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INFLUENCE OF GROOMING ON PERMANENT ARTHROPOD ASSOCIATES OF BIRDS: CATTLE EGRETS, LICE, AND MITES

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Pectinate claw
Behavior

ABSTRACT

Birds have a diverse community of "permanent" arthropods that complete their entire life cycle on the body of the host. Because some of these arthropods are parasites that reduce host fitness, birds control them by grooming, which consists of preening with the beak and scratching with the feet. Although preening is the primary component of grooming, scratching is essential for controlling arthropods on the head and neck, which cannot be preened. Several unrelated groups of birds have evolved comb-like pectinate claws on the middle toenail of each foot. We tested the role of these claws in the control of arthropods by experimentally removing teeth from the claws of captive western cattle egrets (*Bubulcus ibis*) infested with chewing lice (Insecta: Phthiraptera), feather mites (Acari: Sarcoptiformes), and nasal mites (Acari: Mesostigmata). After a period of 4 mo, we compared the abundance of arthropods on experimental birds to that of control birds with intact teeth. We used video to quantify the grooming rates of the captive birds, which groomed twice as much as wild birds. Experimental and control birds did not differ significantly in grooming time. Both groups virtually eradicated the chewing lice, but not feather mites or nasal mites. We found no support for the hypothesis that pectinate claws increase the efficiency of arthropod control by grooming. Experiments with wild birds are needed to test the hypothesis further under conditions in which birds devote less time to grooming.

Birds are host to a diverse community of "permanent" arthropod associates that complete all stages of their life cycle on the body of the host. This community includes chewing lice and different groups of mites, some of which are known to reduce host fitness (Clayton et al., 2010; Proctor and Owens, 2010). In response, birds have evolved defenses for combating ectoparasites that range from antiparasite behavior (Hart, 1992, 1997) to immune defenses (Owen et al., 2010). A first line of defense against ectoparasites is grooming, which includes preening with the beak and scratching with the feet (Fig. 1; Clayton et al., 2010).

Preening plays a critical role in defense against chewing lice (Brown, 1972). One component of beak morphology, the upper mandibular overhang, enhances the effectiveness of preening in combating lice (Clayton et al., 2005). Birds with intermediate overhangs have significantly fewer lice than birds with long or short overhangs, consistent with stabilizing selection on overhang length (Clayton et al., 2010). Preening may also affect the abundance of feather mites; wild birds with deformed beaks have unusually large feather mite populations (Barlow, 1967; Clayton, 1991; Handel et al., 2010). Birds with intermediate overhangs also have significantly fewer feather mites than birds with long or short overhangs (Villa et al., 2018).

Scratching with the feet also plays a role in combating chewing lice on birds (Clayton et al., 2010). Scratching works synergistically with preening by flushing lice from the head and neck onto the rest of the body, where they can be reached by preening (Goodman et al., 2020). Components of foot morphology, such as the comb-like pectinate claws of some birds (Fig. 2a), may enhance the effectiveness of scratching in controlling feather lice and other ectoparasites (Clayton et al., 2010; Bush and Clayton, 2018). A study of barn owls (*Tyto alba*) found mixed support for the role of pectinate claws in combating ectoparasites. Individual owls with lice had fewer teeth on their claws than owls without lice, suggesting that claws with more teeth may be more effective in preventing infestation by lice (Bush et al., 2012). Within infested birds, however, the number of lice was not related to the number of teeth on the claw.

Audubon (1835, p. 499) implied that the pectinate claw of a magnificent frigatebird (*Fregata magnificens*) functions in parasite control: "I had been for years anxious to know what might be the use of the pectinated claws of birds; and on examining both its feet with a glass, I found the racks crammed with insects, such as occur on the bird's head, and especially around the ears." Although Audubon's observation is provocative, an experimental test of the parasite-control hypothesis has not been conducted with frigatebirds, nor any other species of bird with pectinate claws.

Western cattle egrets (*Bubulcus ibis*) are a member of the heron family (Ardeidae), a clade of birds that often have pectinate claws

Figure 1. Cattle egrets (**a**) preening with the beak, and (**b**) scratching with the pectinate middle claw. Photos by Carolyn Wright and Will Wilson. Color version available online.

(Clayton et al., 2010). Like other members of the family, cattle egrets scratch with pectinate claws located on the middle toe of each foot (Fig. 1b). Our study used western cattle egrets sourced from Hilo, Hawaii, where they were introduced in 1959 as biocontrol agents to help control pests of cattle. Subsequently, the egret population in Hawaii has increased dramatically and poses such a threat to aircraft that they are routinely culled by government officials (Breese, 1959; Fellows et al., 1983; Fellows and Paton, 1988).

Cattle egrets at our study site (Lokowaka Pond, Hilo, Hawaii) have 3 groups of permanent arthropod associates: chewing lice (Insecta: Phthiraptera), feather mites (Acari: Sarcoptiformes) and nasal mites (Acari: Mesostigmata). Chewing lice are parasites that feed on feathers, dead skin, and, in some cases, blood; they can decrease the survival and reproductive success of birds, but their effects on the fitness of cattle egrets have not been studied, to our knowledge (Clayton et al., 2015). Feather mites are most often considered commensals, or even mutualists, that do not reduce host fitness (Blanco et al., 2001; Proctor, 2003; Proctor and Owens, 2010; Galván et al., 2012; Doña et al., 2018). Regardless of their effect on the host, feather mites are also affected by preening, perhaps because of collateral damage from louse-mediated preening (Villa et al., 2018). Nasal mites live in nasal passages, where they feed on vascularized epithelial tissue. Although they can cause trauma to the nasal epithelium (De-Rojas et al., 2002), they do not usually cause significant pathology (Knee et al., 2008).

Here we report the results of the first experimental test of the hypothesis that pectinate claws help birds control populations of ectoparasites and other arthropods. More generally, we measured the effectiveness of overall grooming for the control of lice and mites on cattle egrets.

MATERIALS AND METHODS

In June 2022, 43 cattle egrets were captured with mist nets at Lokowaka Pond in Hilo, Hawaii, and transported to our lab in Utah. To document the community of arthropod associates on cattle egrets at this location, a subsample of 14 "Time 0" birds were euthanized soon after capture. The Time 0 birds were subjected to the washing method (Clayton and Drown, 2001), which recovered nasal mites, feather mites, and 2 species of chewing lice. All arthropods were identified and counted using a grid under a dissecting microscope (Clayton and Drown, 2001). Lice were identified by S.E.B.,

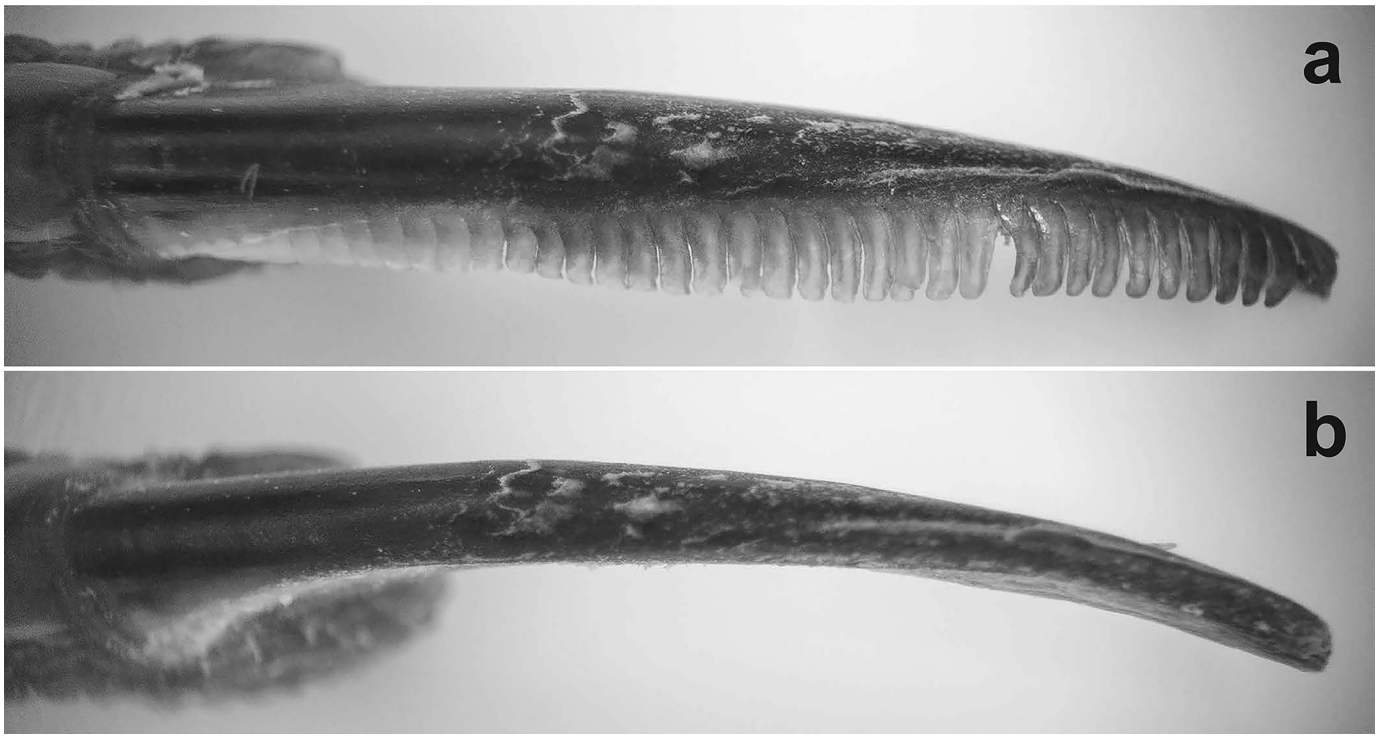

Figure 2. Cattle egret pectinate claw with (**a**) teeth, and (**b**) teeth experimentally removed.

and mites by Heather Proctor, University of Alberta, Canada (Fig. 3). Voucher specimens of all species have been deposited in the Price Institute of Parasite Research, University of Utah (PIPR000993–PIPR000996).

The remaining 29 captive birds were isolated in 29 identical aviaries (1.8 × 1.5 × 1 m). The aviaries were separated by opaque plastic sheets to prevent contact between the feather tips of adjacent birds, which could allow parasites to transmit between birds. The egrets were provided ad libitum water, moistened cat cereal, and a mixture of canned dog food, cooked chicken, and a commercial bird of prey diet. Initially, the birds were kept on a 14-hr light, 10-hr dark photoperiod. After 11 wk this was changed to a 12–12 photoperiod to simulate shortening autumn daylength. Animal houses containing the aviaries were maintained at an average temperature of 21 C and relative humidity of 85%. Birds were weighed approximately once per month with a Pesola® scale (Pesola, Schindellegi, Switzerland).

After about a month in captivity, the egrets were randomly assigned to treatments in blocks of 2. The first bird of each block was randomly assigned to an experimental or control treatment, with the second bird assigned to the opposite treatment, for a total of 15 experimental and 14 control birds. Birds in the experimental treatment had the teeth on the claw of each middle toe harmlessly removed with a Dremel® tool (Dremel, Racine, Wisconsin) (Fig. 2b). Birds in the control group were sham-Dremeled with a buffing wheel that exposed the bird to the stress of handling, but without removing any tissue. The Dremeling procedure was repeated every 3 wk throughout the experiment to prevent regrowth of the teeth.

The experiment lasted 126 days— about the same duration as other recent manipulations of scratching behavior in birds (Goodman et al., 2020). Two birds (1 control and 1 experimental) were removed during the experiment because they injured themselves and had to be euthanized. A third (control) bird was excluded from the analyses because of a problem with its feet (see Discussion). The final sample size for analysis was 14 experimental and 12 control birds.

Between 6 and 9 wk after the start of the experiment, the grooming behavior of each bird was monitored for 6 hr (1500 hr–2100 hr) using 1 of several Koonlung HD609 video cameras (Koonlung, Shenzhen, China). Videos were used to estimate the relative frequency of 7 behaviors at 5-min intervals: preening, scratching, feeding, bill wiping, rousing, motionless but alert/awake, and sleeping (head under wing). These data allowed us to calculate the proportion of time spent preening and scratching by each bird. One (control) bird had to be excluded because of camera failure. Hence, the sample for analysis of behavioral data was 14 experimental and 11 control birds.

At the end of the experiment, all birds were euthanized and frozen. Body washing (Clayton and Drown, 2001) was used to quantify the abundance of arthropods on each bird. It was not possible to estimate louse abundance throughout the experiment with a visual examination, as in some other studies (Tompkins et al., 1996; Clayton and Drown, 2001; Hoi et al., 2012), because *Ardeicola expallidus*, which are snow white lice, were all but invisible against the white plumage of cattle egrets.

Data analyses were performed in R version 4.2.2 (R Core Team, 2022). To test whether the pectinate claw affected the abundance of lice and feather mites, experimental and control birds were compared using generalized linear models (GLMs) with a fixed effect for treatment. A negative binomial link was implemented using the *MASS* package to account for overdispersion of arthropod abundance (Shaw and Dobson, 1995; Venables and Ripley, 2002). Grooming time was included as a fixed effect to account for variations in the amount of time birds spent grooming. Uropygial gland size was also included as a

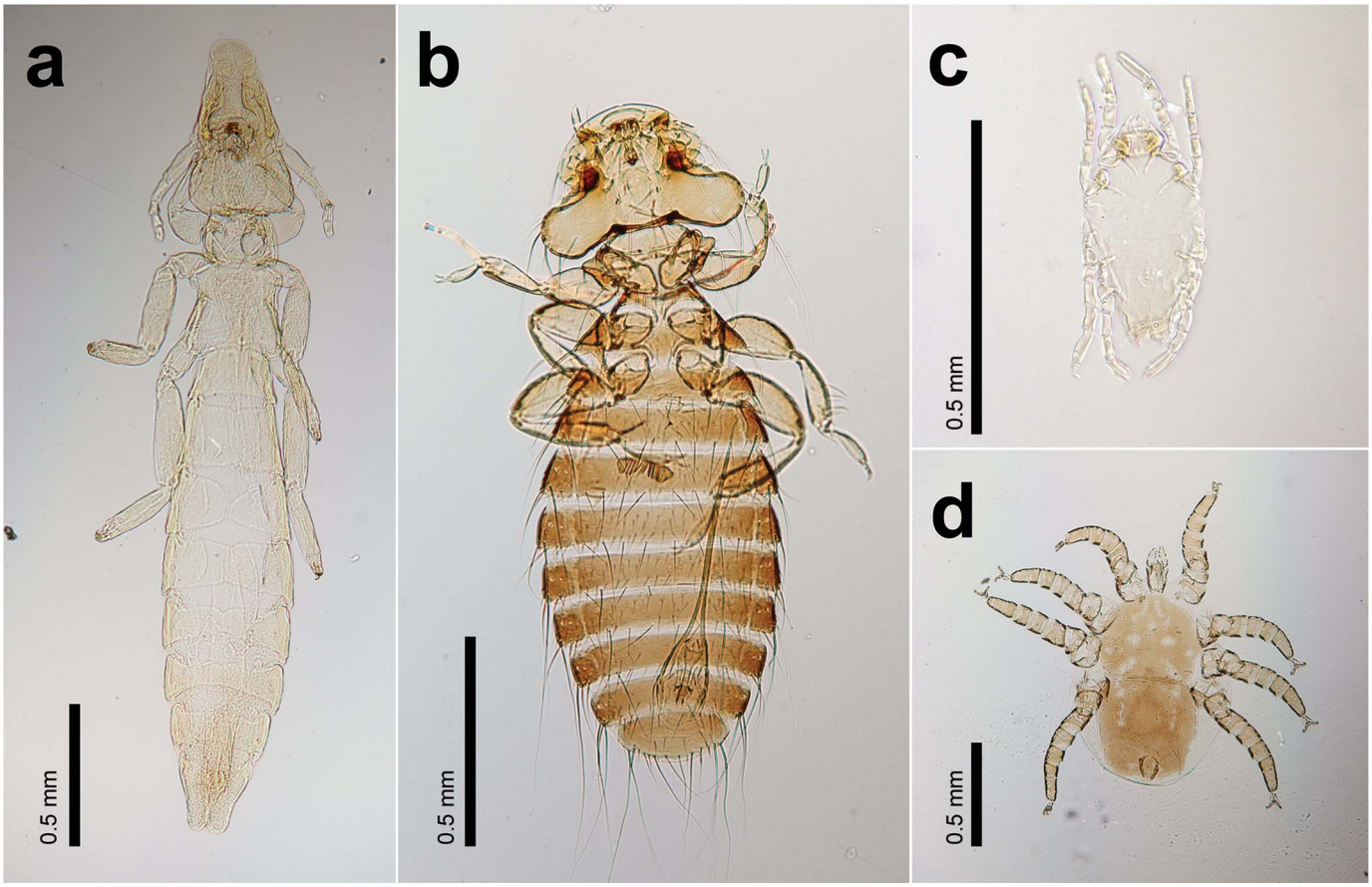

Figure 3. Arthropods found on cattle egrets captured at Lokowaka Pond, Hilo Hawaii. (**a**) Chewing louse *Ardeicola expallidus*; (**b**) chewing louse *Ciconiphilus decimfasciatus*; (**c**) feather mite *Ardeacarus ardeae*; (**d**) nasal mite *Tinaminyssus bubulci*. Voucher specimens of all species are deposited in the Price Institute of Parasite Research, University of Utah (PIPR000993–PIPR000996). Color version available online.

fixed effect in the analysis of feather mites because feather mite abundance has been shown to correlate positively with uropygial gland size (Galván et al., 2008). To quantify uropygial gland size we measured the maximum length, width, and height of the gland and multiplied the 3 dimensions, as in Galván and Sanz (2006).

For nasal mites, which were absent from about a third of the Time 0 birds (Table I), zero-inflated negative binomial regression was used with the *pscl* package to analyze abundance (Zeileis et al., 2008). Zero-inflated regression considers the probability that some captive birds had no nasal mites at the start of the experiment, while comparing the abundance of nasal mites on experimental and control birds. Scratching time was included as a fixed effect because scratching could influence the abundance of nasal mites, which have been observed on the head and beaks of infested birds (Bell, 1996). Preening time was not included in the analysis of nasal mites because preening presumably does not affect nasal mite abundance, as birds cannot preen their heads.

Table I. Prevalence and median abundance of arthropods on 14 "Time 0" cattle egrets from Lokowaka Pond, Hilo, Hawaii.

Arthropod taxa	Prevalence	Abundance (median)
Chewing lice		
Ardeicola expallidus	100%	151
Ciconiphilus decimfasciatus	57%	1.5
Feather mite		
Ardeacarus ardeae	100%	694.5
Nasal mite		
Tinaminyssus bubulci	64%	8

To test if arthropod abundance differed between wild cattle egrets and control birds at the end of the experiment, we compared the arthropod abundance of Time 0 and control birds. We used GLMs with a fixed effect for the 2 groups and a negative binomial link to compare the abundance of both lice and feather mites on the 2 groups of birds. We used zero-inflated negative binomial regression to compare the abundance of nasal mites on the 2 groups.

To test if the removal of the teeth affected grooming time, we compared control and experimental birds. We analyzed time spent preening and time spent scratching separately using GLMs with a binomial link and a fixed effect for treatment.

RESULTS

Two species of chewing lice, 1 species of feather mite, and 1 species of nasal mite were recovered from the cattle egrets (Fig. 3a–d). The prevalence of the louse species *Ardeicola expallidus* and the feather mite *Ardeacarus ardeae* were both 100% and the abundance of both species was high (Table I). We thus assumed that most, if not all, of the 29 captive birds were infested with these 2 arthropod taxa at the

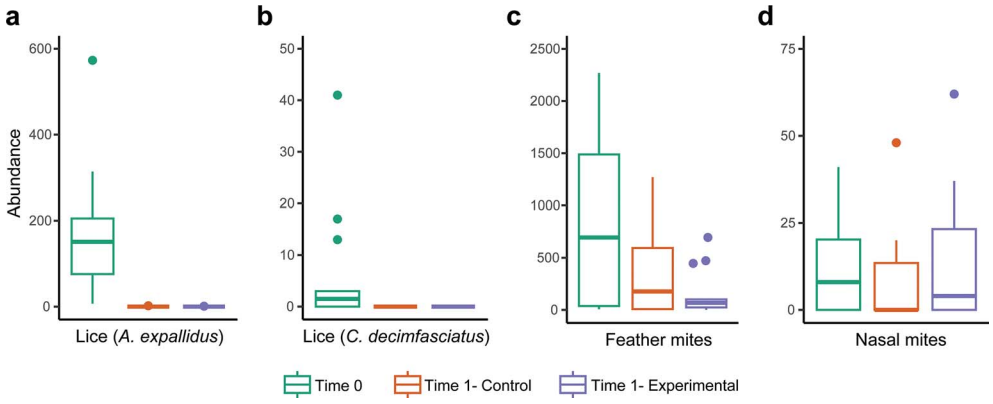

Figure 4. Box plots summarizing the abundance of 4 taxa of arthropods (a–d, as in Fig. 3) among the 3 groups of cattle egrets: 14 Time 0 birds, 12 control birds with intact pectinate claws, and 14 experimental birds with teeth of the pectinate claws removed. Note different y-axes across arthropod taxa. Boxplots show the median, interquartile range, reasonable range of the data, and outliers. Color version available online.

start of the experiment. More than half of Time 0 birds were also infested with the louse *Ciconiphilus decimfasciatus* and the nasal mite *Tinaminyssus bubulci* (Table I). We also assumed that at least some of the captive birds at the start of the experiment were also infested with these 2 arthropod taxa.

At the end of the experiment, nearly all birds, regardless of treatment, were free of lice (Fig. 4). One experimental bird had a single *Ardeicola,* and 1 control bird had 2 *Ardeicola*; none of the birds had *Ciconiphilus*. Given the low prevalence of lice by the end of the study, it was not necessary to use GLMs to compare the abundance of lice on experimental and control birds formally; the virtual extinction of lice on experimental birds shows that pectinate claws are not essential for combatting lice, at least in captive cattle egrets (see Discussion).

At the end of the experiment, the prevalence of feather mites was 83% on control birds and 93% on experimental birds. The median abundance of feather mites was 177 on control birds and 68 on experimental birds (Fig. 4). Experimental removal of teeth from pectinate claws had no significant effect on the abundance of feather mites ($P = 0.20$). Neither preening time ($P = 0.36$), nor uropygial gland size ($P = 0.70$), were significantly related to feather mite abundance. The effect of the experimental removal of teeth on feather mite abundance remained insignificant ($P = 0.16$) when preening time and uropygial gland size were removed from the model.

At the end of the experiment, the prevalence of nasal mites was 42% on control birds and 57% on experimental birds. The median abundance of nasal mites was 0 on control birds and 4 on experimental birds (Fig. 4). Experimental removal of teeth had no significant effect on the abundance of nasal mites ($P = 0.89$), nor was scratching time significantly related to nasal mite abundance ($P = 0.34$). The effect of the experimental removal of teeth on nasal mite abundance remained insignificant ($P = 0.82$) when scratching time was removed from the model.

The grooming time of control and experimental birds was similar (Fig. 5). Control birds spent a mean (±SE) of 14.1% (±2.4) of their time preening, compared to 17.3% (±2.6) by experimental birds ($P = 0.07$). Control birds spent a mean of 0.3% (±0.2) of their time scratching, compared to 0.6% (±0.2) by experimental birds ($P = 0.29$).

DISCUSSION

Over the course of the 4-mo experiment cattle egrets eradicated nearly all of their chewing lice. This was true of control birds, with the pectinate claw intact, as well as experimental birds, with the teeth removed. The lice were presumably removed by grooming (see the following), indicating that the pectinate claw is not essential for egrets to control lice, at least in captivity. These results are similar to an experimental study by Bush and Clayton (2023), which found that captive pigeons (*Columba livia*) are capable of eradicating lice by grooming.

Two apparent factors increased the likelihood of eradication of lice by grooming. First, captive birds, which are released from time constraints such as searching for food, generally double the amount of time they spend grooming (Walther and Clayton, 2005). The cattle egrets in our study spent about twice as much time grooming as wild cattle egrets (Ojija, 2015). Second, birds in our experiment were isolated from conspecifics, eliminating the opportunity for horizontal transmission between birds, which is common (Harbison et al., 2008), especially in colonial birds such as cattle egrets (Rozsa et al., 1996).

Eradication of lice by grooming in our study was further suggested by a (control) cattle egret excluded from the main analyses. The bird in question had swollen feet, perhaps from a chronic infection. Analysis of behavioral video for this bird showed that it groomed only 1.4% of the time, much less than other birds in the study (Fig. 5). Although the bird maintained normal body mass, it had 113 *Ciconiphilus* lice at the end of the study, many more than any other bird

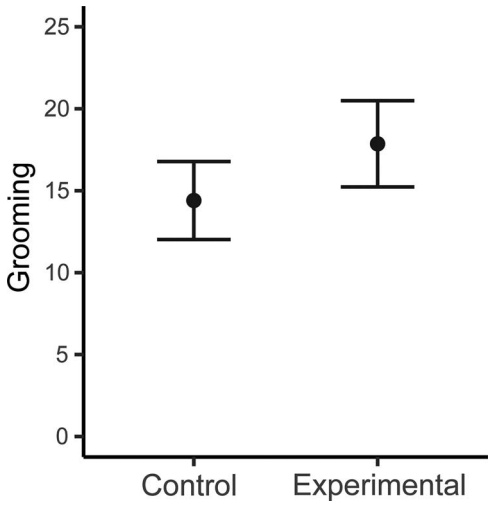

Figure 5. Grooming time (mean ± standard error) of 11 control (at left) and 14 experimental (at right) egrets.

(Fig. 4b). In short, this bird can be viewed as an exception that proves the rule that grooming is required to eradicate lice.

The abundance of feather mites on control vs. experimental birds did not differ significantly at the end of the study, indicating that the pectinate claw had no effect on feather mites. This result is not surprising, because *Ardeacarus ardeae* feather mites are typically found on the wings, which are out of range of scratching. The abundance of feather mites on control vs. Time 0 birds also did not differ significantly, despite the increased rate of grooming by captive birds. In summary, grooming had no effect on feather mites in our study.

Similarly, the abundance of nasal mites on control versus experimental birds did not differ significantly at the end of the study, indicating that the pectinate claw also had no effect on nasal mites. In contrast to the observations by Bell (1996) of nasal mites on the head and beak of Gouldian finches (*Erythrura gouldiae*), we never observed nasal mites outside the nares of cattle egrets. The abundance of nasal mites on control vs. Time 0 birds did not differ significantly, despite the increased rate of grooming by captive birds. Thus, grooming also had no effect on nasal mites in our study.

The results of this study show that the pectinate claw does not play a role in the control of permanent arthropod associates of cattle egrets, at least in captivity. Our experiment may underestimate the role of the pectinate claw in controlling arthropods in wild birds, at least in the case of lice. Our captive birds spent about twice as much time grooming as their wild counterparts, presumably because they had to spend less time looking for food and other challenges faced by natural populations (Ojija, 2015). Scratching with the pectinate claw may be important when birds have less time to devote to grooming.

It would be interesting to repeat our experiment using wild egrets. Such an experiment would be challenging because birds would need to be retrapped and the pectinate claw teeth re-Dremeled (or sham-Dremeled) if the experiment was designed to last more than about a month. Pending such an experiment, the function of the pectinate claw remains unclear. It is a curious structure that has evolved independently several times across birds of the world (Clayton et al., 2010). Although the overall structure of the pectinate claw appears superficially similar across birds, the teeth vary in number, size, and spacing among different taxa of birds (M. M. Waller, pers, obs.). Clues to the function of the pectinate claw may lie in these differences.

The pectinate claw may also serve functions unrelated to arthropod control across independent evolutionary origins. For example, the pectinate claws of some nightjars (Caprimulgiformes) may serve to maintain and clean rictal bristles, whereas the pectinate claws of barn owls (*Tyto alba*) may be used to maintain and arrange feathers of the facial disk. Other potential functions of the pectinate claw, such as the application of colored uropygial oil for cosmetic coloration, would also be interesting to explore (Delhey et al., 2007).

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