (Clayton et al., 2010; Bush and Clayton, 2018). In addition to self-preening, birds preen one another in a behavior known as “allopreening” (Fig. 1). Allopreening, which is thought to serve both social and hygienic functions, is widespread and has been observed in more than 50 families of birds (Harrison, 1965; Clayton et al., 2010; Kenny et al., 2017; Bush and Clayton, 2018). The social functions of allopreening include reducing stress levels (Lewis et al., 2007; Radford, 2008a), reinforcing pair bonds (Kenny et al., 2017), and reinforcing social hierarchies (Gill, 2012; Radford, 2008a, 2008b; Teunissen et al., 2018).

In addition to its social function, allopreening is thought to play a role in the control of ectoparasites. Several studies report negative correlations between allopreening and parasite load (de L. Brooke, 1985; Radford and du Plessis, 2006; Villa et al., 2016b). For example, in captive rock pigeons (*Columba livia*), allopreening rates are negatively correlated with feather lice (*Columbicola columbae*) (Villa et al., 2016b). Whether allopreening does, in fact, control ectoparasites remains uncertain. While allopreening may reduce ectoparasite loads, the dynamics of this behavior are largely unexplored. For example, it is not known whether allopreening occurs at a rate that is independent of parasite load, or whether it is an inducible defense against ectoparasites.

Two models characterize the mechanistic basis of grooming behaviors such as preening. The first model, known as “programmed grooming,” predicts that grooming occurs at a rate that

is independent of the number of parasites on the host. Programmed grooming may serve to remove parasites before they cause too much damage to the host (Hart et al., 1992; Mooring et al., 2004). Programmed grooming is thought to evolve in cases when the threat of parasite infestation is predictably high (Mooring et al., 2004). The second model, known as “stimulus-driven grooming,” predicts that grooming rates will increase when parasite load increases (Mooring, 1995). Stimulus-driven grooming is thought to help hosts conserve energy by allowing them to downregulate grooming when parasite numbers are low (Hawlena et al., 2008).

Patterns of self-preening consistent with both models of grooming have been reported in birds (Brown, 1974; Møller, 1991; Poiani et al., 2000; Dowling et al., 2001; Villa et al., 2016a). For example, self-preening rates increase in pigeons infested with feather-feeding lice, compared to uninfested controls (Villa et al., 2016a). Conversely, Møller (1991) found that Barn swallows (*Hirundo rustica*) do not increase self-preening rates in response to experimental infestation with the hematophagous mite *Ornithonyssus bursa*.

In contrast to the studies of self-preening mentioned above, no test of the inducibility of allopreening with respect to parasites has been conducted to our knowledge. In the current study, we explored the relationship between ectoparasite load and allopreening rates using wild-caught rock pigeons and their ectoparasitic feather lice. We added feather lice to captive pigeons and tested for changes in allopreening rates, compared to the allopreening rates of control birds with no lice added. We also tested for covariation between rates of allopreening and self-preening



Figure 1. Rock pigeons allopreening (*Columba livia*; photo used with permission of Marie Read).

because the 2 forms of preening may control parasites on some of the same body regions (e.g., upper breast). If so, we predict the rates of self-preening and allopreening to be negatively correlated.

Study system

The feather louse *C. columbae* is a host-specific, permanent ectoparasite of rock pigeons that completes all stages of its 24-day life cycle on the body of the host (Clayton et al., 1999). Adult *C. columbae* are typically found on the abdomen, wings, and tail, while immature *C. columbae* congregate more on the head and neck (Nelson and Murray, 1971). *Columbicola columbae* feeds on feathers, which are metabolized with the aid of endosymbiotic bacteria (Clayton et al., 2015). The feather damage caused by *C. columbae* reduces host mating success (Clayton, 1990), thermoregulatory ability (Booth et al., 1993), and survival (Clayton et al., 1999). Because *C. columbae* does not feed on blood or other living tissues, it is “invisible” to the immune system. Rock pigeons control feather lice by killing or removing them with their beaks during regular bouts of self-preening (Clayton et al., 2005). Like self-preening, allopreening is also thought to control feather lice, and allopreening rates are negatively correlated with parasite loads (Villa et al., 2016b). Rock pigeons allopreen their partners regularly (Johnston and Janiga, 1995; Villa et al., 2016b). Allopreening occurs between male-female partners and between parents and their offspring (Goodwin, 1956). Allopreening occurs year-round and is usually initiated by the female in male-female pairs (Goodwin, 1956).

MATERIALS AND METHODS

We live-trapped 80 adult feral rock pigeons in Salt Lake City, Utah (40°45′38.81″N, 111°53′27.78″W) during the fall of 2016. We housed the birds in a free-flight loft with nest boxes. All of the birds were cleared of lice by maintaining the loft at low humidity (<25% relative humidity) for several months. This procedure kills lice and their eggs through desiccation (Harbison et al., 2008).

Following the low-humidity treatment, we visually examined the birds to confirm that each was free of lice and other ectoparasites (Clayton and Drown, 2001). Birds were sexed using the distance between the pelvic bones (Levi, 1945).

Over the course of 18 mo, we removed male-female pairs of birds that were observed to occupy nest boxes and allopreen. We isolated pairs of birds ($n = 24$ pairs) in wire mesh cages ($30 \times 30 \times 56$ cm) separated by plexiglass sheets to prevent feather-feather contact between birds in adjacent cages. Cages were placed in an animal room maintained at approximately 50% humidity, which is sufficient for lice to live and breed (Moyer et al., 2002). Because the molt cycle could influence the results of this study, we examined each bird for signs of molting before entering them into the experiment. None of the birds were molting.

We used instantaneous scan sampling (Altmann, 1974) to collect behavioral data for each pair of birds. In July 2018, one of us (S.A.C.), blind to treatment, conducted 3 observation sessions per day (within the time frames 9:00–10:30, 12:30–14:00, and 16:00–17:30) for 3 days prior to treatment, and again for 3 days following treatment, beginning the first day after treatment. Each observation session began with a 15 min acclimation period, during which the observer sat motionless in a blind erected in our animal facility. The observer quantified rates of self-preening and allopreening.

We defined self-preening as touching the plumage with the bill (Clayton and Cotgreave, 1994). We defined allopreening as touching the plumage of a partner with the bill (Kenny et al., 2017). Because allopreening can be reciprocated quickly by a bird’s mate, allopreening was quantified at the level of pairs rather than individuals, following Villa et al. (2016b). We made a total of 270 instantaneous observations per pair of birds prior to treatment, and 270 observations per pair following treatment. The number of self-preening events was added and divided by 2 to obtain the mean self-preening rate per pair.

Immediately after observations on the third day we “seeded” 12 randomly selected males with 75 lice each, which is 3-fold the number of lice typically found on rock pigeons in Utah (Moyer et al., 2002). Seed lice were collected from infested “donor” rock pigeons also captured in Salt Lake City. We anesthetized lice with CO₂ to remove them from the donor birds and then transferred the live lice to the male of each experimental pair of birds (Moyer et al., 2002). We seeded males both because most allopreening is done by females (G. B. Goodman, pers. obs.) and because females initiate allopreening more frequently than vice versa (Goodwin, 1956). We placed lice on the back of the bird’s neck, then inserted the bird into a paper bag for 20 min. This procedure calmed the bird and restricted its movements while the lice dispersed throughout the plumage. Twelve control males were handled similarly (e.g., placed in a paper bag) but not seeded with lice. Each infested pair was matched with a control pair, in the order in which they were entered into the study. All experimental birds were visually examined 3 days after infestation to ensure that experimental infestations were successful (Clayton and Drown, 2001).

We used a linear mixed-effects model (LMM) to test for a correlation between allopreening and self-preening. Percent time allopreening, percent time self-preening, treatment, and time were fixed effects, while pair identity (ID) was included as a random effect. The mixed model was fit in R using the LME library (Bates et al., 2015; R Core Team, 2016). Model selection was based on

Table I. Mean (\pm SE) percent time spent in each grooming behavior by each pair.

Behavior	Treatment	Before treatment	After treatment
Allopreening	Infested	7.62 \pm 1.00	7.01 \pm 1.31
	Control	5.31 \pm 1.54	5.03 \pm 1.44
Self-preening	Infested	8.97 \pm 1.33	9.88 \pm 1.07
	Control	7.67 \pm 1.00	9.12 \pm 1.01

AIC values. We used matched-pair *t*-tests to compare grooming behavior before and after treatment. We conducted this analysis in JMP® v.13.0. Power was calculated using G*Power 3.1 (Faul et al., 2007).

RESULTS

Experimental infestations were successful: all experimentally infested birds and their partners had lice 3 days following infestation. Grooming rates varied considerably among pairs (Table I). Pairs spent from 2.78% to 20.74% of their total time self-preening, and from 0.37% to 16.30% of total time allopreening. Interestingly, allopreening and self-preening were negatively correlated (Table II; Fig. 2; LMM, $n = 48$, $R^2_{\text{LMM(m,c)}} = 0.25$, 0.71 , $t = -3.790$, $P < 0.001$). However, allopreening did not differ significantly between infested and control birds over time (Fig. 3A; paired *t*-test, $t = 0.23$, $df = 11$, $P = 0.82$). Similarly, self-preening did not differ significantly between infested birds and control birds over time (Fig. 3B; paired *t*-test, $t = 0.35$, $df = 11$, $P = 0.73$). The power to detect a treatment effect of allopreening or self-preening was 0.96, with an effect size of $ES_d = 0.8$ (Cohen, 1988; Thomas, 1997). This effect size is consistent with other avian defenses against lice (Clayton and Vernon, 1993; Dumbacher, 1999; Bush et al., 2006).

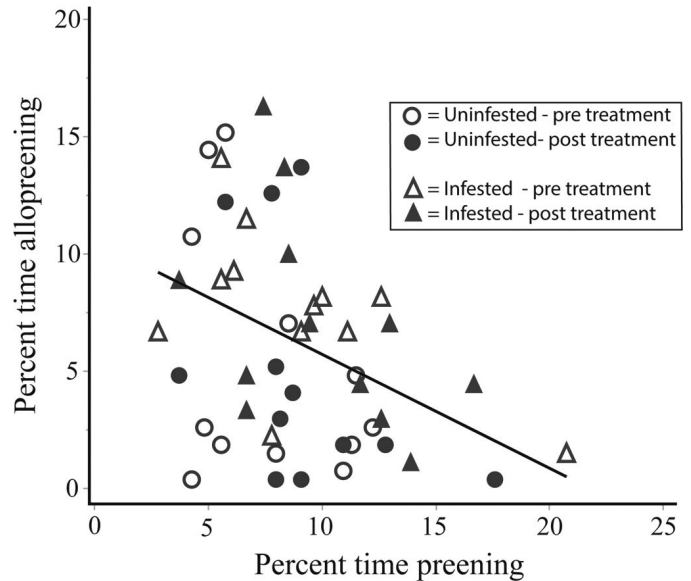
DISCUSSION

The principal goal of this study was to test whether allopreening is an inducible defense against avian ectoparasites. While self-preening is inducible (Villa et al., 2016a), the dynamics of allopreening have not been tested, to our knowledge. In our experiment, infested pairs did not alter their allopreening rates compared to control pairs. One explanation for this result is that pigeons may not be able to detect increases in lice on their partners. Although possible, this seems unlikely as self-preening is known to have a strong visual component (Bush et al., 2010).

Columbicola columbae congregate on different regions of the host depending on their life stage. Allopreening may target the

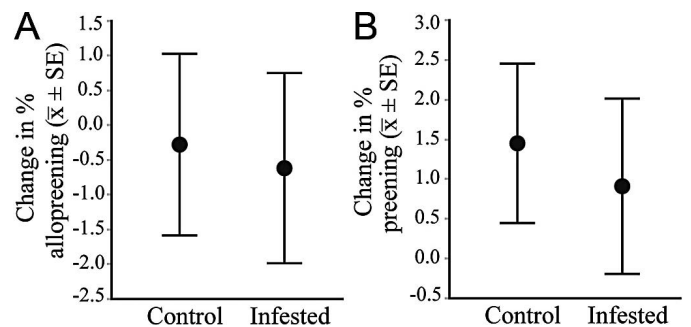
Table II. Linear mixed-effects model of allopreening rates with 48 observations of 24 pairs of birds.

Random effects	Variance	Std deviation		
Pair	10.25	3.20		
Fixed effects	Estimate	Std error	<i>t</i> -value	Pr(> <i>t</i>)
Intercept	10.6326	1.9333	5.500	<0.001
% Time preening	-0.6142	0.1649	-3.726	<0.001
Treatment	2.4397	1.7234	1.416	0.166
Pre-/Post-infestation	-0.6132	1.1419	-0.537	0.597

**Figure 2.** The percent of time each pair spent allopreening was negatively correlated with the amount of time that the pairs spent self-preening, regardless of whether or not the birds were infested with lice ($P < 0.001$; LMM).

developmental stages of lice that occur most frequently on the head and neck, as allopreening is concentrated in these regions (Harrison, 1965). *Columbicola columbae* adults are sometimes found on the head and neck but predominately occur on the abdomen, wings, and tail of their hosts (Nelson and Murray, 1971). In contrast, *C. columbae* nymphs tend to congregate on the head and neck. Unlike adult lice, nymphs lack a fully chitinized exoskeleton (Martin, 1934), making them softer and easier to damage. Our experiment used only adult lice and did not last long enough for nymphs to be produced. An experiment of greater duration might yield different results. It may also be worth repeating this study with a species of “head” lice, which spend all of their time on the head of the host (Bush et al., 2010; Johnson et al., 2012).

The birds in our study spent nearly twice as much time allopreening as the pigeons in Villa et al. (2016b). As a result, they may have reached the upper limit of how much time they can devote to allopreening. One explanation for why the birds in our

**Figure 3.** Change in percent time spent (A) allopreening and (B) self-preening following treatment. Birds experimentally infested with lice did not significantly alter rates of either behavior ($P = 0.82$ and $P = 0.73$, respectively; *t*-tests).

study allopreened more is that they were housed in pairs rather than groups of four, as in Villa et al. (2016b). The birds in their study had to spend time defending territories, building nests, and engaging in behaviors not shown by the birds in our study, which may have spent more time allopreening because they were in smaller cages and not engaged in other behaviors.

Allopreening was negatively correlated with self-preening. This negative correlation indicates that some birds allopreen more, while others self-preen more, regardless of experimental treatment. The negative correlation suggests that birds may adjust their frequency of self-preening in relation to allopreening, or vice versa, regardless of whether grooming is stimulus-driven or occurs at a programmed rate. That is, birds may engage in a given amount of preening over a given period of time but without discriminating between self-preening and allopreening. This result is consistent with a trend reported by de L. Brooke (1985), in which penguins without access to allopreening spent, on average, about 50% more time self-preening than birds with access to allopreening.

Self-preening rates in our study did not change over time, despite the fact that a previous study reported that pigeons adjust self-preening in response to experimental infestation (Villa et al., 2016a). In contrast, Clayton (1990) reported that the rate of preening by pigeons experimentally infested with lice was similar to that of fumigated pigeons without lice. The birds in our study were infested with *C. columbae*, while the birds in Villa et al. (2016a) were infested with both *C. columbae* and another species of feather louse, *Campanulotes compar*. It is possible that the second species of louse, or the combination of the 2 species, is what triggered increased self-preening rates in the Villa et al. (2016a) study. Note, however, that the infested birds in Clayton (1990) had both species of lice yet did not preen more than uninfested birds. Another possible explanation for the differences in results between studies is the duration of each study. The birds in the Villa et al. (2016a) study were observed over the course of 3 mo, while those in our study were infested for just 3 days. It is possible that infestations of longer duration are more likely to elicit a response from the host, possibly due to cumulative feather damage. In addition, the birds in the Villa et al. (2016a) study had nearly twice as many lice as the pairs of birds in our study. Thus, chronic infestations with many lice may be needed to trigger an increase in preening rates in response to feather lice.

In summary, we found that self-preening and allopreening were negatively correlated. This may be caused by a modulation of self-preening in response to allopreening. However, neither allopreening nor self-preening differed between infested and control groups. It is possible that allopreening does not, in fact, control ectoparasites. However, a definitive test of the effect of allopreening on ectoparasites is still needed. Ideally, an experiment manipulating the ability of the birds to allopreen or an experiment manipulating parasite infestation to a greater degree and for a longer duration should determine whether or not allopreening controls ectoparasites.

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