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DOES PREENING BEHAVIOR REDUCE THE PREVALENCE OF AVIAN FEATHER LICE (PHTHIRAPTERA: ISCHNOCERA)?

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ABSTRACT

Animals defend themselves against parasites in many ways. Defenses, such as physiological immune responses, are capable of clearing some infections. External parasites that do not feed on blood, however, are not controlled by the physiological immune system. Instead, ectoparasites like feather-feeding lice (Phthiraptera: Ischnocera) are primarily controlled by behavioral defenses such as preening. Here we test the hypothesis that birds able to preen are capable of clearing infestations of feather lice. We experimentally manipulated preening ability in a captive population of rock pigeons (*Columba livia*) that were infested with identical numbers of feather lice (*Columbicola columbae* or *Campanulotes compar* or both). We then monitored the feather louse infestations for 42 wk. Birds with impaired preening remained infested throughout the experiment; in contrast, the prevalence of lice on birds that could preen normally decreased by 50%. These data indicate that it is indeed possible for birds to clear themselves of feather lice, and perhaps other ectoparasites, by preening. We note, however, that captive birds spend more time preening than wild birds, and that they are less likely to be reinfested than wild birds. Thus, additional studies are necessary to determine under what circumstances wild birds can clear themselves of ectoparasites by preening.

Animals use a diverse array of behavioral defenses to avoid and remove parasites, a strategy often referred to as "behavioral immunity" (Hart, 2011; De Roode and Lefèvre, 2012). Grooming is an important behavioral defense that removes ectoparasites such as fleas, flies, lice, mites, and ticks (Murray, 1987; Mooring et al., 1996; Eckstein and Hart, 2000). Birds groom primarily by "preening," which is when a bird pulls one or more feathers between the mandibles of its beak or nibbles the feathers with the tips of the beak (Bush and Clayton, 2018). Preening is known to help control populations of fleas, flies, lice, and mites (Waite et al., 2012; Bush and Clayton, 2018).

Preening behavior is particularly important in the control of feather lice (Phthiraptera: Ischnocera), which are obligate, "permanent" ectoparasites that complete their entire life cycle on feathers, rarely even venturing even onto the host's skin (Clayton, 1991; Clayton et al., 2015). Feather lice are so closely tied to feathers that transmission typically requires direct contact between the feathers of different host individuals (Harbison et al., 2008). Feather lice feed on the soft, downy regions of feathers, the ingested fragments of which are metabolized with the aid of endosymbiotic bacteria (Fukatsu et al., 2007). Feather lice feed only on feathers, not blood, and they are thus "invisible" to the host's physiological immune system, which plays an important role in the control of other ectoparasites like ticks, fleas, and flies. Feather damage caused by lice increases thermal conductance from the host's body to the surroundings; this energetic stress can reduce host survival and mating success (Clayton, 1990; Booth et al., 1993). These negative effects on host fitness select for efficient preening and other anti-parasite defenses (Clayton et al., 2015).

Louse-infested birds that preen regularly are capable of substantially reducing the number of lice in their plumage (Clayton et al., 2015). Indeed, birds may be capable of removing all lice if they devote sufficient time to preening. Although lice are typically kept at chronic low levels by preening, the complete removal of lice would prevent a surge in the number of lice if the host were to become incapacitated by injury or pathogens in the future. Moreover, the removal of all lice would reduce exposure to pathogens that lice might vector (Clayton et al., 2008). If birds can remove all lice, then preening would reduce louse prevalence (percentage of hosts infested with lice), not just louse abundance (number of lice per host) (Bush et al., 1997). To our knowledge, the hypothesis that preening can reduce the prevalence of feather lice has not been tested. Here, we report the results of a simple experiment designed to test whether preening has the potential to reduce prevalence by eliminating entire infestations of lice from some host individuals. The experiment also tested the influence of preening on competition between lice; see Bush and Malenke (2008) for the competition results.

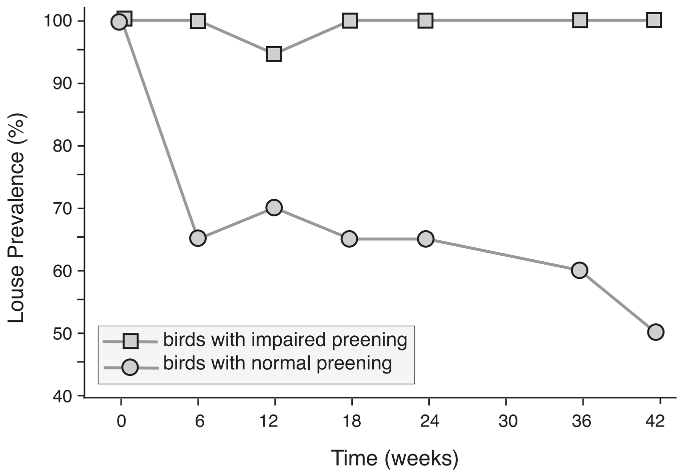

Figure 1. Prevalence of lice over 42 wk on birds with normal preening (circles) vs. impaired preening (squares). Birds were examined for lice every 6 wk, except at the 30-wk mark. The prevalence of lice on birds that preened normally was significantly lower than the prevalence of lice on birds with impaired preening (repeated-measures analysis of variance, effects of preening treatment, time, and preening treatment × time $P < 0.01$ in all cases, see Results for details).

MATERIALS AND METHODS

The experiment used feral rock pigeons (*Columba livia*) captured with walk-in traps in Salt Lake City, Utah. Forty-two pigeons were housed individually in 30 × 30 × 56 cm wire mesh cages in our animal facility. The cages were separated by plexiglass partitions to prevent the transmission of lice between the feathers of birds in adjacent cages. Birds were maintained on a 12-hr light/dark photoperiod and provided ad libitum grain, grit, and water. Before the experiment, freshly trapped birds were cleared of their "background" lice by housing them at <25% relative humidity for ≥10 wk. This method is effective in killing all ischnoceran lice and their eggs, which are glued to the feathers with a glandular cement (Harbison et al., 2008). After clearing the background lice, the ambient humidity of the animal room was raised to 60–70%, which is optimal for the survival and reproduction of feather lice on pigeons (Nelson and Murray, 1971). At the start of the experiment, each bird was infested with 100 feather lice (Bush and Malenke, 2008). The lice consisted of *Columbicola columbae* or *Campanulotes compar* (or both) (Price et al., 2003), which are the two most common species of feather lice found on rock pigeons in Utah (Moyer, 2002).

Before experimental infestation, the preening of half of the 42 pigeons was impaired with small, C-shaped plastic "bits" inserted between the upper and lower mandibles of the beak. Bits spring shut in the nares (nostrils) to prevent dislodging, without interfering with feeding or causing other apparent side effects (Clayton and Tompkins, 1995). Bits create a 1- to 3-mm gap between the mandibles that impairs the forceps-like action of the mandible tips required for the effective control of lice by preening (Clayton et al., 2005). Throughout the experiment, we monitored the number of lice on birds at 6-wk intervals for 42 wk, which is equivalent to about 10 generations of lice (feather lice breed continually on pigeons; Martin, 1934; Marshall, 1981; Moyer, 2002). To quantify lice on birds, we used the visual examination method (Clayton and Drown, 2001), which has proven to be accurate in other studies (Harbison et al., 2008, Koop and Clayton, 2013). The method provides reliable information on both the intensity and prevalence of lice on pigeons. Statistical analyses were conducted with JMP 16.0 (SAS Institute, Cary, North Carolina).

RESULTS

Two of the 42 birds died during the 10-mo-long experiment (one from each treatment), possibly because they were already senescent when captured. The complete experiment thus had a total of 40 birds, 20 with impaired preening (bits) and 20 with normal preening.

The experimental infestation method was successful: all 20 impaired birds (100%) had lice 6 wk after infestation (Fig. 1). By contrast, only 13 (65%) birds with normal preening still had lice at 6 wk, suggesting that preening quickly eliminated lice on 7 of the birds that could preen normally. By the end of the 42-wk experiment only 10 (50%) normal birds had lice, whereas all impaired birds still had lice (Fig. 1). The difference in the prevalence of feather lice on impaired vs. normal birds was significant and increased over time (repeated-measures analysis of variance, effects of preening treatment: $F_{1,38} = 17.57$; $P < 0.001$, time: $F_{6,33} = 3.54$; $P = 0.01$, and the interaction of preening treatment × time: $F_{6,33} = 3.11$; $P = 0.02$).

DISCUSSION

Our results indicate that preening does have the potential to eradicate louse infestations, thus reducing the prevalence of lice in host populations. Reducing prevalence may be particularly advantageous in helping birds avoid pathogenic endoparasites and microbes that are vectored by some lice (Clayton et al., 2008). We hasten to add, however, that the visual examination method is not 100% accurate. We observed 2 cases of apparent increases in the prevalence of lice over the course of the experiment. One case involved an increase in the number of infested (impaired) birds from 19 (95%) to 20 (100%) between weeks 12 and 18 (Fig. 1). The second case involved an apparent increase in the number of infested (normal) birds from 13 (65%) to 14 (70%) between weeks 6 and 12. Since horizontal transmission between birds was not possible (see Methods), these apparent increases were probably the result of overlooking 1 or more lice on a single (impaired) bird at week 12 and on a single (normal) bird at week 6.

Such errors aside, it is very unlikely that the 50% reduction in louse prevalence on normal birds over the course of the experiment was an artifact of imperfect visual examination. Six of the 10 louse-free birds showed no evidence of lice between 18 and 42 wk, a period of nearly 6 mo. One way to guarantee the complete absence of lice on a bird would be to euthanize it and carefully examine every feather on the bird. An interesting alternative would be to impair preening in birds thought to be free of lice by fitting them with bits. If such birds were, in fact, still infested with at least 1 gravid female louse, or viable eggs, the louse population should rebound, making the lice more apparent at subsequent visual examinations.

Our experiment with captive birds probably overrepresents the potential of preening to eradicate lice in wild populations, for at least 2 reasons. First, captive birds spend about twice as much time preening as their wild counterparts (Walther and Clayton, 2005), meaning that preening may be less effective in natural populations. Second, the fact that birds in our experiment were isolated from other birds eliminated the possibility of horizontal transmission between birds, which is relatively common in free-ranging populations of rock pigeons and other species (Harbison et al., 2008). The captive conditions of birds in our study also eliminated the possibility of phoretic dispersal of wing lice on hippoboscid flies, which occurs in many wild populations of feral pigeons and other species (Clayton et al., 2015).

In conclusion, the potential for preening to eradicate lice is perhaps most relevant in the case of relatively solitary birds with reduced opportunities for horizontal transmission. Preening-mediated eradication may be most likely in small-bodied species, such as songbirds, that have relatively small louse populations to begin with (Clayton et al., 2015).

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