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Original Article

Does antiparasite behavior improve with experience? An experimental test of the priming hypothesis

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Behavior is usually the first line of defense against parasites. Antiparasite behaviors, such as grooming, or outright avoidance, have been shown to reduce the risk of parasitism in a wide variety of host–parasite systems. However, despite the central importance of antiparasite behavior, little is known about the extent to which prior exposure to parasites improves effectiveness. Here, we report the results of a 2-year study designed to test whether exposure to parasites can "prime" behavior, loosely analogous to priming of the immune system. We tested whether preening improves with experience by infesting captive-bred rock pigeons (*Columba livia*) with 2 common species of rock pigeon feather lice. We infested "primed" birds in Years 1 and 2 of the study and "nonprimed" birds only in Year 2. Birds with lice preened about a third more, on average, than birds without lice. Birds subsequently cleared of lice resumed preening at the same rate as birds that never had lice. Thus, our results confirm that preening is an inducible, reversible defense that is partly triggered by the presence of lice. Surprisingly, primed birds did not differ significantly from nonprimed birds in the overall rate or the efficacy of preening. Primed and nonprimed birds preened at similar rates and had similar numbers of lice at the end of the study. Our results therefore provide little evidence that antiparasite behavior improves with experience, at least in the case of preening as a defense against feather lice.

Key words: **ectoparasite, feather lice, Phthiraptera, pigeon, preening, Columba livia.**

INTRODUCTION

Pathogens and other parasites have negative effects on the fitness of their hosts (Poulin 2007). In response, hosts evolve a variety of defenses, some of which improve with experience. For example, initial exposure often primes the immune system, allowing it to rapidly recognize and fight subsequent infections (Klein 1982; Siva-Jothy et al. 2005; Iwasaki and Medzhitov 2015). However, the first line of defense against parasites is usually behavioral, not immunological (Hart 1990; Daly and Johnson 2011). Indeed, the immune system has been described as an "emergency service" that gets deployed when parasites circumvent antiparasite behavior (Rigby et al. 2002; Hughes and Cremer 2007). Like many immune responses, antiparasite behavior might improve with experience, that is, it may become more effective after the host has been exposed to parasites at some point in the past. To our knowledge, however, this "priming" hypothesis has not been tested.

The efficacy of antiparasite behavior has been demonstrated for a wide variety of host–parasite systems (Hart 1990). For example, Daly and Johnson (2011) showed that freshwater tadpoles respond to the presence of host-seeking trematode cercariae with bursts of activity that involve fast swimming, twisting, and aggressive turning. These behaviors, which differ markedly from the behavior of unexposed tadpoles, successfully dislodge parasites before they have a chance to penetrate the host (Taylor et al. 2004). While examples such as this one confirm that behavioral defenses can be effective, we are not aware of studies that have tested whether antiparasite behavior improves with experience.

In contrast, many studies have shown that antipredator behavior does improve with experience (Lima and Dill 1990; Tollrian and Harvell 1999; Griffin 2004). Studies have shown that prior exposure to chemical stimuli or visual alarm signals associated with predator species helps prey species better recognize and avoid predators (Kelley and Magurran 2003). For example, Mirza and Chivers (2000) conditioned a group of predator-naive brook trout (*Salvelinus fontinalis*) by exposing them to chemical stimuli from predatory chain pickerel (*Esox niger*), as well as alarm signals released by damaged trout. Another group of brook trout was not conditioned with alarm signals. Upon subsequent exposure to live chain pickerel, the conditioned brook trout showed an increase in antipredator behavior (decreased movement and altered foraging patterns), compared to trout that were not conditioned. The effect of

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conditioning led to a significant increase in survival of individuals both in the lab and the field. Thus, prior experience allowed brook trout to better recognize and avoid predators.

Like antipredator behavior, antiparasite behavior might improve with experience. In this paper, we report the results of a 2-year study designed to test whether antiparasite behavior is "primed" by exposing hosts to parasites. To test this priming hypothesis, we infested captive-bred rock pigeons (*Columba livia*) with feather lice (Phthiraptera: Ischnocera). We used the 2 most common species of pigeon lice, "wing" lice (*Columbicola columbae*) and "body" lice (*Campanulotes compar*). Both species are permanent, feather-feeding ectoparasites that complete all stages of their life cycle on the body of the host (Marshall 1981). The feather damage they cause leads to reductions in the survival and mating success of pigeons (Clayton et al. 2016).

Neither species of louse feeds on blood or living tissue (Marshall 1981). Therefore, they are essentially "invisible" to the immune system and are controlled primarily, if not exclusively, by antiparasite behavior. Preening is the main behavior used by pigeons to control lice, which are crushed and/or removed with the upper mandibular overhang of the beak (Clayton et al. 2005). The behavioral "priming" hypothesis was tested by comparing the rate and efficacy of preening in pigeons infested with lice at different time intervals. We infested "primed" birds with lice in the first and second years of the study; "nonprimed" birds were infested only in the second year of the study. Rates of preening were compared for both groups of birds. The efficacy of preening was also compared by measuring the number of lice on primed and nonprimed birds at the end of the study.

METHODS

Birds used in this experiment were the captive-bred offspring of wild-caught feral rock pigeons trapped in Salt Lake City, UT. Prior to breeding, the parent birds were cleared of lice by keeping them in low-humidity animal rooms (<25% relative humidity) for several months to desiccate their lice and louse eggs (Harbison et al. 2008). Feather lice are transmitted during periods of direct contact between individual hosts, like that between parent birds and their offspring in the nest (Clayton and Tompkins 1994). Because the parent birds in our study had no lice, and their offspring were isolated from any other birds, the offspring were completely free of lice (or other ectoparasites) prior to experimental infestation (see below). This, in turn, eliminated the possibility of experience with lice or other ectoparasites prior to initiation of the experiment.

Twenty birds consisting of 9 pairs of siblings and 1 pair of unrelated birds of similar age were used in the experiment. The members of each pair were randomly assigned to the primed and nonprimed groups to help control for heritable variation in behavior or other characteristics. There were no significant differences between the 2 groups in age, body mass, or length of the bill overhang (Table 1). Length of the bill overhang is closely correlated with the louse-control function of preening (Clayton et al. 2005). During the experiment, birds were housed individually in 30 × 30 × 56 cm wire mesh cages on a 12-h light/dark cycle. They were provided ad libitum grain, grit, and water. To prevent social facilitation of preening, each cage was visually isolated from all other cages using opaque partitions between cages.

Host behavior

Preening was defined as touching of the plumage with the bill (Clayton and Cotgreave 1994). Every 8–10 days, one of us (H.E.C.), who was blind to experimental treatment, collected preening data during each of 3 observation sessions in one of the following time windows: 7:30–10:00, 10:00–12:30, or 12:30–15:00. Each session began with a 15-min acclimation period during which the observer sat motionless within full view of all birds. After this acclimation period, data collection involved instantaneous scan samples (Altmann 1974; Clayton 1990); birds were observed sequentially at 15-s intervals. Each bird was observed 25 times over the course of a session, with each session lasting about 125 min. We divided the number of preening observations by the total number of observations to calculate the proportion of time birds spent preening.

Experimental infestations

Prior to the start of the experiment, birds were carefully examined to confirm that they were free of lice or other ectoparasites (Clayton and Drown 2001). We then infested birds with lice at different intervals (see below). The source of lice was "donor" rock pigeons that were livetrapped in Salt Lake City, UT. The lice were anesthetized with CO_2 to remove them from donor birds and transferred to recipient birds according to the schedule described below (Moyer et al. 2002).

Bout 1 (February–April 2012)

One member of each of the 10 matched pairs of pigeons was randomly chosen and infested (primed) with 100 adult wing lice and 100 adult body lice. The other (nonprimed) member of each pair was handled similarly to the primed birds, but not infested with lice. Following a 3-day acclimation period, we began quantifying the preening rates of all 20 birds as described above.

Immediately following Bout 1, which lasted 3 months, all birds were placed in a low-humidity animal room to kill their lice and louse eggs by desiccation (Harbison et al. 2008). Birds remained in the low-humidity rooms for a period of 8 months, during which time they also molted all of their feathers, thus replacing feathers that had been damaged by lice in Bout 1. Rock pigeons normally molt from May to December (Lowther and Johnston 2014). Once molt was complete, we searched the feathers of each bird thoroughly to ensure that they were free of lice. In January 2013, immediately prior to Bout 2, we quantified the preening rates of all 20 louse-free birds over a period of 30 days.

Bout 2 (February–April 2013)

In Bout 2, which began 1 year after the start of Bout 1, all 20 birds were infested with 100 adult wing lice and 100 adult body lice. After a 3-day acclimation period, the preening behavior of the birds was quantified, as in Bout 1. At the end of Bout 2, all birds were euthanized and louse abundance was determined using the washing method (Clayton and Drown 2001). This method recovers ($\bar{x}$ ± standard error [SE]) 82.1 (±1.1)% of wing lice and 76.3 (±12.4)% of body lice. The raw number of wing and body lice recovered by washing were entered into regression equations that predict the total number of lice on each bird (r^2 = 0.99 for wing and for body lice, see Clayton and Drown 2001; Bush et al. 2006). In short, this approach is extremely accurate, accounting for 99% of variation in total lice on a bird.

Data analysis

Repeated-measures analyses of variance with post hoc paired *t*-tests were used to compare the rate of preening for primed versus nonprimed birds over the course of the experiment. A paired *t*-test was used to compare the (ln transformed) abundance of lice

on primed versus nonprimed birds as a measure of the relative efficacy of preening. Statistical analyses were conducted in JMP® v.11.0.

RESULTS

In Bout 1, birds that were experimentally infested with lice preened significantly more than birds without lice (Figure 1; Table 2). Birds with lice preened an average (±SE) of 19.5% (±9.47) of the time, while birds without lice preened an average of 14.1% (±7.39) of the time. Both groups of birds increased their preening rates over the course of Bout 1; however, the magnitude of this increase did not depend on treatment (the interaction between treatment and time was not quite significant; Table 2).

When we quantified the behavior of birds in January 2013 (immediately prior to Bout 2), we found no significant difference in the rates of preening by birds cleared of lice (de-infested) versus birds that had never been infested with lice (Figure 1; Table 2). Indeed, rates of preening by the 2 groups were virtually identical. Birds de-infested after Bout 1 preened an average (±SE) of 15.4% (±9.1), while birds that were never infested preened an average of 15.4% (±6.1) of the time.

Over the first 10 days of Bout 2, primed birds preened significantly more than nonprimed birds (Figure 1; mean (±SE): 27.73% (±9.63) vs. 21.47% (±9.29); post hoc paired *t*-test; degrees of freedom [df] = 9; $t = -3.07$; $P = 0.013$). However, at no time during the rest of Bout 2 did the primed and nonprimed birds preen at significantly different rates. Overall, there was no significant difference in the rate of preening by primed versus nonprimed birds in Bout 2 (Table 2). Primed birds preened an average of 22.3% (±9.6) and nonprimed birds an average of 19.7% (±9.9) over the course of Bout 2.

Both primed and nonprimed birds decreased their rate of preening over much of the latter half of Bout 2 (Figure 1). There was a significant effect of time, and a significant interaction between time and treatment (Table 2), with primed birds decreasing their rate of preening more than nonprimed birds.

The efficacy of preening did not differ significantly between primed and nonprimed birds; there was no significant difference in the number of lice on the 2 groups of birds at the end of the experiment (Figure 2; paired *t*-test; df = 9; $t = -0.055$; $P = 0.59$; power = 0.84, $d_z = 0.70$; Cohen 1988). Primed birds had a mean (±SE) of 129 (±117) lice, while nonprimed birds had a mean of 127 (±51) lice.

Table 1

Comparative age, size, and bill morphology of primed versus nonprimed pigeons

Measurement	Primed	Nonprimed	*P* value
n	10	10	
Age (days) (mean ± SE)	475.40 ± 94.23	459.00 ± 79.70	1.00
Mass (g) (mean ± SE)	327.00 ± 38.68	329.00 ± 30.12	0.92
Bill overhang length (mm) (mean ± SE)	1.34 ± 0.78	1.24 ± 0.38	0.69

Nine pairs of birds were siblings; the remaining pair consisted of unrelated birds of similar age. One randomly chosen member of each pair was primed (experimentally infested with lice during Bout 1); the other member of the pair was not primed. None of the measurements differed significantly between primed and nonprimed birds (Wilcoxon signed-rank test for all comparisons).

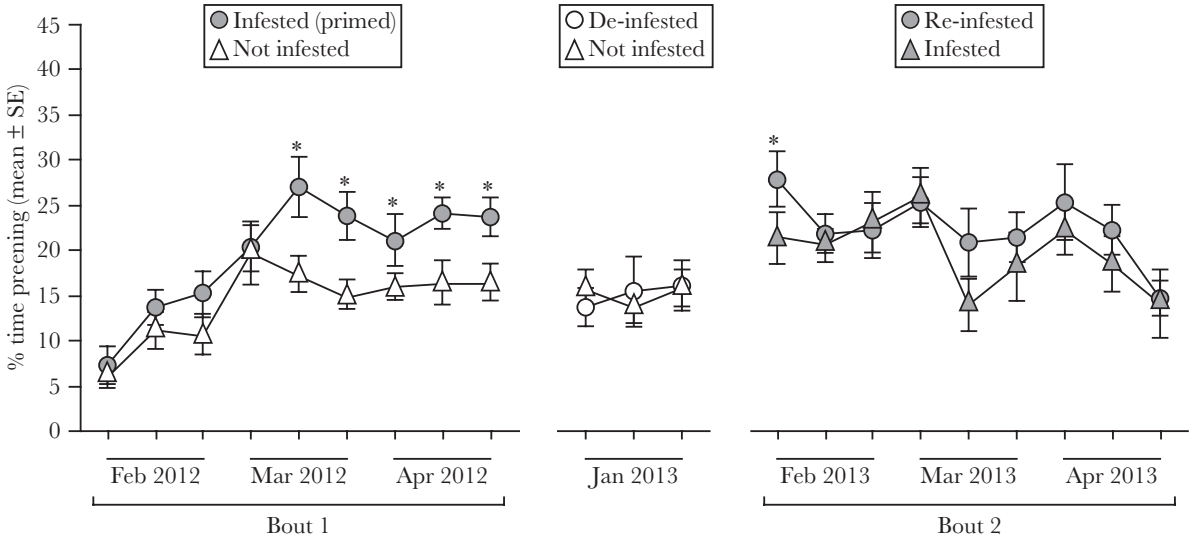

Figure 1

Test of the effect of prior exposure ("priming") on preening rates of pigeons. Ten matched pairs of birds were observed over the course of the 2-year experiment. At the start of Bout 1, one member of each pair was experimentally infested with lice; the other member was handled but not infested. Following Bout 1, all birds were cleared of lice ("de-infested"; see Methods). At the start of Bout 2, both members of each pair were experimentally infested with lice. Preening rates were measured 3 times every 8–10 days throughout the study. Birds with lice preened significantly more than birds without lice. Birds cleared of lice resumed preening at the same rate as birds without lice. At the very start of Bout 2, primed birds preened significantly more than nonprimed birds. However, this difference soon disappeared and there was no overall effect of priming on rates of preening. Open symbols (circles and triangles) are birds without lice; filled symbols are birds with lice. *$P < 0.05$, repeated-measures analyses of variance with post hoc paired *t*-tests.

Table 2

Repeated-measures ANOVAs testing the effects of treatment and time on the preening rates of pigeons

	df	*F* ratio	*P* value
Bout 1			
Treatment	1, 18	4.6940	0.0439
Time	8, 11	56.4978	<0.0001
Interaction	8, 11	2.5683	0.0746
January 2013			
Treatment	1, 18	0.0003	0.9854
Time	2, 17	1.7214	0.2086
Interaction	2, 17	1.2135	0.3216
Bout 2			
Treatment	1, 18	0.7357	0.4023
Time	8, 11	92.8045	<0.0001
Interaction	8, 11	15.3826	<0.0001

In Bout 1, the treatments were infested (primed) versus not infested; in Bout 2, the treatments were re-infested versus infested. In the interim (January 2013), the treatments were de-infested versus not infested; see Figure 1. ANOVA, analysis of variance; df, degrees of freedom.

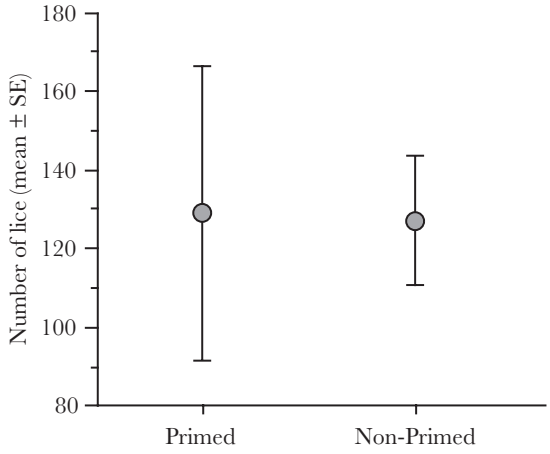

Figure 2

Test of the effect of prior exposure ("priming") on the efficacy of preening. Efficacy was measured by comparing the number of lice on primed (n = 10) and nonprimed (n = 10) birds at the end of the study. There was no significant difference in the number of lice on the 2 groups (paired t-test; df = 9; t = –0.055; P = 0.59).

DISCUSSION

The goal of this study was to test whether antiparasite behavior improves with experience; that is, is behavior "primed" by exposure to parasites? Behavioral priming is loosely analogous to immunological priming, in which prior exposure to parasites increases the speed and effectiveness of the adaptive immune response (Klein 1982; Owen et al. 2010; Iwasaki and Medzhitov 2015). Earlier studies show that antipredator behavior can also be primed (Lima and Dill 1990; Tollrian and Harvell 1999; Griffin 2004). Exposure to predators improves the antipredator response of some prey species, leading to increased survival. We tested the hypothesis that antiparasite behavior can also be primed; we compared the rate and efficacy of preening by birds exposed to lice at different times.

Our results showed that primed birds initially preened more than nonprimed birds; however, this difference did not persist and, overall, there was no significant difference in preening rates between primed and nonprimed birds. It is possible that the initial increase in preening by primed birds allowed them to quickly reduce their lice, compared to nonprimed birds. However, this is unlikely because lice tend to be reduced more gradually by preening (Clayton et al. 2005). Unlike Clayton et al. (2005), we did not attempt to quantify lice by visual examination repeatedly over the course of the study. Visual censusing, which requires the deflection of feathers, could have influenced the preening behavior of birds trying to straighten their feathers.

The results of our study were somewhat unexpected. The fact that pigeons did not alter preening with experience suggests that they may already be proficient at removing lice at first infestation. Alternatively, it may be that preening can be primed, but only in the presence of more acute ectoparasites. For example, pigeons are often also infested with blood-feeding hippoboscid flies (*Pseudolynchia canariensis*) (Harbison et al. 2008). In addition to biting the skin, these flies cause anemia (Jones 1985), emaciation (Lloyd 2002), and slow nestling development (Bishopp 1929). Hippoboscid flies also transmit blood parasites that can have negative effects on birds, such as malaria (Sol et al. 2003), trypanosomes (Baker 1967), and possibly West Nile virus (Farajollahi et al. 2005). In short, hippoboscids probably represent a greater immediate threat to host fitness than feather lice. It would be interesting to repeat our test of the priming hypothesis using pigeons infested with flies in addition to, or instead of, lice.

Although pigeons do not appear to improve their ability to control feather lice with experience, our results confirm that pigeons do respond to feather lice with increased preening. In Bout 1, experimentally infested birds increased their rate of preening by approximately 38%, compared to birds with no lice (Figure 1). Our results contrast with those of Clayton (1990), who reported no difference in the preening rates of male pigeons with and without lice. In Clayton's study, "stimulus" pairs of tethered male pigeons competed for females from the opposite sides of single mate choice arenas. The study showed a strong correlation between the preening rates of the 2 males in each arena, suggesting social facilitation of preening. It is possible, therefore, that the effects of indirect male–male completion overwhelmed any differences in the preening rates of males with and without lice. In the current study, birds were visually isolated from one another, reducing the likelihood of such effects.

Although there was an overall difference in the preening rates of infested and non-infested birds in Bout 1, the 2 groups did not differ in the rate of preening until about halfway through Bout 1. During the first few weeks of Bout 1, the rate of preening tripled (from about 6% to 20%; Figure 1). We speculate that an observer effect may account for the initial low rates of preening by the 2 groups of birds. Preening data were collected by one of us (H.E.C.) sitting in plain view of all birds. It may have been the case that during the first few week of Bout 1, the birds were not yet completely accustomed to the presence of the observer. This explanation could account for the lack of any apparent observer effect during the latter half of Bout 1, January 2013, or Bout 2.

Our results show that preening to control lice is both inducible and reversible. In Bout 1, birds with lice increased their preening more than birds without lice. Once lice were removed by "de-infestation," however, even previously infested birds reduced their rate of preening (Figure 1). At the end of Bout 1, the birds that were initially infested (primed) were cleared of lice by placing them in a dry room for 8 months. After the primed birds were louse-free, they reduced the time they spent preening from 20% to about 15%. The rate of preening when birds are free of lice is presumably the amount required for basic cleaning and straightening of the plumage (Figure 1; Johnston and Janiga 1995). The changes

we observed in preening with the addition and subsequent removal of lice are consistent with a "stimulus-driven grooming" model of antiparasite defense (Riek 1962; Willadsen 1980; Wikel 1984).

Stimulus-driven grooming contrasts with the "programmed grooming" model, in which grooming is upregulated by intrinsic mechanisms that are independent of parasite load (Mooring and Samuel 1998; Hawlena et al. 2008). For example, an experimental study comparing the grooming rates of impala (*Aepyceros melampus*) showed that differences in grooming rates among adults and juveniles are more a product of body size rather than tick abundance (Mooring and Hart 1997). Therefore, grooming rates in impala are governed by a programmed timing mechanism, which evokes grooming as a preventative parasite defense that is dependent on body size, and not on cutaneous stimulation. While programmed grooming also combats ectoparasites, it is a costly strategy when parasites are not abundant from reasons other than grooming (Hart 1990; Heeb et al. 1998; Mooring and Samuel 1998). The reversibility of preening may allow birds to spend more time in other important behaviors, such as feeding, mating, and antipredator vigilance (Redpath 1988).

In summary, our results show that antiparasite behavior does not necessarily improve with experience. Our study highlights the complex dynamics of host behavioral defenses and argues for the importance of a better understanding of the behavioral processes that shape host–parasite interactions.

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