How Birds Combat Ectoparasites

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Abstract: Birds are plagued by an impressive diversity of ectoparasites, ranging from feather-feeding lice, to feather-degrading bacteria. Many of these ectoparasites have severe negative effects on host fitness. It is therefore not surprising that selection on birds has favored a variety of possible adaptations for dealing with ectoparasites. The functional significance of some of these defenses has been well documented. Others have barely been studied, much less tested rigorously. In this article we review the evidence - or lack thereof - for many of the purported mechanisms birds have for dealing with ectoparasites. We concentrate on features of the plumage and its components, as well as anti-parasite behaviors. In some cases, we present original data from our own recent work. We make recommendations for future studies that could improve our understanding of this poorly known aspect of avian biology.

INTRODUCTION

As a class, birds (Aves) are the most thoroughly studied group of organisms on earth. Nevertheless, the adaptive function of many intriguing features of avian morphology, physiology, and behavior are still uncertain. Some of these features are thought to play a role in defense against harmful ectoparasites. Examples include the pectinate middle claw of many birds, the strange odors of some birds, and the odd "maintenance" behaviors, such as sunning, anting or dusting, performed by many birds. In this article we review the ways in which birds are thought to combat ectoparasites. We pay particular attention to possible anti-parasite features of the plumage itself, as well as various forms of anti-parasite behavior. Although the immune system also plays an important role in defense against some ectoparasites, such as blood-feeding mites [1], we do not cover immune defenses in this review. Instead, we refer readers to other papers in this volume, and recent reviews of immunology published elsewhere, e.g. [2] and [3].

In the classic work *Fleas, Flukes and Cuckoos*, Rothschild and Clay [4] catalogued the incredibly rich diversity of parasitic organisms inhabiting birds, including groups as different as viruses, fungi, bacteria, protozoa, worms and arthropods. The major groups with *ectoparasitic* forms are as follows:

1) Insects: Four orders, including lice (Phthiraptera), fleas (Siphonaptera), true bugs (Hemiptera), and flies (Diptera) [5].

2) Mites and ticks (Acari): *many* families [6-9].

3) Leeches: four families [10].

4) Fungi: keratinophilic and cellulose decomposing forms [11].

5) Bacteria: several unrelated groups that decompose feathers [12].

Relatively little was known about the impact of ectoparasites on non-game wild birds until about 25 years ago, when ornithologists began to take a strong interest in parasites. One catalyst was Hamilton and Zuk's influential 1982 [13] paper arguing that the elaborate visual and acoustic displays of many birds evolved as a result of parasite-mediated sexual selection. Since then, dozens of papers testing the impact of parasites on wild birds have been published. For reviews, including the topic of sexual selection, which we will not cover here, see [3, 14-21].

These studies confirm that many ectoparasites are potent agents of selection on birds, affecting both the survival and reproductive components of avian fitness. Not surprisingly, therefore, birds appear to have evolved a wide variety of defenses for controlling ectoparasites. Moyer and Clayton [22] provided a succinct review of defenses involving plumage as a barrier, and antiparasite behaviors of birds. Since their review, several dozen new papers have been published with information pertinent to these kinds of defenses. We review these papers below, and in some cases we report original data relevant to purported defenses.

We consider ectoparasites to include taxa that spend at least some of their life cycle in close association with the host, as opposed to more ephemeral "parasites", such as mosquitoes. We do not cover defenses aimed primarily at

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these ephemeral species, such as fly repelling behavior, defensive sleeping postures, microhabitat choice, territoriality, and "selfish herd" effects. For reviews of these topics see Lehane [23], Hart [24] and Weldon and Carroll [25].

We use parasite *load* in reference to any of the following more precise measures: *richness* (the number of species of parasites present); *prevalence* (the fraction of parasitized individuals in a host population); *intensity* (the number of individual parasites in an infested host); *abundance* (the number of individual parasites in a host, regardless of infestation). Hence, *mean intensity* is the average number of individual parasites across infested hosts in a population, and *mean abundance* is the average number of parasites across all host individuals, regardless of infestation. For further details see Bush *et al.* [26].

PLUMAGE AS A BARRIER

Most ectoparasites are in contact with the plumage, at least some of the time. Some ectoparasites, such as feather lice (Phthiraptera: suborder Ischnocera), are in contact with the plumage *all* of the time. Indeed, they even feed on feathers, which are digested with the aid of endosymbiotic bacteria [27]. It is therefore reasonable to expect that some chemical or mechanical features of the plumage may have evolved to deter ectoparasites, similar to the many features of foliage known to deter herbivorous insects [28]. Plumage related defenses might include feather molt, analogous to the abscission of plant leafs reducing infestations of leaf miners and other endophytic and sessile herbivorous insects (reviewed in Stiling *et al.* [29]).

Feather Molt

Conventional wisdom has it that feather molt helps reduce ectoparasite loads [5]. Indeed, molt presumably does help birds jettison immobile parasites, such as fungi and bacteria that live in the plumage. Burtt and Ichida [30] showed that the abundance of feather-degrading bacteria fluctuates seasonally, with the smallest infestations in the autumn, which is consistent with this hypothesis. But it remains unclear whether molt plays an important role in controlling more mobile parasites, such as mites and lice.

Records of lice on molted feathers suggest that molt may indeed reduce arthropod ectoparasite loads [31]. Post and Enders [32] attributed the low prevalence of lice on Sharp-tailed Sparrows (*Ammodramus caudacutus*), compared to Seaside Sparrows (*A. maritimus*), to the fact that the former molt twice a year, while the latter molt once a year. Several researchers have carried out longitudinal studies in which they documented an apparent reduction in ectoparasite load over the course of the host's molting period [33]. Baum [34] reported an 85% drop in the abundance of lice on molting Eurasian Blackbirds (*Turdus merula*). Markov [35] observed a decrease in the number of ectoparasites on European Starlings (*Sturnus vulgaris*) during the autumn, and argued that feather molt caused this decrease. However, Boyd [36] suggested that seasonal changes in climate were actually responsible for the autumn reductions. Changes in climatic factors - particularly ambient humidity - are known to have a significant impact on ectoparasite abundance, at least in the case of lice [22, 37, 38].

A recent longitudinal study of ectoparasite loads on House Finches (*Carpodacus mexicanus*) indicates that the relationship between molt and ectoparasite abundance can be complicated [39]. The results of this study show that the abundance of two species of feather mites (*Strelkoviacarus* sp. and *Dermoglyphus* sp.) increased, rather than decreased, during the molting season. The louse *Menecanthus alaudae* also increased during the molting season on male House Finches. The authors argued that the energetic cost of molt reduced the amount of energy birds could expend on activities such as preening, leading to an increase in ectoparasites. The authors also compared the ectoparasite loads of birds in various degrees of molt. Molting males had more feather mites than non-molting males, whereas the number of mites on molting vs. non-molting females did not differ significantly. In addition, the study showed that molting males had more lice than molting females. The authors suggest that these patterns are driven by the additional energetic costs associated with the possession of showy plumage in males.

Moyer *et al.* [40] conducted an experimental test of the impact of molt on ectoparasites. The authors manipulated photoperiod to trigger early molt in captive Rock Pigeons (*Columba livia*) infested with lice. They then tracked the abundance of lice on molting and non-molting (control) birds over the course of several weeks. Visual examination of lice on different body regions indicated that feather molt reduced louse abundance. However, body washing, a more robust method of quantifying lice [41], showed that molt did not, in fact, reduce the abundance of lice. Two factors caused visual examination to underestimate the number of lice on the molting birds. First, molt replaced worn feathers with new, lush plumage that obscured lice during visual examination. Second, lice sought refuge inside the sheaths of newly developing feathers, where they could not be seen. The illusion of reduced louse abundance documented by Moyer *et al.* [40] calls into question observational studies documenting apparent reductions in lice during molt. This may also be true for other ectoparasites.

A few studies of molt have used methods for quantifying ectoparasites that are more rigorous than visual examination. For example, Chandra *et al.* [42] fumigated Common Mynas (*Acridotheres tristis*), ruffled their plumage, and quantified the lice. McGroarty and Dobson [43] used body washing to determine the number of lice on House Sparrows (*Passer domesticus*). Both studies showed a reduction in louse abundance in late summer, coincident with the postnuptial molt of the host. However, experimental manipulations are still needed to establish molt as the cause of these decreases, rather than some third factor that covaries with both molt and ectoparasite reductions. One such factor could simply be transmission of lice from parent to offspring birds. Lice typically move in large numbers from parent birds to their offspring at the end of the breeding season, leading to a decrease in the abundance of lice on adult birds around the time of molt [44-47]. Dispersal of lice to juveniles could also explain why fewer newly deposited feather louse eggs are found on adult feathers near the end of the host's breeding season [48].

Host physiological constraints may give many ectoparasites time to circumvent molt, which tends to be a gradual process in most birds because thermal insulation and aerody-

namic efficiency are both compromised in proportion to the number of missing feathers [49, 50]. Energy is also required, of course, to create each new feather [51]. Feather quality can be inversely proportional to the rate of molt, further suggesting constraints on rapid molt [52]. If feathers are lost gradually, then it may be possible for ectoparasites to avoid feathers that will soon be molted. A survey of feather mite distributions on the flight feathers of molting passerines shows that mites can, in fact, avoid molting feathers [53]. Similarly, mites that live inside the quills of feathers (Syringophilidae) are known to abandon the old feathers in favor of new ones before the old ones molt [54, 55].

Two mechanisms have been proposed to explain how ectoparasites detect and avoid molting feathers [56]. The "vibration" hypothesis proposes that the cue used by the ectoparasites is the vibration caused by rocking of the old feather as it is pushed out of a follicle by the newly emerging feather. The "window" hypothesis proposes that ectoparasites on sequentially molting flight feathers can detect changes in movement or airflow caused by absence of the adjacent, molted feather. Pap *et al.* [57] addressed both hypotheses in a clever experiment. To test the window hypothesis they removed the sixth primary feather from non-molting Barn Swallows *(Hirundo rustica)*. To test the vibration hypothesis they cut part way through the shaft of the sixth primary feather of the opposite wing to simulate vibration in a molting feather. The simulated window did not cause mites to leave the adjacent (seventh) primary on the first wing, suggesting that the vibration hypothesis might be the correct explanation. Unfortunately, the authors did not report whether mites left the partially cut sixth primary on the opposite wing, nor did they report the number of mites on the fifth primary, which is one place the mites would be expected to move in response to vibration. The authors did note a decrease in the number of mites on the eighth primary, but the relevance of this observation is unclear. Interestingly, experimental birds with pulled or cut feathers had significantly fewer mites on the flight feathers than did control birds at the end of the experiment. The authors suggested that the mites may have moved from flight feathers onto body feathers to escape molt, but there were no data with which to test this hypothesis.

Jovani *et al.* [56] also evaluated the two hypotheses using mites on Barn Swallows. As in many birds, there is a time lag between molting of a primary feather, which creates a window, and hypothesized vibration in the adjacent feather before that feather also molts. Jovani *et al.* [56] found that mites stayed on feathers near the window for a long time, moving only when the feather was nearly ready to drop. As in the case of Pap *et al.*'s study [57] this observation suggests that vibration may be a more important cue than the appearance of a window. However, additional experimental manipulations of cues that ectoparasites could use to detect molt are needed for a more complete understanding of this question.

Feather Toughness

Feathers containing melanin—the pigment typically responsible for brown, gray or black colors [58]—are more resistant to mechanical abrasion than feathers without melanin [59, 60]. This toughness makes melanin rich feathers more resistant to wear and tear, and may also deter feather-feeding ectoparasites. Two studies suggest that melanin can limit damage by feather feeding lice [61, 62]. Kose and colleagues [61] surveyed feather damage in Barn Swallow (*Hirundo rustica*) populations and found that the holes chewed by lice were significantly more likely to occur in the white (melanin-free) spots on the tail feathers, compared to black (melanin-rich) regions of the tail. The authors conducted a louse-preference trial *in vitro* and found that the lice preferred to be on white portions of the tail feathers. Unfortunately, recent evidence indicates that the louse genus studied by Kose *et al.* [61] is not the one that creates holes in the feathers, thus bringing into question the relevance of their experiment. Kose *et al.* [61] studied preferences of the louse *Machaerilaemus malleus* (synonym: *Hirundoecus malleus*), in the family Menoponidae, whose members often feed on blood and feathers [63]. The holes in Barn Swallow tail feathers appear to be caused by members of the genus *Brueelia* [64], in the family Philopteridae, whose members typically feed on feathers and dead skin. The experiments performed by Kose *et al.* [61] need to be repeated using *Brueelia*.

Experiments conducted by Bush *et al.* [65] indicate that melanin does not have an effect on feather-feeding lice from Rock Pigeons. The authors captured pigeons of different color morphs ranging from white to black. Feather-feeding lice (*Columbicola columbae,* and *Campanulotes compar*) were fed feathers from these birds *in vitro*. After two weeks, there was no significant difference in the amount of feather material consumed, nor in the survival of lice on feathers with different amounts of melanin. Additional experiments with *C. columbae* showed that there was no significant difference in reproduction of lice on white vs. black feathers, nor did the lice exhibit a preference for different colored feathers.

Melanized feathers may be more resistant to feather-degrading bacteria (FDB). Three studies have addressed this question by exposing *Bacillus licheniformis*, a common strain of FDB, to melanized and unmelanized feathers. Goldstein *et al.* [66] suggested that melanized feathers resisted degradation by FDB; however, this study was performed without adequate controls or replicates [67]. In contrast, Grande *et al.* [68] found that FDB actually degraded melanized feathers faster than unmelanized feathers; however, in this study feather degradation was scored visually, which may be problematic because color could bias human perception of degradation. In an attempt to remedy these shortcomings, Gunderson *et al.* [67] conducted an experiment where goose feathers were inoculated with *B. licheniformis*. They found that melanized feathers had lower bacterial densities, degraded more slowly, and had less degradation than unmelanized feathers, indicating that melanin does, in fact, deter at least one strain of FDB *in vitro*.

Many species of birds have melanic morphs, and the darker morphs typically live in more humid regions – a pattern known as *Gloger's rule* [69]. Burtt and Ichida [70] hypothesized that this pattern may be driven by FDB, which thrive in humid conditions. They compared the degradation rates of *B. licheniformis* isolated from darkly colored Song Sparrows (*Melospiza melodia*) from a humid region and more lightly colored Song Sparrows from an arid region. By growing

these bacterial isolates on chicken feathers under "common garden" laboratory conditions, the authors showed that the bacteria from the humid region degraded feathers faster than bacteria from the arid region. Burtt and Ichida [70] suggested that Song Sparrows in humid regions (where bacteria do better) evolved more melanin because of increased pressure from the more detrimental strain of *B. licheniformis*.

In another study, Cristol *et al.* [71] inoculated the feathers of live birds with *B. licheniformis* to test the impact of sunning behavior on FDB. They noticed that darkly colored European Starlings (*Sturnus vulgaris*) had far less damage than more lightly colored Northern Cardinals (*Cardinalis cardinalis*). However, as the authors themselves point out, these data are only suggestive, since the experiments with starlings and cardinals were run at different temperatures, humidities, and for different lengths of time.

In summary, studies with *B. licheniformis* [70, 71] suggest that melanin may be an important defense against FDB. However, experiments manipulating bacteria *in vivo* on light and dark birds are needed for a more convincing test of this hypothesis, as well as to test the fitness consequences of FDB for birds [72]. Moreover, studies are needed to understand how melanin affects bacterial communities. Interactions between bacteria could alter how we interpret the role of melanin as a bacterial defense. Experiments done *in vivo* should, if possible, incorporate whole communities of FDB, not just *B. licheniformis,* which is often studied because it can be cultured *in vitro*. Work is also needed to elucidate the precise mechanism(s) by which melanins deter bacteria [67]. It is entirely possible that an antibacterial role of melanin could have more to do with its influence on the avian immune system [3] than it's influence on feather hardness (see other articles in this volume).

FEATHER TOXINS

Toxins in the plumage of some birds may help combat ectoparasites [25, 73]. The best-known example is batrachotoxins in the feathers and skin of several species in the New Guinea passerine genera *Pitohui* and *Ifrita* [74, 75]. Batrachotoxins, which are also found in the skin of poison dart frogs, (*Phyllobates spp.*) are thought to play a role in deterring predators. Experimental evidence suggests that the toxins also deter ectoparasites [76-78]. Dumbacher [78] conducted a series of *in vitro* trials in which he exposed feather lice from a variety of bird species to feathers of *Pitohui* and other non-toxic birds. He found that lice avoid feeding or resting on *Pitohui* feathers when they are given a choice. Lice on *Pitohui* feathers also show higher mortality than lice on non-toxic feathers. Since batrachotoxin detrimentally affects a wide variety of invertebrates [78], it may deter other ectoparasites in addition to lice. Interestingly, a survey of 30 New Guinea passerine genera showed that *Pitohuis* had the lowest tick loads [79]. Another study showed that the family Pachycephalidae, which includes the genus *Pitohui,* has comparatively few arthropod-vectored haematozoan parasites [80].

Odorous Feathers

At least 80 genera of birds in 17 orders produce odors that humans can readily detect [81]. It is possible that one adaptive function of such odors is to combat ectoparasites.

This hypothesis has been tested most thoroughly in Crested Auklets (*Aethia cristatella*) (Fig. **1**), which emit a pungent citrus-like odor that humans can detect at a considerable distance from breeding colonies [82]. Douglas *et al.* [83] identified the odor constituents as a series of short-chained, saturated and monounsaturated aldehydes, which are corrosive irritants that are volatile and reactive. The authors suggested that the citrus odor might repel ectoparasites since two of the major constituents, hexanal and octanal, are known arthropod repellents.

Douglas *et al.* [84] tested the effect of synthetic versions of auklet odorant compounds on two genera of auklet lice (*Austomenopon* sp. and *Quadraceps* sp.). Lice exposed to 1µl of either octanal or Z-4-decanal became moribund in seconds. In contrast, when Douglas *et al.* [85] exposed Rock Pigeon lice (*Columbicola columbae* and *Campanulotes compar*) to fresh auklet feathers placed in covered petri dishes with lice, or to fresh auklet carcasses sealed in beakers with lice, there was no effect on parasite survival. Douglas *et al.* [85] also compared the relative abundance of lice on Crested Auklets to lice on Least Auklets *(A. pusilla)*, which do not emit a noticeable odor (the birds were from the same mixed breeding colony). They found that Crested Auklets actually had significantly more lice than Least Auklets, even after controlling for a difference in host body size.

Douglas *et al.* [84] also tested the effect of synthetic versions of auklet odorant compounds on two species of ticks. Laboratory reared ticks (*Amblyomma americanum*) were exposed to octanal on an artificial host consisting of filter paper attached to a heated, rotating drum. Ticks detached

Fig. (1). Crested Auklets (*Aethia cristatella*), such as the one shown here, emit a citrus-like odor that may deter ectoparasites. Photo by Hector Douglas.

significantly faster from artificial hosts treated with 10% octanal than from artificial hosts treated with ethanol. Ticks were also exposed to a synthetic cocktail designed to mimic the diverse chemical composition of auklet odorant. Ticks challenged with this cocktail (40% octanal, 21% hexanal, 8% Z-4 decenal, 3% decanal, 7% hexanoic acid, and 3% octanoic acid) showed a dose dependent response. Ticks exposed to at least a 10% dilution of the cocktail remained attached to the artificial host for a shorter period of time than controls. Douglas *et al.* [84] also conducted experiments with *Ixodes uriae*, the tick found on Crested Auklets in nature. The results were similar to the experiments conducted with *A. americanum.* Moreover, when these ticks were placed in a vial with 5μl octanal, they became moribund within an hour.

In another study involving *I. uriae* ticks, Douglas [86] quantified the relative odor emissions from 57 live Crested Auklets. Interestingly, the individual with the lowest emission level was infested with 14 ticks. Only one other bird was infested (with two ticks), out of 96 birds surveyed in the same breeding colony. In contrast, Hagelin [87] found no evidence that *I. uriae* ticks are repelled by fresh Crested Auklet feathers placed in petri dishes, compared to feathers of Least Auklets or Parakeet Auklets *(A. psittacula),* neither of which emit a noticeable odor.

Hagelin and Jones [81] have argued that the repellency studies conducted by Douglas *et al.* [84] used synthetic compounds that exceed natural concentrations (c.f. those measured in auklet odorant by Hagelin *et al* [88]). In response, Douglas [89] argued that Hagelin *et al.*'s study underestimated the quantity of volatiles in auklet feathers because the samples were kept under suboptimal conditions, during which time they may have degraded (and see Hagelin [90]).

Douglas [91] published data indicating that natural concentrations of auklet odor are, at least in some cases, greater than those published by Hagelin *et al* [88]. He also conducted *in vitro* experiments with ticks (*A. americanum*) exposed to low doses (0.5% and 1%) of a synthetic cocktail. Douglas [91] argued that these doses simulate natural conditions because the 1% solution exposed ticks to lower concentrations of octanal than he isolated from the crown and nape feathers of Crested Auklets. Locomotion of ticks at both doses in this study was significantly less than that of controls, and there was evidence of paralysis in some of the ticks exposed to the 1% treatment. These results suggest that the compounds in Crested Auklet odorant do have the potential to deter ticks. What is needed for a more definitive study, if possible, is a test of the impact of the odorant on ticks under natural conditions in the field. Ideally, this test would involve some kind of experimental manipulation of odorant levels. Tests for an impact of odorants on ectoparasites in other groups of birds are also needed.

Uropygial Oil

Most birds have a nipple-like uropygial (preen) gland on their rump. They squeeze this protuberance with their bill during preening and spread its oil throughout the plumage. The oil is known to help maintain plumage strength and flexibility, but it has long been thought that the oil may also deter ectoparasites [77, 92, 93]. Uropygial oil could combat ectoparasites by reducing their mobility on feathers or skin. If the oil coats the exterior of a parasite, or at least plugs the spiracles (breathing holes) of arthropod parasites, it might also suffocate them [94]. In some species of birds the oil is associated with noxious or repellent odors, which could conceivably affect ectoparasites [73].

Moyer *et al.* [94] tested whether preen oil helps Rock Pigeons combat feather lice. They compared the survival of lice raised in an incubator on feathers treated with uropygial oil to the survival of lice on control feathers without oil. They found that lice on oiled feathers died more rapidly than controls. They also compared the population dynamics of lice on captive pigeons with intact uropygial glands to lice on pigeons with their glands surgically removed. Removal of the gland had no significant effect on louse populations over a period of four months (about 5 louse generations). This finding suggests that birds do not "fumigate" themselves with preen oil, despite the fact that the oil does, in fact, have the capacity to kill lice when applied *in vitro* [94].

Uropygial oil may inhibit the growth of certain pathogenic bacteria and fungi that inhabit the plumage of birds [11,95-99]. Jacob *et al.* [99] demonstrated that constituents of Pelecaniform uropygial oil, applied *in vitro*, have a dose-dependent inhibitory effect on Gram-positive bacteria and fungal dermatophytes (*Trichophyton* sp., *Microsporum gypseum*). The Red-billed Woodhoopoe (*Phoeniculus purpureus*), like other species of woodhoopoes, emits a malodorous secretion from its uropygial gland [73]. Law-Brown [98] identified 17 chemical constituents found in the uropygial oil of this species. Using disc-diffusion assays, she tested the *in vitro* activity of each constituent against 13 pathogenic bacterial strains (e.g., *Salmonella enteritidis, Staphylococcus aureus,* and *Streptococcus faecalis*), and against a strain of the feather-degrading bacterium *Bacillus licheniformis* [30]. Seven of the constituents significantly inhibited bacteria, suggesting that uropygial oil has the potential to combat bacterial infections and concommitant feather degradation.

Interestingly, most of the chemical constituents of the uropygial oil of Red-billed Woodhoopes are synthesized by yet another bacterium, *Enterococcus phoeniculicola*, which lives in the bird's uropygial gland. Law-Brown [98] treated the glands of this species with an antibiotic, and then compared the chemical composition of their uropygial oil to that of untreated controls. Her results showed that only two of 17 constituents were still present following antibiotic treatment. Furthermore, the ones that remained in the oil (e.g., cholesterol) were present at elevated levels, suggesting they were no longer metabolized in the absence of the bacteria. This pioneering study is the first to document a bacterial symbiont that metabolizes constituents of uropygial oil.

Uropygial oil affects different strains of parasitic bacteria and fungi in different ways. Pugh and Evans [96] tested the impact of European Starling (*Sturnus vulgaris*) "feather fats" on four species of keratinophilic fungi. They made the interesting observation that, while sporulation of *Chrysosporium keratinophilum* increased, the same oils inhibited the growth of *Arthroderma quadrifidum, A. uncinatum* and *Ctenomyces serratus*. Pugh [11] found that the feather fats of Blackbirds (*Turdus merula*) inhibited the growth of *C. serratus*, while stimulating the growth of *A. curreyi*. In a similar study, Bandyopadhyay and Bhattacharyya [100] tested the effects of uropygial oil on several fungal species cultured from the skin

of white leghorn fowl. They found that surgical removal of the uropygial gland led to an increase in the populations of all but one species of fungi.

Shawkey *et al.* [101] suggest that uropygial oil might benefit birds by promoting the growth of bacteria or fungi that out compete or otherwise exclude more virulent microbes. The authors identified 13 bacterial isolates from the feathers of wild house finches (*Carpodacus mexicanus*), and measured the feather-degrading activity of each. They tested the effects of uropygial oil on the survival and growth of each strain through a disc-diffusion assay. They found that uropygial oil inhibited the growth of three feather degrading strains, including *Bacillus licheniformis*, but it had less of an effect on more benign strains. Future studies should aim to clarify the impact of uropygial oil on bacterial and fungal strains both in isolation, and in the context of the full microbial community.

Feather mites may have an entirely different relationship with uropygial oil. Blanco *et al.* [102] suggested that feather mites are commensals, or even mutualists, rather than parasites. The main food resource of certain feather mites is uropygial oil on the feathers. Along with the oil, the mites consume microbes such as fungi and bacteria [9]. If these microbes include forms that are dangerous to the bird, the consumption of uropygial oil by feather mites may be beneficial to the host [103, 104]. This interesting hypothesis should be tested experimentally.

BODY MAINTENANCE BEHAVIOR

Grooming behavior, defined as preening and scratching combined [105], is known to be critical for defense against ectoparasites [5, 24]. Preening is of two types: self-preening (Fig. **2a**) and allopreening (Fig. **2b**). Water bathing, dusting, sunning, anointing and cosmetic behaviors may also play a role in ectoparasite defense. Below we review the evidence relevant to each of these behaviors, as well as the evidence relevant to the different types of grooming.

Grooming: Self-Preening

Preening is the most common defensive behavior that birds use against ectoparasites. Preening involves the bird pulling its feathers between the two mandibles of the bill, or nibbling the feathers with the bill tips. Birds can spend a significant portion of their daily time budget preening; e.g. Losito *et al.* [106] showed that juvenile mourning doves spend up to 23% of their time preening. This is a considerable amount of time and energy, given that the cost of preening can be about twice the basic metabolic rate [107]. Croll and McLaren [108] documented a nearly 200% increase in the metabolic rate of preening Thick-billed Murres (*Uria lomvia*), compared to resting individuals. The increase was higher than that associated with either feeding (49%) or diving (140%).

Many studies have shown that preening is a critical defense against ectoparasites. The defensive role of preening was initially suggested by natural "experiments" in which birds with bill deformities have very high ectoparasite loads [4, 5, 31, 34, 36, 109-113]. For example, Clayton *et al.* [113] observed that among 150 wild Rock Pigeons, the three individuals with the most feather lice all had minor bill deformi-
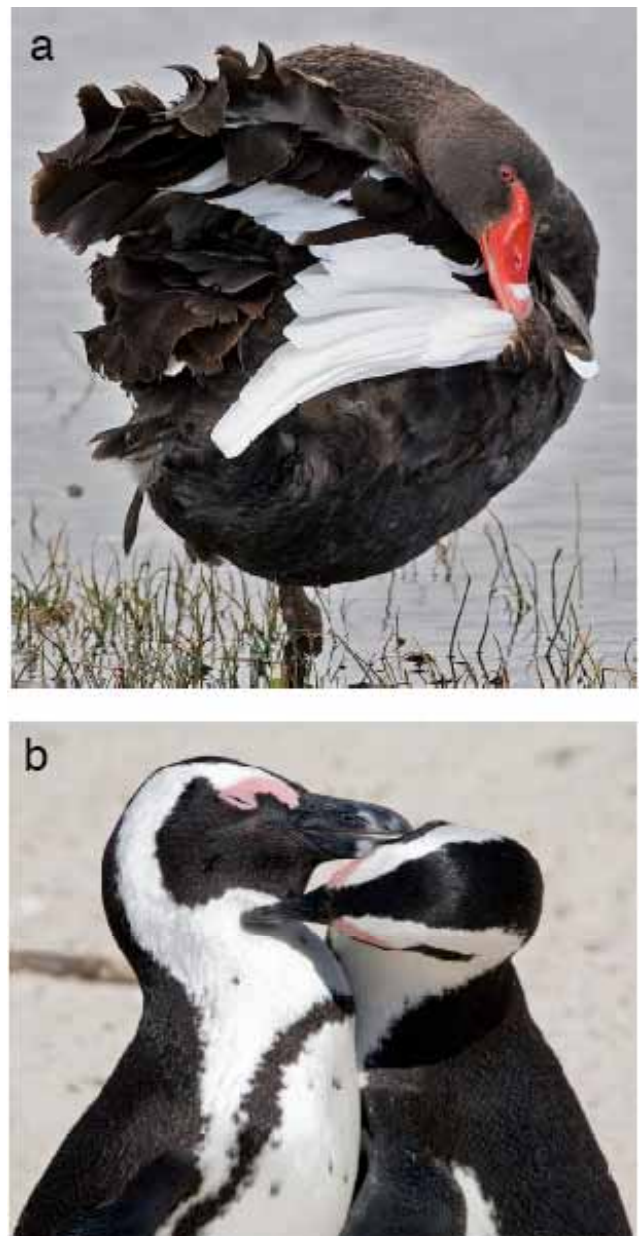

Fig. (2). (**a**) Preening Black Swan (*Cygnus atratus*). Photo by Noodle Snacks (commons.wikimedia.org). (**b**) Allopreening between Magellanic Penguins (*Spheniscus magellanicus*). Photo by Andreas Edelmann (fotolia.com).

ties. One of the deformed individuals had more than 10,000 lice, compared to a mean of 631 lice on birds without deformities. Of course, birds with deformed mandibles may have other problems, such as impaired foraging ability, which could contribute to increases in ectoparasite load [114-117]. Therefore, a rigorous test of the role of preening in ectoparasite control requires an experimental approach that alters only preening efficiency.

Early such tests impaired preening crudely by clipping ca. 1 cm from the upper mandible of domestic chickens or pigeons, leading to dramatic increases in ectoparasite load [118-121]. Subsequent tests impaired preening in a less invasive way, using poultry "bits," which are small, C-shaped

pieces of metal or plastic. Bits are inserted between the upper and lower mandibles and crimped slightly in the nostrils to prevent dislodging, but without damaging the tissue. They create a 1-3 mm gap between the mandibles that impairs the forceps-like action of the bill required for efficient preening. Bitting triggers a dramatic increase in feather louse populations on pigeons [112, 113, 122, 123]. This increase is not due to side effects of bits, such as an impact on feeding, because pigeons feed on whole grain (corn, peas, etc.) that can be picked up despite the small mandibular gap created by the bits. Clayton and Tompkins [123] showed that bits have no effect on the survival or reproductive success of (unparasitized) Rock Pigeons, compared to non-bitted controls.

The importance of preening for ectoparasite control is also apparent from comparative studies. The size of the bill overhang varies markedly across species of birds (Fig. **3**). For example, Clayton and Walther [124] compared the diversity of lice among 52 species of Peruvian birds belonging to 13 families. Phylogenetically independent comparisons revealed a significant negative correlation between louse abundance and degree to which the upper mandible (maxilla) overhangs the lower mandible. This correlation suggests that birds with slightly longer overhangs are better at controlling

lice by preening. Extreme overhangs, such as the hooked bills of raptors and parrots, are adaptations for feeding that do not enhance preening efficiency [124].

Clayton *et al.* [125] demonstrated how the maxillary overhang functions to control lice. Experimental removal of the tiny (1-2 mm) overhang (Fig. **3e,f**), triggered a dramatic increase in louse population size (Fig. **4a**). Regrowth caused the louse populations to subsequently crash (Fig. **4a**). In a series of measurements using magnetic transducers glued to the mandibles of birds, the authors showed that the lower mandible moves forward during preening (Rock Pigeon preening at 1/4th actual speed, Rock Pigeon preening at 1/24th actual speed) (suppl 1). This forward motion, which was remarkably fast, at up to 31 times per second, created a shearing force against the overhang that damaged the lice (Fig. **4b-e**). Without the maxillary overhang, birds were unable to generate this force. Additional experiments showed that removal of the overhang had no impact on feeding efficiency, suggesting that the overhang is a specific adaptation for ectoparasite control. Overhangs longer than a mean of 1.5mm broke significantly more often than shorter overhangs, further suggesting that stabilizing selection favors overhangs of intermediate length. Considering the critical
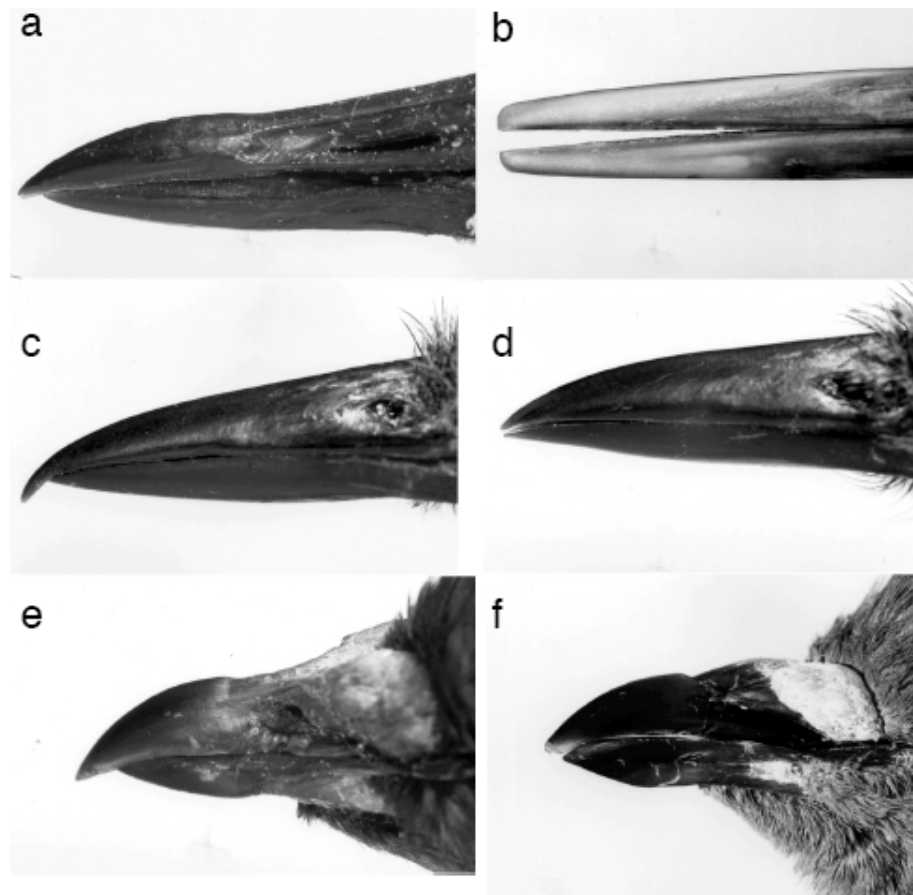

Fig. (3). Natural and experimentally induced variation in the bill overhang. Within the family Charadriidae, the Black-bellied Plover (*Pluvialis squatarola*) has a pronounced overhang (**a**), whereas the Black Oystercatcher (*Haematopus bachmani*) lacks an overhang (**b**). Within the species Western Scrub-Jay (*Aphelocoma californica*), populations living in scrub oak have a pronounced overhang (**c**), whereas those living in pinyon pine have no overhang (**d**). Rock Pigeons (*Columba livia*) have a pronounced overhang (**e**), which Clayton *et al.* [125] trimmed using a Dremel® rotary tool (**f**). Trimming is a harmless procedure, and the overhang regrows in 1-2 weeks. The results of trimming are shown in Fig. (**4**). Photos by C. Beittel.
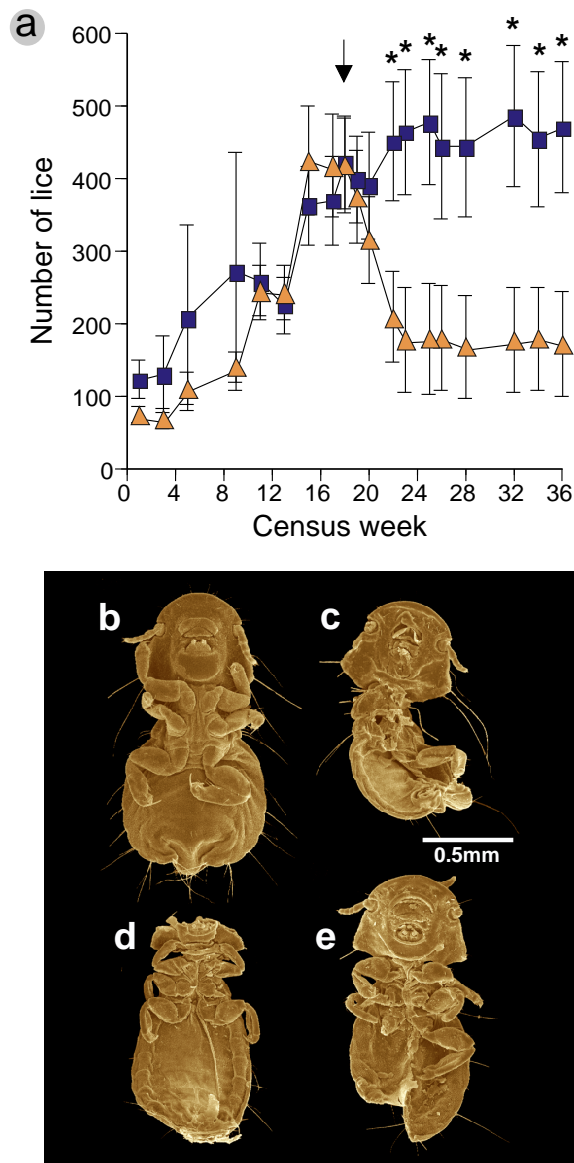
Fig. (4). (**a**) Mean (± 1 SE) number of lice on 26 adult pigeons in an experiment to test the impact of the bill overhang on preening efficiency. The overhangs of all birds were trimmed for 17 weeks; at week 18 (arrow), half the birds (orange triangles) were allowed to regrow their overhangs, while the remaining half (blue squares) continued to be trimmed weekly. Data were analyzed using a 2 (treatment: trim, regrow) X 11 (post-treatment census) ANOVA with repeated measures on the second factor (census). There were significant overall effects of treatment ($P = 0.003$) and census ($P < 0.0001$), and a significant interaction ($P < 0.0001$). Birds allowed to regrow their overhangs had significantly fewer lice than trimmed birds at each of the final eight censuses = weeks 22-36 (Protected $t > 1.97$, df = 240, *$P < 0.001$). (**b**) SEM of an undamaged louse (*Campanulotes compar*), compared to lice that have had most of their legs removed (**c**), or been decapitated (**d**), or lacerated (**e**) by birds with normal overhangs. Reprinted from Clayton *et al.* [125].

importance of the maxillary overhang for controlling lice, Clayton *et al.* [125] concluded that the adaptive radiation of beak morphology in birds should be re-assessed with both feeding and preening in mind.

Interestingly, a negative correlation between length of the bill overhang and ectoparasite abundance is also apparent among populations within species. Populations of the Western Scrub-jay (*Aphelocoma californica*) have bills specialized for feeding in their respective habitats [126, 127]. Scrub-jays in oak habitat have hooked bills (Fig. **3c**), whereas the bills of populations in pinyon habitat are pointed (Fig. **3d**). Moyer *et al.* [128] quantified lice on 170 freshly collected jays and found a significant relationship between bill morphology and louse load. Although louse prevalence was low, infested birds with pointed bills had significantly more lice than infested birds with hooked bills. More recent work using better methods of quantifying parasites further suggests that lice also exert stabilizing selection on the bill morphology of jays (Fig. **5**).

Grooming: Allopreening

In addition to preening themselves, birds sometimes "allopreen" one another (Fig. **2b**). Allopreening helps reduce ectoparasites on the head and neck, which are impossible to self-preen. Allopreening is a widespread behavior observed in many species of birds [129]. It is most common between courting and mated individuals, and between parents and their offspring. Harrison [129] argued that allopreening serves mainly a social function, such as reinforcement of the pair bond, and is of little or no importance for ectoparasite control. However, subsequent studies indicate a role for allopreening in parasite control [130-133]. Radford and Du Plessis [134] suggested a dual function for allopreening in the Green Woodhoopoe (*Phoeniculus purpureus*). Allopreening of the head and neck regions occurs at similar rates for dominant and subordinate individuals, suggesting a hygienic function. However, allopreening of self-accessible body regions, such as the wings, back or breast, are influenced by group size and dominance status, suggesting a social function.

Among the most convincing demonstrations of the importance of allopreening for controlling parasites is Brooke's [131] study of tick-infested Macaroni Penguins *(Eudyptes chrysolophus)*. Brooke reported that individual birds, which could only self-preen, had two to three times more ticks than paired birds, which engaged in frequent allopreening. The ticks were found mainly on the head and neck, suggesting that the larger numbers on unpaired birds were due to the lack of allopreening, rather than inefficient self-preening. It is important to keep in mind, however, that the author could not control for possible covariates of tick load, such as genetic resistance. Such resistance, if present, might have contributed to the low tick loads of some individuals, as well as to their ability to attract mates. Hence, inability to attract mates could lead to a spurious inverse correlation between tick load and allopreening. A more rigorous test of the role of allopreening requires analysis of covariation between allopreening and parasite load [cf. 135] or - even better - experimental manipulation of allopreening and its impact on ectoparasites.

Grooming: Scratching

Scratching with the feet is an important means of controlling ectoparasites on regions that cannot be self-preened, such as the head. Birds with a deformed or missing foot of-
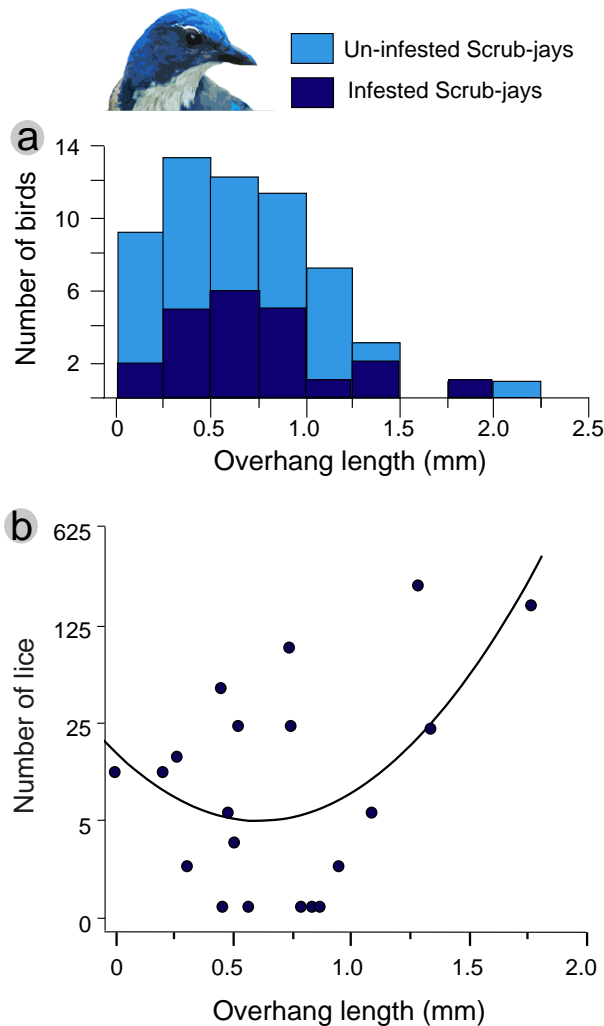
Fig. (5). Overhang lengths of Western Scrub-jays, in relation to ectoparasite abundance. Jay specimens (n = 57) were collected in 2002-03 at five localities in Utah and Nevada (Utah: Oquirrh Mountains, n = 8; Lookout Pass, n = 4; La Sal National Forest, n= 6, Stansbury Mountains, n = 2; Nevada: vicinity of Austin, n = 37). Bills were measured with calipers and the number of lice on each bird was determined using the body washing method [41]. Panel (**a**) shows the distribution of overhang length (mean of three measurements per bird) across all 57 birds, as well as across the 20 birds (35%) that were infested with lice. Factors other than preening, such as ambient humidity, are known to influence the prevalence of feather lice on Western Scrub-jays [38]. Nevertheless, of the twenty birds that had lice, those with intermediate overhangs had the fewest lice (Fig. **5b**; quadratic regression R^2 = 0.30, *P*< 0.05). This intriguing relationship suggests that lice exert stabilizing selection for intermediate overhang length, presumably because intermediate overhangs are best at controlling lice (cf. Clayton *et al*. [125]). An experimental test of this hypothesis is needed.

ten have large numbers of ectoparasites (and their eggs) concentrated around the head and neck [112]. The obvious explanation is that, although birds can preen themselves while standing on one leg, they cannot scratch themselves. Although the precise impact of scratching on ectoparasites has not been measured, scratching is known to kill or damage fleas on domestic chickens (Suter cited in Marshall [5]).

Birds may use scratching to compensate for a lack of other methods of ectoparasite control. The unpaired penguins in Brooke's [131] study spent significantly more time scratching than did paired individuals with access to allopreening. Scratching also appears to compensate for inefficient preening in species with unwieldy bills. Clayton and Cotgreave [105] reported that long-billed species average 16.2% of their grooming time scratching, compared to 2.3% in short-billed species. In a series of paired taxonomic comparisons, long-billed species scratched significantly more than short-billed taxa. In another comparative study, Clayton and Walther [124] investigated the relationship of relative foot length and toenail flange width to the louse loads of Peruvian birds, but neither feature was correlated with louse species richness or abundance.

The efficiency of scratching for ectoparasite control may be enhanced by the presence of a comb-like pectinate claw on the middle toes of some birds (Fig. **6**) [136-138]. But the possible ectoparasite control function of this "louse comb" has long been controversial [139]. Other possible functions include a role in feeding [140], removal of stale powder down from the plumage [141], or straightening of rictal bristles [137, 142]. To our knowledge, however, none of these functional hypotheses, including ectoparasite control, has ever been tested. Even the distribution of the pectinate claw among bird taxa has not been carefully documented.

One of us (BRM) recently examined 1421 study skins for pectinate claws in the collection of the Division of Birds, National Museum of Natural History, Washington DC. At
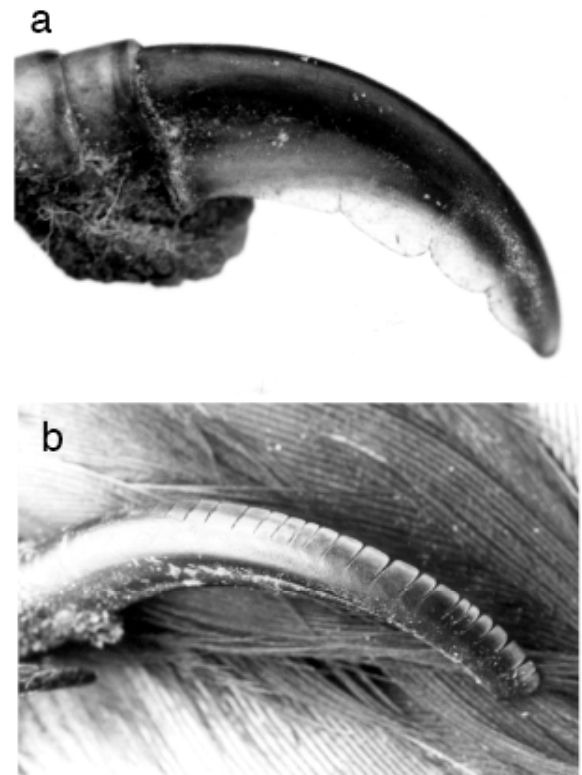

Fig. (6). Variation in the structure of the pectinate claw, ranging from (**a**) the coarsely serrated claw of the American Dipper (*Cinclus mexicanus*) to (**b**) the finely serrated claw of the Magnificent Frigatebird (*Fregata magnificens*). Photos by C. Beittel.

least one representative species from each of 118 (82%) of the 144 bird families recognized by Sibley and Ahlquist [143] was selected (haphazardly), and all of the claws of one male and one female specimen were examined under 6x magnification. Skins of species noted in the literature to have a pectinate claw were also examined [138, 144-146] . A pectinate claw was considered to be present if any portion of any claw was serrate. If a pectinate claw was detected in a given family during the initial survey, at least one representative species from every available genus in this family was subsequently examined to assess within family variation (5 males and 5 females were examined when possible).

Most birds lack a pectinate claw. Only 17 of 118 families contained individuals with pectinate claws (Table **I**), and of the Passeriformes, only dippers (Cinclidae) had them (Fig **6a**). The claw has probably evolved repeatedly, given its scattered distribution across bird families. It is also variable within families; only a minority of genera possess it within most of the 17 families. For example, a pectinate claw is present in one of four genera of Heliornithidae, two of 12 genera of Scolopacidae, four of six genera of Glareolidae, four of 16 genera of Laridae, and one of ten genera of Threskiornithidae (Table **I**).

In addition to within-family variation, we discovered within-species variation in pectinate claws. In 15 species some individuals had the claw, while others lacked it (Table **I**). This intraspecific variation did not appear to be related to the sex, geographic distribution, or season in which the bird was collected. We did not examine variation in relation to the bird's age, but this would also be interesting to explore. The structure of the pectinate claw varied considerably among taxa. Pectinations ranged from scalloping, as in the American Dipper (*Cinclus mexicanus*) (Fig. **6a**), to fine serrations, as in the Magnificent Frigatebird (*Fregata magnificens*) (Fig. **6b**).

Serrations on some pectinate claws are somewhat similar to the teeth of combs designed to remove human head lice. Clay [138] believed that species with pectinate claws might be more efficient at removing lice from the head by scratching. She predicted that birds with pectinate claws would be parasitized by fewer species of head lice than those species without pectinate claws. We tested Clay's hypothesis using an analysis that compared the species richness of head lice on birds with pectinate claws to that of sister taxa without pectinate claws. We selected 14 phylogenetically independent comparisons of bird species with and without pectinate claws. We then asked a louse taxonomist colleague to tally the number of species of head lice known from each species of bird using Price *et al.* [63]. Because louse species richness is influenced by sampling effort, we corrected for this factor as described in Walther *et al.* [147].

Our analysis revealed no significant difference in the number of species of head lice on birds with and without claws (Wilcoxon signed-rank test on residuals, T = 24.5, $P = 0.15$). In eight of the 14 comparisons, the species with the pectinate claw had fewer (residual) species of head lice, and in five comparisons the reverse was true (one tie). In retrospect, it is unclear why one should necessarily expect a negative correlation between the pectinate claw and louse species richness, or a positive correlation. If richness decreases on birds that evolve pectinate claws, then selection maintaining

the claw would be relaxed, leading to disappearance of the claw. Hence, this comparative analysis is perhaps not the most convincing test of the hypothesis that pectinate claws help to control ectoparasites.

We have also investigated the relationship between louse abundance and pectinate claw morphology within species. We used 24 road-killed Barn Owls (*Tyto alba*) salvaged by colleagues along highways in southern Idaho. We counted the number of teeth on the pectinate claw of each foot (Fig **7a**), and we measured the length and width of each claw's flange. The number of lice on each owl was quantified using "body washing" [41]. Fourteen (58%) of the owls had lice, but one was missing the pectinate claw on one foot. Since we could not be sure whether this was natural, or a consequence of post-mortem road damage, this individual bird was excluded from the analysis.

There was no significant difference in the number of teeth or the length or width of the flange, between infested and uninfested owls ($n = 23$, $df = 1$, $P > 0.27$). Similarly, there was no significant relationship between the abundance of lice on infested owls, and the mean number of teeth per claw (Fig. **7c**). Finally, there was no relationship between louse abundance and mean claw length ($n = 13$, $R^2 = 0.006$, $P = 0.81$), or width ($n = 13$, $R^2 = 0.02$, $P = 0.63$). The results of this study indicate that natural variation in the size and shape of the pectinate claw does not correlate with louse prevalence or intensity, at least in the case of Barn Owls from southern Idaho.

In summary, these comparative and correlational studies indicate that the pectinate claw plays no role in parasite control. However, a more definitive test would be to conduct an experiment in which parasite populations are monitored on birds with normal claws, versus birds from which the pectinations have been removed, perhaps by filing them off. There are several common species that could be used for this experiment, such as Cattle Egrets (*Bubulcus ibis*) (Table **I**).

Bathing

Another form of maintenance behavior practiced by most birds is bathing in water.

Rothschild and Clay [4] wrote, "Bathing in water and dust and the subsequent preening helps the bird to rid itself of parasites." However, we are not aware of any evidence suggesting that water bathing has a detrimental effect on ectoparasites. If anything, it might be expected to have a positive effect, given that high humidity favors ectoparasites ranging from feather lice [37] to bacteria [70]. It is conceivable that substances detrimental to ectoparasites might be dissolved in some water sources, but we know of no support for this speculation.

Dusting

Members of at least a dozen orders of birds are known to engage in dusting (Table **II**), during which fine dirt or sand is ruffled through the plumage [148-150] (Fig. **8**). Dusting appears to remove excess feather oil that can cause matting of plumage [151-153]. It is also thought to help control ectoparasites. Several mechanisms for such control have been proposed, including (1) reducing feather lipids upon which some ectoparasites feed [152]; (2) directly dislodging para

Table I. **Occurrence of Pectinate Claws Among 1421 Study Skins of Birds Representing 278 Species in 250 Genera (118 Families, 23 Orders). Species with Pectinate Claws are in Boldface. Presence (+) or Absence (-) of a Maxillary Overhang on the Bill is also Indicated in the Final Column; Lack of a Symbol Means the Species was not Checked for an Overhang. Classification and Nomenclature Follow Sibley and Monroe [252]**

Higher Taxa	Bird Species	# With Claw/ # Examined (%)	Bill Overhang Present (+), Absent (-), or Unexamined ( )
Struthioniformes			
Struthionidae	Ostrich, *Struthio camelus*	0/2 (0)	+
Rheidae	Greater Rhea, *Rhea americana*	0/2 (0)	+
Casuariidae	Dwarf Cassowary, *Casuarius bennetti*	0/2 (0)	+
	Emu, *Dromaius novaehollandiae*	0/2 (0)	+
Apterygidae	Brown Kiwi, *Apteryx australis*	0/2 (0)	+
Tinamiformes			
Tinamiidae	Variegated Tinamou, *Crypturellus variegatus*	0/2 (0)	+
	Elegant Crested-Tinamou, *Eudromia elegans*	0/2 (0)	
Craciformes			
Cracidae	Grey-headed Chachalaca, *Ortalis cinereiceps*	0/2 (0)	+
	Blue-knobbed Curassow, *Crax alberti*	0/2 (0)	
Megapodiidae	Brown-collared Brush-turkey, *Talegalla jobiensis*	0/2 (0)	+
Galliformes			
Phasianidae	Green Peafowl, *Pavo muticus*	0/2 (0)	
	Spruce Grouse, *Dendragapus canadensis*	0/2 (0)	+
	Ruffed Grouse, *Bonasa umbellus*	0/2 (0)	
	Wild Turkey, *Meleagris gallopavo*	0/2 (0)	+
Numididae	Crested Guineafowl, *Guttera pucherani*	0/2 (0)	+
Odontophoridae	Northern Bobwhite, *Colinus virginianus*	0/2 (0)	+
Anseriformes			
Anhimidae	Southern Screamer, *Chauna torquata*	0/2 (0)	+
Anatidae	Emperor Goose, *Anser canagica*	0/2 (0)	+
	Common Teal, *Anas crecca*	0/2 (0)	
Turniciformes			
Turnicidae	Barred Buttonquail, *Turnix suscitator*	0/2 (0)	+
Piciformes			
Indicatoridae	Lesser Honeyguide, *Indicator minor*	0/2 (0)	+
Picidae	Black-cheeked Woodpecker, *Melanerpes pucherani*	0/2 (0)	
	Greater Flameback, *Chrysocolaptes lucidus*	0/2 (0)	-
Lybiidae	Green Barbet, *Stactolaema olivacea*	0/2 (0)	+
Ramphastidae	Yellow-eared Toucanet, *Selenidera spectabilis*	0/2 (0)	+
Galbuliformes			

Table 1. Contd….

Higher Taxa	Bird Species	# With Claw/ # Examined (%)	Bill Overhang Present (+), Absent (-), or Unexamined ( )
Galbulidae	Great Jacamar, *Jacamerops aurea*	0/2 (0)	+
Bucconidae	White-whiskered Puffbird, *Malacoptila panamensis*	0/2 (0)	+
Bucerotiformes			
Bucerotidae	Helmeted Hornbill, *Buceros vigil*	0/2 (0)	
	White-crowned Hornbill, *Aceros comatus*	0/2 (0)	+
Upupiformes			
Upupidae	Eurasian Hoopoe, *Upupa epops*	0/2 (0)	+
Phoeniculidae	White-headed Woodhoopoe, *Phoeniculus bollei*	0/2 (0)	+
Trogoniformes			
Trogonidae	Diard's Trogon, *Harpactes diardii*	0/2 (0)	+
Coraciiformes			
Coraciidae	Purple-winged Roller, *Coracias temminckii*	0/2 (0)	+
Leptosomidae	Courol, *Leptosomus discolor*	0/2 (0)	+
Momotidae	Turquoise-browed Motmot, *Eumomota superciliosa*	0/2 (0)	+
Todidae	Broad-billed Tody, *Todus subulatus*	0/2 (0)	+
Dacelonidae	Laughing Kookaburra, *Dacelo novaeguineae*	0/2 (0)	+
Cerylidae	Belted Kingfisher, *Megaceryle alcyon*	0/2 (0)	+
Meropidae	Madagascar Bee-eater, *Merops superciliosus*	0/2 (0)	+
Coliiformes			
Coliidae	Blue-naped Mousebird, *Urocolius macrourus*	0/2 (0)	+
Cuculiformes			
Cuculidae	Large Hawk-cuckoo, *Cuculus sparverioides*	0/2 (0)	+
Opisthocomidae	Hoatzin, *Opisthocomus hoazin*	0/2 (0)	+
Psittaciformes			
Psittacidae	Common Kaka, *Nestor meridionalis*	0/2 (0)	+
Apodiformes			
Apodidae	White-throated Swift, *Aeronautes saxatalis*	0/2 (0)	+
Hemiprocnidae	Grey-rumped Treeswift, *Hemiprocne longipennis*	0/2 (0)	+
Trochiliformes			
Trochilidae	Black-hooded Sunbeam, *Aglaeactis pamela*	0/2 (0)	-
Musophagiformes			
Musophagidae	Knysna Turaco, *Tauraco corythaix*	0/2 (0)	+
Strigiformes			
Tytonidae	**Barn Owl, *Tyto alba***	**12/12 (100)**	+
	Oriental Bay-Owl, *Phodilus badius*	**3/3 (100)**	

Table 1. Contd….

Higher Taxa	Bird Species	# With Claw/ # Examined (%)	Bill Overhang Present (+), Absent (-), or Unexamined ( )
Strigidae	Eastern Screech-Owl, *Otus asio*	0/2 (0)	+
	Great Horned Owl, *Bubo virginianus*	0/2 (0)	
	Short-eared Owl, *Asio flammeus*	0/10 (0)	
Aegothelidae	Australian Owlet-Nightjar, *Aegotheles cristatus*	0/2 (0)	+
Podargidae	Tawny Frogmouth, *Podargus strigoides*	0/10 (0)	+
Batrachostomidae	Philippine Frogmouth, *Batrachostomus septimus*	0/2 (0)	+
Steatornithidae	Oilbird, *Steatornis caripensis*	0/2 (0)	+
Nyctibiidae	Great Potoo, *Nyctibius grandis*	0/2 (0)	+
Eurostopodidae	**Great Eared-Nightjar, *Eurostopodus macrotis***	**10/10 (100)**	+
Caprimulgidae	**Short-tailed Nighthawk, *Lurocalis semitorquatus***	**9/9 (100)**	
	Common Nighthawk, *Chordeiles minor*	**10/10 (100)**	+
	Band-tailed Nighthawk, *Nyctiprogne leucopyga*	**5/5 (100)**	
	Nacunda Nighthawk, *Podager nacunda*	**10/10 (100)**	
	Paraque, *Nyctidromus albicollis*	**10/10 (100)**	
	Common Poorwill, *Phalaenoptilus nuttallii*	**10/10 (100)**	
	Ocellated Poorwill, *Nyctiphrynus ocellatus*	**2/2 (100)**	
	Whip-Poor-Will, *Caprimulgus vociferus*	**10/10 (100)**	
	Standard-winged Nightjar, *Macrodipteryx longipennis*	**2/2 (100)**	
Columbiformes			
Columbidae	Rock Pigeon, *Columba livia*	0/2 (0)	
	Pied Imperial-Pigeon, *Ducula bicolor*	0/2 (0)	+
Gruiformes			
Eurypygidae	Sunbittern, *Eurypyga helias*	0/2 (0)	+
Otididae	Black-bellied Bustard, *Eupodotis melanogaster*	0/2 (0)	+
Gruidae	Common Crane, *Grus grus*	0/2 (0)	+
Heliornithidae	Limpkin, *Aramus guarauna*	0/2 (0)	+
	African Finfoot, *Podica senegalensis*	**4/4 (100)**	
	Masked Finfoot, *Heliopais personata*	0/4 (0)	+
	Sungrebe, *Heliornis fulica*	0/10 (0)	
Psophiidae	Grey-winged Trumpeter, *Psophia crepitans*	0/2 (0)	+
Cariamidae	Red-legged Seriema, *Cariama cristata*	0/2 (0)	+
Rhynochetidae	Kagu, *Rhynochetus jubata*	0/2 (0)	+
Rallidae	King Rail, *Rallus elegans*	0/2 (0)	+
	Giant Coot, *Fulica gigantea*	0/2 (0)	

Table 1. Contd….

Higher Taxa	Bird Species	# With Claw/ # Examined (%)	Bill Overhang Present (+), Absent (-), or Unexamined ( )
Mesitornithidae	Brown Roatelo, *Mesitornis unicolor*	0/2 (0)	+
Ciconiiformes			
Pteroclidae	Lichtenstein's Sandgrouse, *Pterocles lichtensteinii*	0/2 (0)	+
Thinocoridae	Grey-breasted Seedsnipe, *Thinocorus orbignyianus*	0/2 (0)	+
Pedionomidae	Plains-Wanderer, *Pedionomus torquatus*	0/2 (0)	+
Scolopacidae	Common Snipe, *Gallinago gallinago*	0/10 (0)	
	Jack Snipe, *Lymnocryptes minimus*	0/10 (0)	
	Black-tailed Godwit, *Limosa limosa*	**10/12 (83)**	
	Long-billed Curlew, *Numenius americanus*	0/21 (0)	
	Upland Sandpiper, *Bartramia longicauda*	0/10 (0)	
	Greater Yellowlegs, *Tringa melanoleuca*	0/2 (0)	+
	Lesser Yellowlegs, *Tringa flavipes*	0/10 (0)	
	Terek Sandpiper, *Tringa cinerea*	0/10 (0)	
	Black Turnstone, *Arenaria melanocephala*	0/10 (0)	
	Short-billed Dowitcher, *Limnodromus griseus*	0/11 (0)	
	Surfbird, *Aphriza virgata*	**11/17 (65)**	
	Red Knot, *Calidris canutus*	0/10 (0)	
	Ruff, *Philomachus pugnax*	0/10 (0)	
	Red-necked Phalarope, *Phalaropus lobatus*	0/10 (0)	
Rostratulidae	Greater Painted-Snipe, *Rostratula benghalensis*	0/2 (0)	+
Jacanidae	Wattled Jacana, *Jacana jacana*	0/2 (0)	+
Chionididae	Snowy Sheathbill, *Chionis alba*	0/2 (0)	+
Burhinidae	Double-striped Thick-knee, *Burhinus bistriatus*	0/2 (0)	+
	Beach Thick-knee, *Burhinus giganteus*	0/15 (0)	
Charadriidae	Black Oystercatcher, *Haematopus bachmani*	0/2 (0)	-
	American Avocet, *Recurvirostra americana*	0/2 (0)	+
	Killdeer, *Charadrius vociferus*	0/2 (0)	
	Northern Lapwing, *Vanellus vanellus*	0/14 (0)	+
Glareolidae	**Crab Plover, *Dromas ardeola***	**7/10 (70)**	+
	Crocodile-bird, *Pluvianus aegyptius*	0/4 (0)	
	Three-banded Courser, *Rhinoptilus cinctus*	**7/7 (100)**	
	Cream-colored Courser, *Cursorius cursor*	**10/11 (91)**	
	Indian Courser, *Cursorius coromandelicus*	**2/2 (100)**	
	Collared Pratincole, *Glareola pratinicola*	**10/19 (53)**	+
	Oriental Pratincole, *Glareola maldivarum*	**10/12 (83)**	

Table 1. Contd....

Higher Taxa	Bird Species	# With Claw/ # Examined (%)	Bill Overhang Present (+), Absent (-), or Unexamined ( )
	Australian Pratincole, *Stiltia isabella*	0/5 (0)	
Laridae	South Polar Skua, *Catharacta maccormicki*	0/12 (0)	
	Pomarine Jaeger, *Stercorarius pomarinus*	0/2 (0)	+
	Long-tailed Jaeger, *Stercorarius longicaudus*	0/10 (0)	
	Black Skimmer, *Rynchops niger*	0/12 (0)	-
	Laughing Gull, *Larus atricilla*	0/12 (0)	+
	Sabine's Gull, *Xema sabini*	0/10 (0)	
	Gull-billed Tern, *Sterna nilotica*	0/10 (0)	
	Caspian Tern, *Sterna caspia*	0/10 (0)	
	Black-naped Tern, *Sterna sumatrana*	**9/10 (0)**	
	Black Tern, *Chlidonias niger*	0/10 (0)	
	Large-billed Tern, *Phaetusa simplex*	0/10 (0)	
	Brown Noddy, *Anous stolidus*	**16/20 (80)**	
	Black Noddy, *Anous minutus*	0/2 (0)	
	Blue Noddy, *Procelsterna cerulea*	**9/10 (90)**	
	Common White-Tern, *Gygis alba*	0/10 (0)	
	Inca Tern, *Larosterna inca*	**6/7 (86)**	
	Dovekie, *Alle alle*	0/10 (0)	
	Razorbill, *Alca torda*	0/2 (0)	+
	Pigeon Guillemot, *Cepphus columba*	0/10 (0)	
	Tufted Puffin, *Fratercula cirrhata*	0/2 (0)	
Accipitridae	Osprey, *Pandion haliaetus*	0/2 (0)	+
	Mississippi Kite, *Ictinia mississippiensis*	0/2 (0)	+
	Cooper's Hawk, *Accipiter cooperii*	0/2 (0)	
Sagittariidae	Secretary-Bird, *Sagittarius serpentarius*	0/2 (0)	+
Falconidae	Crested Caracara, *Polyborus plancus*	0/2 (0)	+
	American Kestrel, *Falco sparverius*	0/11 (0)	
Podicipedidae	**White-tufted Grebe, *Rollandia rolland***	**7/8 (88)**	
	Australasian Grebe, *Tachybaptus novaehollandiae*	**7/7 (100)**	
	Least Grebe, *Tachybaptus dominicus*	**10/10 (100)**	
	Pied-billed Grebe, *Podilymbus podiceps*	**12/12 (100)**	+
	Western Grebe, *Aechmophorus occidentalis*	**12/12 (100)**	
Phaethontidae	Red-tailed Tropicbird, *Phaethon rubricauda*	0/12 (0)	+
	White-tailed Tropicbird, *Phaethon lepturus*	0/10 (0)	
Sulidae	**Northern Gannet, *Morus bassanus***	**9/9 (100)**	+

Higher Taxa	Bird Species	# With Claw/ # Examined (%)	Bill Overhang Present (+), Absent (-), or Unexamined ( )
	Masked Booby, *Sula dactylatra*	**2/2 (100)**	
	Brown Booby, *Sula leucogaster*	**11/11 (100)**	
Anhingidae	**Anhinga, *Anhinga anhinga***	**10/10 (100)**	
	Oriental Darter, *Anhinga melanogaster*	**2/2 (100)**	-
Phalacrocoracidae	**Little Cormorant, *Phalacrocorax niger***	**2/2 (100)**	
	Brandt's Cormorant, *Phalacrocorax penicillatus*	**10/10 (100)**	
	Neotropic Cormorant, *Phalacrocorax brasilianus*	**2/2 (100)**	+
	Double-crested Cormorant, *Phalacrocorax auritus*	**10/10 (100)**	
Ardeidae	**Great Blue Heron, *Ardea herodias***	**12/12 (100)**	-
	Cattle Egret, *Bubulcus ibis*	**13/13 (100)**	
	Chinese Pond-Heron, *Ardeola bacchus*	**10/10 (100)**	
	Yellow-crowned Night-Heron, *Nyctanassa violacea*	**10/10 (100)**	
	Black-crowned Night-Heron, *Nycticorax nycticorax*	**10/10 (100)**	
	Boat-billed Heron, *Cochlearius cochlearius*	**10/10 (100)**	
	Bare-throated Tiger-Heron, *Tigrisoma mexicanum*	**10/10 (100)**	
	White-crested Bittern, *Tigriornis leucolophus*	**2/2 (100)**	
	Zigzag Heron, *Zebrilus undulatus*	**1/1 (100)**	
	Stripe-backed Bittern, *Ixobrychus involucris*	**4/4 (100)**	
	Great Bittern, *Botaurus stellaris*	**8/8 (100)**	
Scopidae	**Hamerkop, *Scopus umbretta***	**10/10 (100)**	+
Phoenicopteridae	Greater Flamingo, *Phoenicopterus ruber*	0/12 (0)	+
Threskiornithidae	White Ibis, *Eudocimus albus*	0/10 (0)	
	White-faced Ibis, *Plegadis chihi*	**12/12 (100)**	
	Plumbeous Ibis, *Theristicus caerulescens*	0/5 (0)	
	Buff-necked Ibis, *Theristicus caudatus*	0/9 (0)	
	Green Ibis, *Mesembrinibis cayennensis*	0/10 (0)	
	Hadada Ibis, *Bostrychia hagedash*	0/12 (0)	
	Wattled Ibis, *Bostrychia carunculata*	0/5 (0)	
	Spot-breasted Ibis, *Bostrychia rara*	0/1 (0)	
	Bald Ibis, *Geronticus calvus*	0/2 (0)	
	Sacred Ibis, *Threskiornis aethiopicus*	0/10 (0)	
	Straw-necked Ibis, *Threskiornis spinicollis*	0/5 (0)	
	White-shouldered Ibis, *Pseudibis davisoni*	0/13 (0)	+
	Giant Ibis, *Pseudibis gigantea*	0/4 (0)	
	Crested Ibis, *Nipponia nippon*	0/6 (0)	

Table 1. Contd….

Higher Taxa	Bird Species	# With Claw/ # Examined (%)	Bill Overhang Present (+), Absent (-), or Unexamined ( )
	Roseate Spoonbill, *Ajaia ajaja*	0/12 (0)	
Pelecanidae	**Shoebill, *Balaeniceps rex***	**2/2 (100)**	+
	American White Pelican, *Pelecanus erythrorhynchos*	**3/11 (27)**	
	Brown Pelican, *Pelecanus occidentalis*	**11/11 (100)**	+
Ciconiidae	Turkey Vulture, *Cathartes aura*	0/2 (0)	+
	Andean Condor, *Vultur gryphus*	0/2 (0)	
	White Stork, *Ciconia ciconia*	0/9 (0)	+
	Lesser Adjutant, *Leptoptilos javanicus*	0/2 (0)	
Fregatidae	**Magnificent Frigatebird, *Fregata magnificens***	**12/12 (100)**	+
	Great Frigatebird, *Fregata minor*	**10/10 (100)**	
Spheniscidae	Gentoo Penguin, *Pygoscelis papua*	0/12 (0)	+
	Jackass Penguin, *Spheniscus demersus*	0/2 (0)	
Gaviidae	Red-throated Loon, *Gavia stellata*	0/7 (0)	
	Arctic Loon, *Gavia arctica*	0/6 (0)	+
	Common Loon, *Gavia immer*	0/12 (0)	
	Yellow-billed Loon, *Gavia adamsii*	0/4 (0)	
Procellariidae	Southern Fulmar, *Fulmarus glacialoides*	0/2 (0)	+
	Juan Fernandez Petrel, *Pterodroma externa*	0/2 (0)	
	Common Diving-Petrel, *Pelecanoides urinatrix*	0/2 (0)	+
	Black-footed Albatross, *Diomedea nigripes*	0/2 (0)	+
	Light-mantled Albatross, *Phoebetria palpebrata*	0/2 (0)	
	Leach's Storm-Petrel, *Oceanodroma leucorhoa*	0/2 (0)	+
Passeriformes			
Acanthisittidae	Rifleman, *Acanthisitta chloris*	0/2 (0)	+
Pittidae	Ivory-breasted Pitta, *Pitta maxima*	0/2 (0)	+
Eurylaimidae	Dusky Broadbill, *Corydon sumatranus*	0/2 (0)	+
Philepittidae	Velvet Asity, *Philepitta castanea*	0/2 (0)	+
Tyrannidae	Highland Elaenia, *Elaenia obscura*	0/2 (0)	+
	Black-necked Red-Cotinga, *Phoenicircus nigricollis*	0/2 (0)	+
	Rufous-tailed Plant-cutter, *Phytotoma rara*	0/2 (0)	+
	Sharpbill, *Oxyruncus cristatus*	0/2 (0)	+
	Long-tailed Manakin, *Chiroxiphia linearis*	0/2 (0)	+
Thamnophilidae	Black-backed Antshrike, *Sakesphorus melanonotus*	0/2 (0)	+
Furnariidae	Azara's Spinetail, *Synallaxis azarae*	0/2 (0)	+
	Long-billed Woodcreeper, *Nasica longirostris*	0/2 (0)	+

Table 1. Contd….

Higher Taxa	Bird Species	# With Claw/ # Examined (%)	Bill Overhang Present (+), Absent (-), or Unexamined ( )
Rhinocryptidae	Moustached Turca, *Pteroptochos megapodius*	0/2 (0)	+
Climacteridae	White-throated Treecreeper, *Cormobates leucophaeus*	0/2 (0)	+
Menuridae	Superb Lyrebird, *Menura novaehollandiae*	0/2 (0)	+
	Rufous Scrub-bird, *Atrichornis rufescens*	0/2 (0)	+
Ptilonorhynchidae	Green Catbird, *Ailuroedus crassirostris*	0/2 (0)	+
Meliphagidae	Wattled Honeyeater, *Foulehaio carunculata*	0/2 (0)	+
Irenidae	Golden-fronted Leafbird, *Chloropsis aurifrons*	0/2 (0)	+
Vireonidae	Yellow-throated Vireo, *Vireo flavifrons*	0/2 (0)	+
Corvidae	Daurian Jackdaw, *Corvus dauuricus*	0/2 (0)	+
	Raggiana Bird-of-Paradise, *Paradisaea raggiana*	0/2 (0)	+
	Grey Currawong, *Strepera versicolor*	0/2 (0)	+
	Dusky Wood-Swallow, *Artamus cyanopterus*	0/2 (0)	+
	Black-hooded Oriole, *Oriolus xanthornus*	0/2 (0)	+
	Bar-bellied Cuckoo-Shrike, *Coracina striata*	0/2 (0)	+
	Square-tailed Drongo, *Dicrurus ludwigii*	0/2 (0)	+
	Magpie-Lark, *Grallina cyanoleuca*	0/2 (0)	+
	White Helmetshrike, *Prionops plumatus*	0/2 (0)	+
	Rufous Vanga, *Schetba rufa*	0/2 (0)	+
	Coral-billed Nuthatch, *Hypositta corallirostris*	0/2 (0)	+
Callaeatidae	Kokako, *Callaeas cinerea*	0/2 (0)	+
Bombycillidae	Palmchat, *Dulus dominicus*	0/2 (0)	+
	Grey Silky-Flycatcher, *Ptilogonys cinereus*	0/2 (0)	+
	Cedar Waxwing, *Bombycilla cedrorum*	0/2 (0)	+
Cinclidae	**White-throated Dipper, *Cinclus cinclus***	**3/15 (20)**	
	Brown Dipper, *Cinclus pallasii*	**3/22 (14)**	
	American Dipper, *Cinclus mexicanus*	**10/20 (50)**	+
Muscicapidae	Swainson's Thrush, *Catharus ustulatus*	0/20 (0)	
	White-bellied Short-wing, *Brachypteryx major*	0/2 (0)	+
Sturnidae	Red-winged Starling, *Onychognathus morio*	0/2 (0)	+
	Grey Catbird, *Dumetella carolinensis*	0/2 (0)	+
Sittidae	Wood Nuthatch, *Sitta europaea*	0/2 (0)	+
	Wallcreeper, *Tichodroma muraria*	0/2 (0)	+
Certhiidae	Eurasian Tree-Creeper, *Certhia familiaris*	0/2 (0)	+
	Cactus Wren, *Campylorhynchus brunneicapillus*	0/2 (0)	+
Paridae	African Penduline-Tit, *Anthoscopus caroli*	0/2 (0)	+

Table 1. Contd….

Higher Taxa	Bird Species	# With Claw/ # Examined (%)	Bill Overhang Present (+), Absent (-), or Unexamined ( )
	Carolina Chickadee, *Parus carolinensis*	0/2 (0)	+
Aegithalidae	Bushtit, *Psaltriparus minimus*	0/2 (0)	+
Hirundinidae	Caribbean Martin, *Progne dominicensis*	0/2 (0)	+
Pycnonotidae	Red-whiskered Bulbul, *Pycnonotus jocosus*	0/2 (0)	+
Zosteropidae	White-breasted White-eye, *Zosterops abyssinicus*	0/2 (0)	+
Sylviidae	Gray's Warbler, *Locustella fasciolata*	0/2 (0)	+
	Ferruginous Babbler, *Trichastoma bicolor*	0/2 (0)	+
	Brown Parrotbill, *Paradoxornis unicolor*	0/2 (0)	+
	Stripe-sided Rhabdornis, *Rhabdornis mysticalis*	0/2 (0)	+
	Wrentit, *Chamaea fasciata*	0/2 (0)	+
Alaudidae	Austral-Asian Lark, *Mirafra javanica*	0/2 (0)	+
Nectariniidae	Yellow-sided Flowerpecker, *Dicaeum aureolimbatum*	0/2 (0)	+
	Purple-throated Sunbird, *Nectarinia sperata*	0/2 (0)	+
Passeridae	Russet Sparrow, *Passer rutilans*	0/2 (0)	+
	Yellow Wagtail, *Motacilla flava*	0/2 (0)	+
	Alpine Accentor, *Prunella collaris*	0/2 (0)	+
	White-breasted Negrofinch, *Nigrita fusconota*	0/2 (0)	+
Fringillidae	Iiwi, *Vestiaria coccinea*	0/2 (0)	+
	Nashville Warbler, *Vermivora ruficapilla*	0/2 (0)	+
	Grass-green Tanager, *Chlorornis riefferii*	0/2 (0)	+
	Swallow Tanager, *Tersina viridis*	0/2 (0)	+
	Grey-bellied Flower-piercer, *Diglossa carbonaria*	0/2 (0)	+
	Rose-breasted Grosbeak, *Pheucticus ludovicianus*	0/2 (0)	+
	Audubon's Oriole, *Icterus graduacauda*	0/2 (0)	+

sites [154, 155]; (3) plugging parasite spiracles (breathing pores), leading to poor respiration; and (4) abrading the cuticle, leading to desiccation [132,149]. Desiccation is an intriguing possibility, given that inert dusts, such as volcanic ash, are known to kill insects by abrading their cuticles [156, 157]. Surprisingly, however, no rigorous test of this hypothesis has been conducted. Indeed, to our knowledge, no direct test of the impact of dusting behavior on ectoparasites has ever been performed. Such a study is feasible because many birds dust readily in captivity [153, 158-161]. It should be possible to "seed" parasite-free birds with identical numbers of parasites, such as feather lice, and then provide experimental birds with containers of dust. It might even be possible elicit dusting behavior in control birds by providing them a substance that is known to be harmless to ectoparasites.

Sunning

At least 50 families of birds are known to adopt stereotyped postures and expose themselves to solar radiation, which is known as "sunning" [162] (Fig. **9**). Sunning is thought to control ectoparasites, either by killing them directly or by increasing their vulnerability to preening as they try to escape from the heat [163]. Sunning has intriguing parallels to "behavioral fever," which is when ectothermic animals exploit warm microclimates to combat parasites [164-166]. For example, in response to bacterial infections, Desert Iguanas (*Dipsosaurus dorsalis*) move to warm microclimates and generate a 2°C fever, which increases their survival [167]. Goldfish (*Carassius auratus*) increase their survival in the face of bacterial infection by frequenting warm water, which elevates their body temperature [168].

In warm environments many birds sun to the point of apparent hyperthermia [163, 169-172]. Some birds sun when it is hottest outside, not when it is coolest, suggesting that such sunning has little or nothing to do with conserving body heat. For example, Black Noddies (*Anous minutus*) in tropical Australia sun most frequently during periods of high temperature rather than low temperature [163], and several species of swallows sun only on hot summer days [172 -
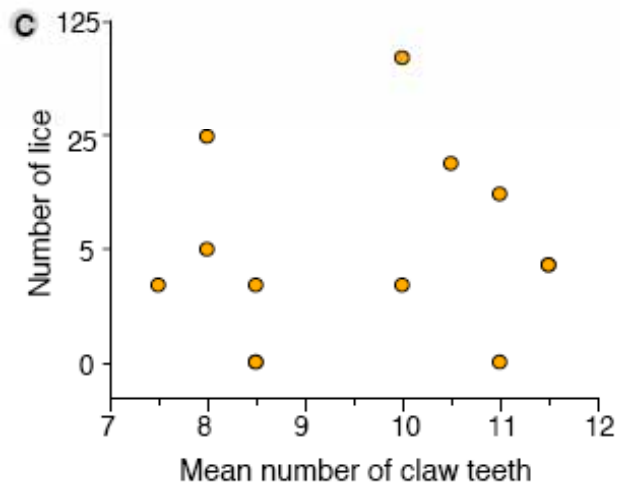
Fig. (7). Barn Owls (*Tyto alba*) have a pectinate claw on their middle toe (**a**, photo by S. Bush), which is used in scratching (**b**, photo by Mike Read, naturepl.com). One adaptive function of this claw may be to remove ectoparasites. We studied natural variation in louse load and pectinate claw morphology of Barn Owls from Southern Idaho. (**c**) The relationship between the number of lice and the mean number of teeth per claw is not significant ($n = 13$, $R^2 = 0.01$, $P = 0.72$).

175]. Both noddies and swallows pant during these sunning episodes, indicating heat stress.

Table II. Examples of Birds Known to Dust; from Moyer and Clayton [22]

STRUTHIONIFORMES	STRIGIFORMES
STRUTHIONIDAE	STRIGIDAE
Ostrich *(Struthio)*	Owl
RHEIFORMES	**CAPRIMULGIFORMES**
RHEIDAE	CAPRIMULGIDAE
Rhea *(Rhea)*	Nightjar
FALCONIFORMES	**COLIIFORMES**
ACCIPITRIDAE	COLIIDAE
Hawk	Mousebird
FALCONIDAE	**CORACIIFORMES**
Falcon	MOMOTIDAE
GALLIFORMES	Motmot
PHASIANIDAE	MEROPIDAE
Grouse *(Lagopus)*	Bee-eater
Bobwhite *(Colinus)*	CORACIIDAE
Fowl *(Gallus)*	Roller
Quail *(Coturnix)*	UPUPIDAE
Partridge *(Alectoris)*	Hoopoe
Pheasant *(Chrysolophus, Phasianus)*	BUCEROTIDAE
GRUIFORMES	Hornbill
TURNICIDAE	**PASSERIFORMES**
Buttonquail	ALAUDIDAE
CARIAMIDAE	Lark
Seriema	TROGLODYTIDAE
OTIDIDAE	Wren
Bustard	TIMALIIDAE
CHARADRIIFORMES	Wrentit *(Chamaea)*
THINOCORIDAE	**EMBERIZIDAE**
Seedsnipe	Sparrow (Spizella, Pooecetes)
COLUMBIFORMES	ICTERIDAE
COLUMBIDAE	Grackle *(Quiscalus)*
Dove	PLOCEIDAE
PTEROCLIDIDAE Sandgrouse	Sparrow (Passer, Petronia, Montifringilla)
	GRALLINIDAE
	Chough *(Corcorax)*

Fig. (8). Southern Ground-hornbill (*Bucorvus leadbeateri*) dusting itself. Photo by T. Laman (naturepl.com).

Fig. (9). White-rumped Shama (*Copsychus malabaricus*) sunning itself. Photo by Michael Luckett (fotolia.com).

Two lines of evidence are consistent with the hypothesis that sunning helps control ectoparasites. Blem and Blem [172] compared the rate of sunning in Violet-green Swallows (*Tachycinete thalassina*); experimentals were fumigated to remove ectoparasites, while controls were not. Fumigated birds sunned less frequently than controls [172], suggesting that the motivation to sun decreases with a reduction in ectoparasite load. Moyer and Wagenbach [163] exposed lice, placed on model Black Noddy wings, to sun and shade. The duration of exposure was typical of those sunning bouts, and the temperature of the model wings did not exceed that of the wings of actual sunning noddies (temperature was measured from a distance with an infrared thermometer). Significantly more lice died in the sun than in the shade.

Although this work suggests that one adaptive function of sunning is ectoparasite control, additional research is needed to determine exactly how effective sunning is for controlling different parasites, and under different conditions. For example, it would be interesting to explore whether sunning by birds with dark plumage is more effec-

tive than sunning by birds with light plumage. Preliminary work by one of us (BRM) indicates that dark feathers heat up more rapidly, and to a higher temperature, than white feathers when exposed to the sun. Furthermore, Rock Pigeon wing lice abandon interbarb refuges of dark feathers sooner than those on white feathers when exposed sunlight. It is tempting to speculate that one cost associated with the evolution of light colored plumage might be that light colored birds have more difficulty controlling ectoparasites by sunning.

Anointing

Another hypothesized defense against ectoparasites is anointing behavior, during which birds and mammals "...apply scent-laden materials to their integument" [25]. A particularly intriguing form of anointing is "anting" behavior, during which birds crush and smear ants on their feathers (active anting), or allow ants to crawl through the plumage (passive anting) [176-181] (Fig. **10**). Anting has been re-

ported in over 200 bird species, most of them Passeriformes [24, 182, 181]. The fact that birds ant exclusively with ants that secrete formic acid, or other pungent fluids, suggests that anting may kill or deter ectoparasites.

Among the most compelling observations suggesting a role of anting in parasite control is Dubinin's [183] account of anting Meadow Pipits (*Anthus pratensis*) (cited in Kelso and Nice, [179]). Dubinin observed four pipits grasping Wood Ants (*Formica rufa*) in their bills and rubbing them through their plumage. He collected these birds shortly thereafter and examined them along with several other pipits that had not been seen anting. The wing feathers of the anting birds were splotched with liquid that Dubinin presumed to be formic acid. Feather mites (*Pterodectes* spp.) on these birds were actively moving across the feathers, and a large proportion of the mites in the moist regions of the feathers were dead. In contrast, mites on the four non-anting birds were positioned between the feather barbs and were undisturbed. More than 25% (163 of 642) of live mites taken
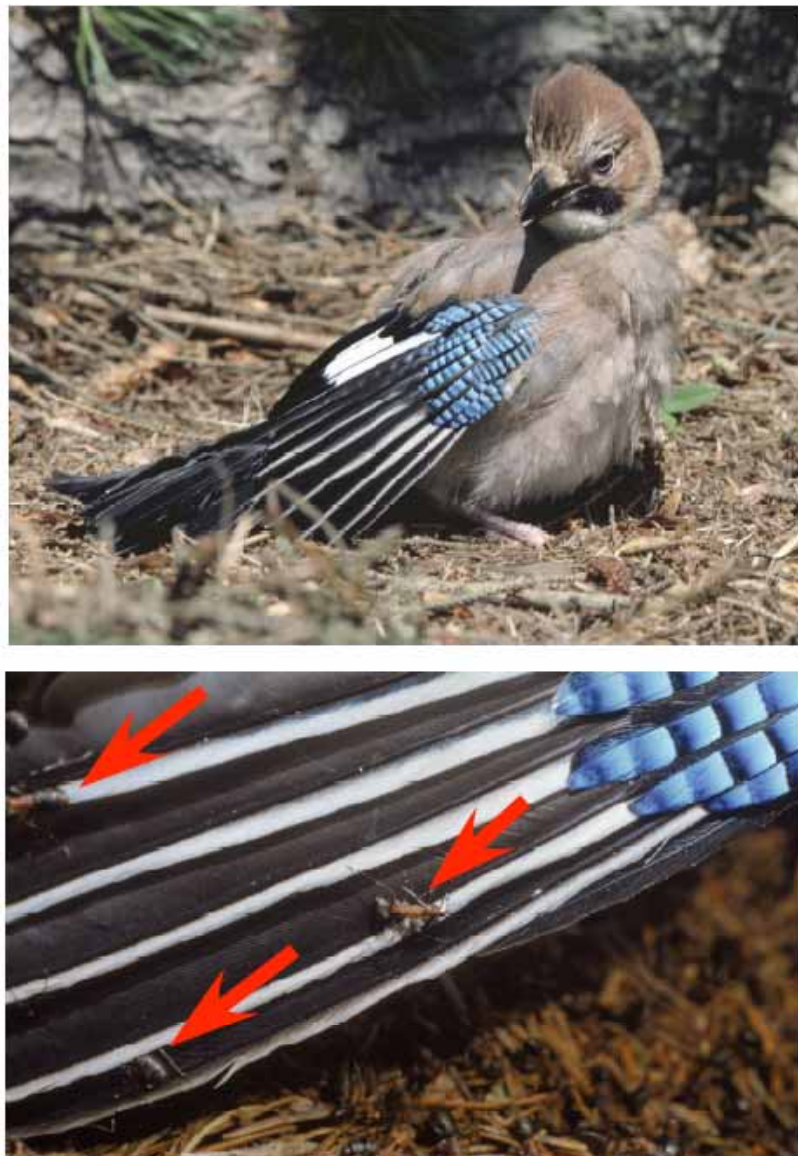

Fig. (10). Jay (*Garrulus glandarius*) anting. Ants (arrows) crawling on the primaries. Photos by A. Cooper (naturepl.com).

from the anting birds died within 12 hr, compared with less than 1% (5 of 758) of those taken from the non-anting birds. Dubinin's observations are consistent with the hypothesis that anting helps control ectoparasites. However, Dubinin's work certainly does not represent a rigorous test of the hypothesis.

Clayton and Wolfe [181] provided a brief synopsis of the results of a field experiment designed to test the impact of anting by European Starlings *(Sturnus vulgaris)* on feather mites and lice. The experiment was conducted using 32 wild-caught birds, half of which were placed in cages (0.8x0.8x0.9 m) directly over natural Wood Ant *(Formica rufa)* trails, while the other half (controls) were placed in identical cages adjacent to ant trails ([184]; Bennett *et al.* unpublished ms). The bottomless cages allowed birds direct access to ants on the ground. The lower portions of the cages were coated with Fluon™, a Teflon-coated liquid that dries to a film ants cannot cross, thus preventing them from swarming up the cage and disturbing the bird. Experimental birds (over ant trails) were observed in frequent anting behavior over the course of the field trials, which lasted three days (birds were removed from the field enclosures at night). By the end of the field trials, experimental birds had plumage that smelled strongly of formic acid. In contrast, control birds did not have access to ant trails and they seldom engaged in anting-like behavior. They did not smell of formic acid at the end of the field trials.

Ectoparasite abundance was quantified on all birds using the visual examination method [41] both the day before field trials started, and again three days after the conclusion of the field trials. The three-day interval allowed birds time to preen dead or damaged ectoparasites, while allowing parasites time to return to normal plumage microhabitats prior to the second visual census. All feather mites visible on each primary and secondary feather of each outstretched wing, as well as mites on the tail feathers, were counted with the aid of a 2x magnifying headset. All of the mites were *Pteronyssoides truncates*. Lice were quantified by tallying only those observed during timed visual counts of specific body regions, including the crown, face, gulum, breast, pectoral region, nape, back (60 s each), as well as the flank and rump (30 s each). Four species of lice were observed: *Menacanthus eurysternus*, *Myrsidea cucullaris*, *Brueelia nebulosa*, and *Sturnidoecus sturni*. Parasite counts were done "blind" to treatment by using Vicks™ Vaporub in the nostrils of the person doing the parasite counts. A few birds escaped or died over the course of the experiment, which left complete data sets for 25 of the 32 birds (14 experimentals and 11 controls).

Despite the fact that experimental birds anted extensively over the three day field trials, there was no significant impact of anting on mites (Fig. **11a**), nor on lice (Fig. **11b**). Since the post-treatment census occurred three days after the final day of formic acid exposure, there should have been ample time for any effect of acid on parasites to occur. *In vitro* studies show that formic acid kills more than 90% of ectoparasites within 15 minutes [177]. In addition to comparing the number of ectoparasites on birds, the condition of all of the lice was noted, as well as a haphazard sample of 25 mites on each wing of each of 14 birds (under magnification). All of the parasites appeared to be in good condition.
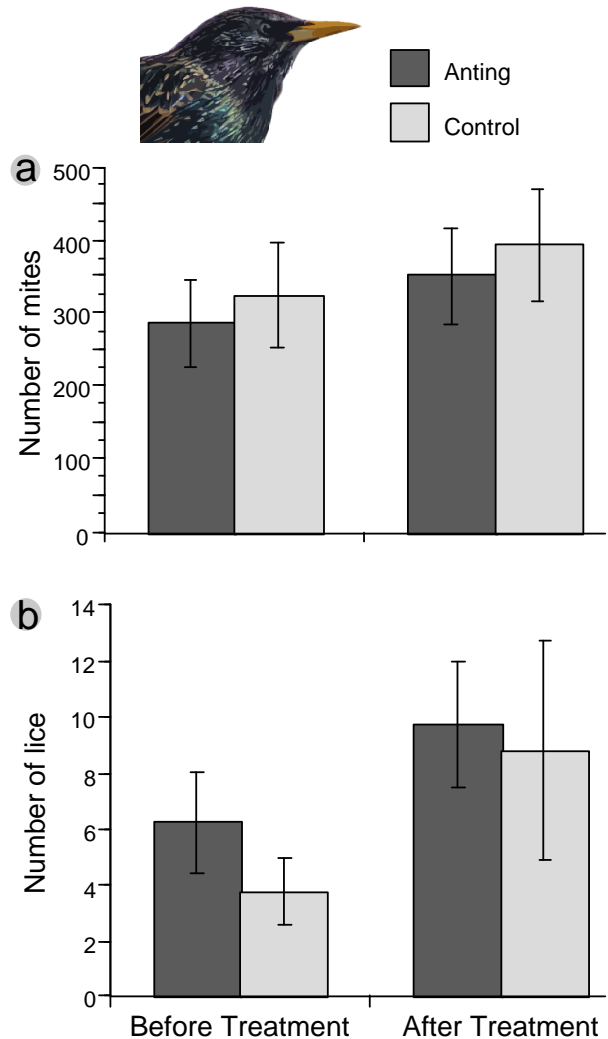

Fig. (11). Mean (± SE) number of (**a**) feather mites and (**b**) lice on European Starlings (*Sturnus vulgaris*) before and after experimental birds were allowed to engage in anting behavior. There was no significant relationship between anting and either mite or louse loads.

These observations indicate that anting has little or no effect on mites or lice, at least on starlings. Interestingly, the number of mites and lice actually increased between the first and second visual censuses, presumably as a result of improvement on the part of the observer, and/or displacement of ectoparasites from refugia where they may have been hiding prior to the initial census and field procedures. It would be worthwhile repeating this experiment using birds that are euthanized and washed after the experiment in order to obtain more accurate estimates of total ectoparasite abundance [41].

Ehrlich *et al.* [185] proposed that anting behavior helps control harmful plumage bacteria or fungi. In a series of inhibition trials, Revis and Waller [186] tested polar and non-polar ant secretions, as well as pure formic acid, for bactericidal and fungicidal effects. Although the formic acid strongly inhibited all bacteria and fungal hyphae tested, concentrations of formic acid approximating those actually found in the bodies of formicine ants did not have an effect.

There was also no detectable effect of hexane ant-chemical extracts, nor ant suspensions in deionized water, on plumage microbes. These results suggest that anting is unlikely to control microbes. Nevertheless, an "*in vivo*" experiment, analogous to the one with starlings described above, is needed for a more definitive test.

Birds also anoint themselves with a bizarre list of other items, including millipedes [187, 188], caterpillars [189], garlic snails [190], bombardier beetles [191], citrus fruits [192, 193, 194], walnut juice [195], flowers [196, 197], lawn chemicals [198] and even mothballs placed in gardens to repel vegetarian pests [199-201]. Many of these items reportedly have anti-parasite properties [201], but few careful tests have been carried out.

Clayton and Vernon [194] performed one such test. The authors observed a Common Grackle (*Quiscalus quiscula*) anointing itself with half a lime fruit. The bird pecked at the fruit repeatedly, then preened itself while holding pieces of lime in its bill. The authors subsequently tested the effect of lime on pigeon lice in the lab. Although lime juice had no effect, exposure to vapor from the lime rind rapidly killed the lice. This result is not surprising, given that lime peel contains D-limonene, a monoterpene present at high concentrations in the peel oil of many citrus fruits, and which is known to be toxic to a wide variety of arthropods [194]. Nevertheless, the hypothesis that birds use citrus peel, or any of the other substances listed above, as a means for actually controlling their ectoparasites is still in need of *in vivo* testing. Experiments using parasitized captive birds engaging in anointing behavior would be informative.

Cosmetic behavior

At least 13 bird families are known to apply "cosmetic" substances to their bodies [202]. The function of this cosmetic behavior is largely unknown, but some examples suggest that the behavior may help combat ectoparasites. For example, Bearded Vultures (*Gypaetus barbatus*) stain their plumage with soils that are rich in iron oxide Fig. (**12**), [203, 204]. They either rub their plumage in dry red soil, or rub damp red soil into their plumage following a bath. Vultures spend as much as an hour applying the soil [204]. Captive Bearded Vultures return to their nests following episodes of soil bathing and rub their newly stained feathers on eggs and offspring [205]. Frey and Roth-Callies [203] [cited in Negro *et al.* [204]] tested for an effect of iron oxide on lice, but there was no significant difference in the survival of lice exposed to a suspension containing iron oxide vs. water controls. Arlettaz *et al.* [205] argued that, since Bearded Vultures are often the last species to feed upon carcasses, they may also be exposed to dangerous quantities of bacteria left behind by earlier scavengers. The oxidative properties in iron oxide rich soils may reduce the negative effects of such bacteria on egg development and nestling growth [205]. However, experimental tests are needed to investigate the effects of iron oxides on bacterial strains.

In a recent review of cosmetic coloration, Delhey and colleagues [202] describe two other kinds of cosmetic behavior that might deter ectoparasites. Shortly before breeding, the Japanese Crested Ibis (*Nipponia nippon*) secretes a black substance from the skin of its head and neck, which is then preened into the plumage [206]; whether this substance has

Fig. (12). Bearded vultures (*Gypaetus barbatus*) stain their plumage with soil rich in iron oxide; captive birds without access to such soil have white underparts. Photo by Richard Bartz (commons.wikimedia.org).

any effect on ectoparasites has not been tested. Other species of birds, such as Cinnamon Bitterns (*Ixobrychus cinnamomeus*) and Night Herons (*Nycticorax nycticorax*), apply powder down - specialized feathers that degrade into a powder - to their head and neck regions [207, 208]. The powder down alters the color of these regions, suggesting an intraspecific signaling function. However, since these are also the areas that the bird cannot reach with its bill to preen, it is conceivable that the application of substances to these regions could also help deter parasites. No test of this hypothesis has been conducted.

NEST MAINTENANCE BEHAVIOR

In addition to combating ectoparasites on their bodies, birds must defend themselves from parasites in their nests. Parasites such as fleas, flies, true bugs, and some mites spend portions of their life cycle in the nest material and make brief forays onto nestlings and parents to feed [5]. It is not uncommon for such parasites to kill nestlings or fledglings [45, 209]. Birds have several kinds of nest maintenance behavior that may deter ectoparasites.

Territoriality and Colony Size

Parasite transmission is often more efficient in dense host populations [210]. For this reason, antisocial behavior, such as territoriality, may provide benefits in terms of defense against ectoparasites [211]. Similarly, in colonial species, nesting in smaller colonies can help control ectoparasites because parasite load is proportional to colony size [212].

Nest Site Avoidance

The most effective defense against nest parasites may be to simply avoid them in the first place. A number of studies have shown that birds can detect and avoid nesting (and roosting) sites containing ectoparasites [24, 212-221]. For example, Oppliger *et al.* [214] experimentally investigated the effects of the hematophagous Hen Flea (*Ceratophyllus gallinae*) on nest-site choice in the Great Tit *(Parus major)*. When offered a choice between adjacent nest boxes, one flea-infested and one flea-free, significantly more Great Tits chose parasite-free boxes.

Cliff Swallows (*Hirundo pyrrhonota*) show a similar preference for uninfested nests. Brown and Brown [212] noted that during the early spring, overwintering fleas (*Ceratophyllus celsus*) and Swallow Bugs (*Oeciacus vicarius*) congregate in plain view at the entrances of old swallow nests. This location is a good position from which to infest swallows that enter the nest, or even swallows that come too close to inspect the nest opening, allowing the fleas to leap onto such birds. When they return from the wintering grounds, Cliff Swallows often hover a few centimeters in front of old nests, rather than entering them. This behavior appears to allow the birds to safely inspect the nest opening for ectoparasites [212].

Another way in which birds can avoid ectoparasites is by choosing to breed when fewer ectoparasites are present at nest sites. For example, Great Tits delay reproduction to minimize infestations by Hen Fleas [222], which - like swallow fleas - overwinter in the nest cavity. If a host does not use the cavity, the fleas emigrate [223]. Hence, by delaying reproduction, birds can reduce exposure to fleas. In an experimental test of this delayed-reproduction hypothesis, Oppliger *et al.* [214] found that Great Tits whose nest boxes were infested with fleas started laying eggs 11 days later than birds occupying uninfested nest boxes.

Nest Sanitation

In some cases, birds are known to engage in nest "sanitation" behavior [24]. Female Great Tits and Blue Tits (*Parus caeruleus*) exhibit this behavior, which Christe *et al.* [224] described as "a period of active search with the head dug into the nest material." It is unclear whether this kills or simply disperses ectoparasites, but female Great Tits devote significantly more time to sanitation in flea-infested nests than in uninfested nests [224]. Similarly, female Blue Tits spend more time in sanitation of nests infested with blowfly (*Protocalliphora*) larvae [225] or fleas [226] than in uninfested nests [225]. Another form of nest sanitation is to clean out nests that have been used before; for example, male House Wrens (*Troglodytes aedon*) remove old nest material from their nest boxes prior to each reproductive bout. Pacejka *et al.* [227] showed that this behavior effectively reduces the abundance of mites (*Dermanyssus*) in the nest.

Nest Fumigation

An interesting purported adaptation for controlling ectoparasites in nests is the use of aromatic vegetation to fumigate the nest [24, 25, 73, 181, 228]. Clark and Mason [229] showed that European Starlings (*Sturnus vulgaris*) select species of plants that contain volatile chemicals with antibac-

terial and insecticidal properties. The authors found that the hatching success of lice (*Menacanthus* sp.) and the growth of several strains of bacteria (*Streptococcus aurealis, Staphylococcus epidermis*, and *Pseudomonas aeruginosa*) were significantly reduced when exposed to volatiles from plants preferred by starlings, compared to a random sample of nearby vegetation. A subsequent study showed that emergence of a mite (*Ornithonyssus sylviarum*) was significantly decreased when wild carrot (*Daucus carota*) or fleabane (*Erigeron philadelphicus*) was added to the nesting material [230].

A recent study of Bonelli's Eagles (*Hieraaetus fasciatus*) showed that nests with higher percentages of pine greenery had fewer blow fly larvae (*Protocalliphora*) and higher host breeding success [231]. The results of this observational study are intriguing, but they have not yet been tested by experimental manipulation. In another study, which did use an experimental approach, Shutler and Campbell [232], added yarrow (*Achillea millefolium*) to the nests of Tree Swallows (*Tachycineta bicolor*); this manipulation reduced the number of fleas in the nest by half, compared to control nests. However, the authors did not find that the use of green vegetation and the subsequent reduction in fleas had any effect on nestling survival or fledgling success. Gwinner *et al.* [233] manipulated green vegetation in European Starling (*Sturnus vulgaris*) nests and found no difference in the number of ectoparasites (mites, lice, fleas) between experimental and control nests; however, nestlings from nests with vegetation did have higher red blood cell counts and body masses than nestlings from nests without vegetation. The authors argued that the vegetation may stimulate the immune system of nestlings, which could ameliorate the detrimental effects of blood-feeding ectoparasites, even though it did not change parasite number, per se. This hypothesis has not been tested.

Yet another recent study, this one with Blue Tits (*Cyanistes caeruleus*), showed that in enlarged broods, nestling mass gain was positively affected by the addition of green vegetation [234]. However, there was no difference in fledgling body mass between chicks in nests with added vegetation versus control nests. In conclusion, these various studies reveal a link between green vegetation and decreased ectoparasite loads, and a link between vegetation and increased nestling condition. However, there is still no rigorous experimental evidence that fumigation of nests with green vegetation actually increases the fitness of birds by deterring parasites.

Heterospecific Cleaning

Birds can conceivably reduce ectoparasites using what Hart [24] referred to as "heterospecific cleaning". Both of the known cases involve nest maintenance. The most remarkable example was reported in a paper by Smith [235]. He observed that brood parasitic Giant Cowbirds (*Scaphidura oryzivora*) are tolerated by some nesting colonies of foster species, such as Yellow-rumped Caciques (*Cacicus cela*) and oropendolas (*Psarocolius wagleri, P. decumanus, Gymnostinops montezuma*). Smith [235] reported that the cost of brood parasitism was offset by the fact that the nestling cowbirds remove and consume parasitic botflies (*Philornis*) from the foster parents' offspring, thus enhancing the fledging success of the foster species. Selection for cowbird egg mim-

icry was relaxed under these conditions, explaining a higher frequency of non-mimetic eggs in colonies parasitized by flies. This "advantage of being parasitized" (by cowbirds) was reportedly lost in the case of cacique or oropendola colonies adjacent to large wasp nests, because the wasps deterred the flies from parasitizing bird nests. In such cases, cowbirds were not tolerated by the foster species and the frequency of mimetic eggs was higher. These interactions, which are among the most complex ever documented, need additional study and confirmation.

Gehlbach and Baldridge [236] reported another form of heterospecific cleaning. They documented higher growth rates of nestling Eastern Screech Owls (*Otus asio*) in nests with Blind Snakes (*Leptotyphlops dulcis*). Superficial scars on the snakes suggested they were transported to the nest by adult owls, yet not eaten. The authors argued that growth rates of young in nests containing snakes were higher because the snakes fed on parasitic larvae that are harmful to the nestlings. However, other factors could covary with snake presence and owlet growth, e.g., parental hunting ability. An experimental manipulation of snake presence is needed to test Gehlbach and Baldridge's [236] hypothesis.

Cleaning of one species of bird by another species, analogous to the cleaning symbioses of marine fishes, has also been suggested. Bowman and Billeb [237] speculated that the bizarre feeding behavior of "vampire" Sharp-beaked Ground Finches *(Geospiza difficilis)*, which puncture the pin-feathers of boobies to feed upon their blood, may have originated from finches feeding on the large, numerous hipoboscid flies that plague the boobies. This is an intriguing idea, but the authors were quick to point out that they did not actually observe finches feeding on hippoboscid flies. We are unaware of any other documented cases of cleaning interactions between different species of birds.

Nest Desertion

If all else fails, an ultimate strategy for dealing with nest parasites is simply to abandon the nest, rather than continuing to invest in offspring that may be doomed. Nest desertion in the face of high ectoparasite loads has been documented for many bird species [45, 212, 214, 238-245]. Duffy [242] showed that argasid ticks (*Ornithodoros amblus*) cause large-scale desertion of colonial seabird nesting colonies, which raises interesting questions. How often do adult birds desert because they are cutting their losses, versus simply escaping intolerable irritation? Because short-lived birds have fewer breeding seasons in which to reproduce, short-lived birds should be slower to abandon their nests than long-lived birds, all else being equal. Comparative and experimental studies are needed to investigate how life span affects the decision to desert nests, in the face of high ectoparasite load.

DISCUSSION

As we have tried to show, birds have an impressive array of possible defenses against ectoparasites. Different species of birds may use very different combinations of these defenses, but the extent to which this actually occurs is not known. Most work has focused on demonstrating what the various defenses are, and, in some cases, exactly how they function. A more complete understanding of how birds com-

bat ectoparasites requires a broader perspective that considers how the different defenses interact, and the relationship of ectoparasite defense to the many other life history challenges birds face. The optimum strategy undoubtedly depends on various life history tradeoffs. Multiple defenses and how they interact are also important to document in order to better understand the nature of coevolutionary responses to host defense by the parasites themselves. The evolution of effective counterstrategies should be more difficult, all else being equal, if a host has more than one effective defense strategy.

Environmental constraints will also limit the defenses available to different species. Opportunities for sunning are more limited for birds that live in regions with an average of 300 days per year of rain (e.g., Seattle, Washington), compared to regions with an average of 300 days/year of sun (e.g., Salt Lake City, Utah). Redundant defenses may also be important in the face of environmental variability. Sunning and dusting may combat similar ectoparasites, but dusting is an option on a cloudy day, while sunning may be effective in habitats devoid of dust or loose dirt.

Composition of the ectoparasite community will also influence the defenses used by a given host. Ectoparasite species richness and abundance vary markedly among birds, even within single groups of ectoparasites [124]. Some species of tinamous (Tinamiidae) can be infested with a dozen species of lice, while ostriches (Struthionidae) have but one species [5, 63]. Defense strategies against a single species probably differ from those against a more diverse community. Consistent with this prediction, bird species known to host more species of lice appear to devote more time to maintenance behavior than birds with few species of lice [246]. This kind of relationship probably holds for other kinds of ectoparasites, as well.

Ectoparasite species richness can also vary within a single bird species. Brown and Wilson [247] compared the ectoparasite communities of House Sparrows in Europe and North America. They found that 34 of the 69 species of ectoparasites found on the European sparrows were "lost" when House Sparrows were introduced to North America. It would be interesting to test whether North American sparrows have lost certain defenses as a result of the reduction in the richness of their ectoparasite community.

Ectoparasite prevalence also varies across environments. A worldwide comparison of louse prevalence among 22 species of pigeons and doves (Columbidae) revealed a positive relationship between louse prevalence and ambient humidity [22]. For example, lice were found on fewer than 3% of birds in the Sonoran Desert of Arizona, whereas 92% and 100% of birds in Philippine and Peruvian rainforests, respectively, were infested. Moyer *et al.* [37] showed that pigeons and doves in arid habitats also have lower louse abundance than conspecifics in humid habitats. To confirm humidity as the causal agent, the authors experimentally manipulated the ambient humidity of captive feral Rock Pigeons. Louse infestations decreased greatly on birds kept at low humidity, compared with those at higher humidities.

The "arsenal" of defenses employed by a given bird species will also depend on adaptations that are not immediately

related to parasite control. Ornithologists have traditionally interpreted bill shape mainly as it relates to foraging [126, 248-250]. However, recent studies (e.g. Clayton *et al.* [125]; Fig. **4**) make it clear that selection for efficient preening can also play a role in the evolution of bill morphology. In environments with high ectoparasite pressure, selection for preening-efficient bills may be strong. Some species of birds have foraging ecology that precludes a maxillary overhang (e.g. woodpeckers, hummingbirds, oystercatchers (Fig. **2b**), skimmers, darters, and herons; Table **I**). These taxa are presumably under selective pressure to evolve other mechanisms for controlling ectoparasites.

Finally, ectoparasite defense may also vary in terms of investment in particular defenses, independent of other defenses. For example, preening birds cannot simultaneously forage or engage in courtship. Preening also reduces vigilance [251], increasing the risk of predation. Given these costs of preening, we predict that birds in areas of low ectoparasite pressure should spend less time preening than birds in areas of high ectoparasite pressure. This hypothesis would be easy to test simply by comparing preening rates of birds in different localities (e.g., Clayton and Cotgreave [105]). We expect that tradeoffs of this kind may be common for many of the different adaptations birds have for controlling ectoparasites.

CONCLUSION

Birds have a wide variety of defenses for combating their diverse communities of ectoparasites. In some cases there is overwhelming evidence that a particular trait is important in ectoparasite defense (e.g., preening). In other cases the purported defense has not been tested (e.g, dusting). In still other cases, recent evidence suggests that the purported defense may, in fact, have little to do with ectoparasite control (e.g. pectinate claws). Multiple defenses allow birds to target different types of ectoparasites and to defend themselves in the face of environmental variability. Birds should also modulate the use of particular defenses, as well as combinations of defenses, in response to the many life history demands they face.

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SUPPLEMENTARY MATERIAL

Supplementary material is available on the publishers Web site along with the published article.

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