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Avian Defences Against Ectoparasites

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Introduction

Birds are infested by a variety of detrimental ectoparasites (Janovy, 1997). A good deal of information concerning the impact of ectoparasites on birds has been summarised in several recent reviews (Loye & Zuk, 1991; Lehmann, 1993; Clayton & Moore, 1997). These reviews show that ectoparasites can have severe effects on birds, selecting for efficient host defences. Unfortunately, the literature on avian defences against ectoparasites is scattered. The first goal of this chapter is to provide a comprehensive catalogue of these defences. The second goal is to critically evaluate the evidence supporting the defensive function of each trait. The third and final goal is to argue that future research should investigate how defensive traits interact, rather than continuing to focus on each defensive trait in isolation. Studying defences in isolation can lead to misleading interpretations regarding their adaptive function.

Birds are exploited by a diverse community of ectoparasites, including insects such as lice (Phthiraptera), fleas (Siphonaptera), true bugs (Hemiptera), and flies (Diptera) (Marshall, 1981), as well as ticks and other mites (Acari) (Walter & Proctor, 1999). These taxa vary in the resources they exploit (skin, feathers, blood, etc.), and in the intimacy of their association. For example, feather lice (Phthiraptera: Ischnocera) specialise on feathers and spend their entire life cycle on the bird. Other taxa, like flat flies (Diptera: Hippoboscidae) and swallow bugs (Hemiptera: Cimicidae), feed on blood and are more transient parasites. In this review, we focus on more 'permanent' parasites, such as lice. Generally speaking, defences against permanent parasites are likely also to help defend against more ephemeral parasites.

Many recent studies have demonstrated detrimental effects of ectoparasites on avian fitness (Møller *et al.*, 1990; Loye & Zuk, 1991; Lehmann, 1993; Clayton & Moore, 1997). Ectoparasites can influence several components of host reproductive success. These components include nest desertion (Moss & Camin, 1970; Duffy, 1983; Oppliger *et al.*, 1994), as well as reductions in mating success (Andersson, 1994; Hillgarth & Wingfield, 1997), clutch size (Møller, 1993), hatching success (Oppliger *et al.*, 1994; Clayton & Tompkins, 1995), nestling survival (Møller, 1987; Shields & Crook, 1987; Richner *et al.*, 1993), and fledgling success (Clayton & Tompkins, 1995). Adult survival can also be reduced by ectoparasites (Brown *et al.*,

1995; Clayton *et al.*, 1999). Owing to these detrimental effects, avian traits that minimise infestations have a selective advantage.

Birds combat ectoparasites in a variety of ways. All else being equal, the simplest way to minimise the detrimental effects of ectoparasites is to avoid them in the first place. Once infested, however, various defensive mechanisms exist to minimise the detrimental impact. These mechanisms include morphological barriers, immune responses, and behavioural defences. This review will focus mainly on morphological and behavioural defences against ectoparasites. Wikel (1996) and Wakelin & Apanius (1997) provide recent reviews of immune defences in birds.

Habitat choice

One defence against parasites is to occupy environments that are relatively free from parasites. For example, avian blood parasites (Haematozoa) are scarce on open tundra (Greiner *et al.*, 1975; Bennett *et al.*, 1992), in arid regions (Little & Earle, 1995; Tella, 1996), and at high elevations (van Riper III *et al.*, 1986). The main reason for the paucity of Haematozoa in these habitats is low abundance of vectors, such as mosquitoes.

Another defence may be to occupy environments too extreme for the survival of the parasites themselves. For instance, the abundance of fleas on dogs in Egypt is positively correlated with the relative humidity of the environment (Amin, 1966). Similarly, in a comparison of the feather lice on birds in habitats ranging from desert to rainforest, Moyer *et al.* (*in press*) found a positive correlation between louse prevalence (% of individuals infested) and relative humidity (*Figure 18.1*). Inca doves (*Columbina inca*) and mourning doves (*Zenaida macroura*) were sampled from the Sonoran Desert (Arizona, USA) and from the more humid Rio Grande Valley (Texas, USA). Only 3% of Arizona birds (n = 346) had lice, compared to 80% of the Texas birds (n = 62) (Moyer *et al.*, 2002). Moyer *et al.* (2002) further showed experimentally that lice cannot survive on birds kept at low relative humidity (<35% RH).

Avoidance of parasites also operates on a more local scale. For example, quite a few studies have now shown that birds avoid nesting or roosting in sites that are infested with ectoparasites (Christe *et al.*, 1994; Oppliger *et al.*, 1994, Merilä & Allandar, 1995; Merino & Potti, 1995; Hart, 1997; Loye & Carroll, 1998; Rytkonen *et al.*, 1998; Thompson, 1999). Recent evidence further demonstrates that the microclimate of nest cavities influences colonisation by ectoparasites. Heeb *et al.* (2000) manipulated the humidity of uninfested nest boxes of blue tits (*Parus caeruleus*). More hen fleas (*Ceratophyllus gallinae*) subsequently colonized the dry nests than humid nests.

Mate choice

Another anti-parasite defence is for the members of one sex (often females) to choose mates that are parasite-free. Since the publication of Hamilton & Zuk's (1982) seminal paper, parasite-mediated mate choice has been a topic of widespread interest and research (Hillgarth & Wingfield, 1997). Hamilton & Zuk argued that parasite-free males are more likely to carry genes for resistance to parasites, genes that will be passed on to a choosy female's offspring. According to the Hamilton–Zuk hypo
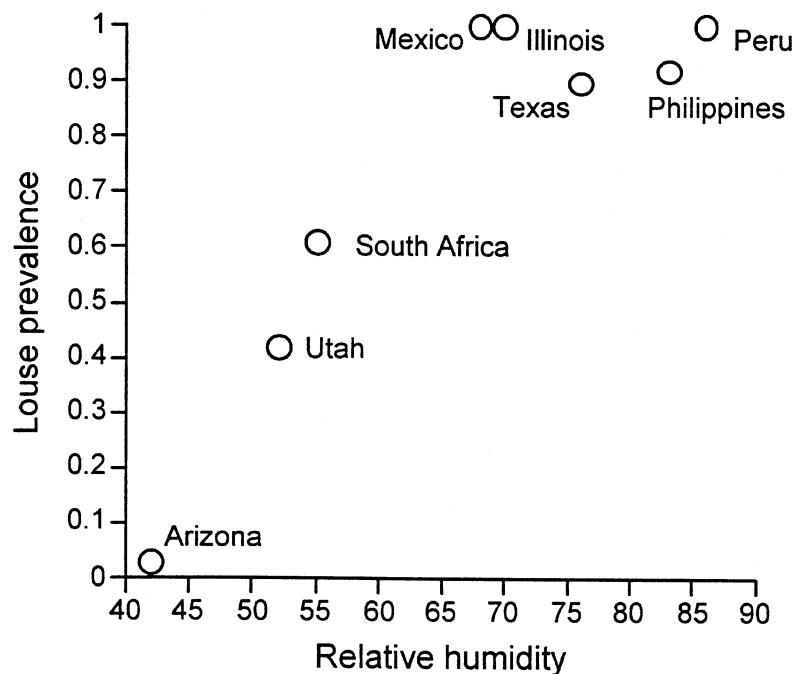
Figure 18.1.   Louse prevalence (% birds infested) plotted against the average annual relative humidity near the site of capture (n = 1,295 birds). Sampling localities are as follows: Tucson, Arizona, USA; Salt Lake City, Utah, USA; Free State and Mpumalanga, South Africa; Campeche, Mexico; Manteno, Illinois, USA; Weslaco, Texas, USA; Cagayan de Oro City, Philippines; and near Manu, Peru (Moyer *et al.*, *in press*).

thesis, females choose resistant males on the basis of secondary sexual traits whose full expression depends on health and vigour. Examples of such traits are brightly coloured plumage that is subject to fading, or vigorous courtship displays that parasitised individuals cannot perform. Hamilton & Zuk argued that, over time, sexual selection will lead to the elaboration of parasite-indicative traits that improve the ability of females to identify resistant males.

The Hamilton–Zuk hypothesis is a 'good-genes' model of sexual selection which assumes that choice of resistant males benefits females indirectly through the inheritance of resistance by offspring. Parasite-mediated mate choice could also yield more direct fitness benefits. For example, females might choose unparasitised males simply to avoid the direct transmission of parasites to themselves and/or their offspring (Able, 1996). Females might also benefit directly from the choice of unparasitised males if they require a healthy mate to provide resources such as parental care (Milinski & Bakker, 1990). Further information on this intriguing subject, including work involving birds and ectoparasites, can be found in recent reviews by Andersson (1994) and Hillgarth & Wingfield (1997).

Plumage as a barrier

FEATHER TOUGHNESS

A tough integument could conceivably be another defence against ectoparasites. Literally 'having a thick skin' might deter blood-feeding ectoparasites, although we

know of no data relevant to this hypothesis. Tough plumage could also deter feather-feeding ectoparasites, analogous to foliage containing cellulose which helps deter feeding by herbivores (Howe & Westley, 1988). Some recent work suggests that feather toughness may be an important defence against ectoparasites.

Feathers that contain melanin are known to be more resistant to mechanical abrasion than feathers without this pigment (Burtt, 1986; Bonser, 1995). Two recent studies suggest that melanin may also limit damage by feather-feeding lice (Kose & Møller, 1999; Kose et al., 1999). Kose and colleagues studied the interaction between the barn swallow (Hirundo rustica) and its louse Hirundoecus malleus, which chews holes in the host's tail feathers (Møller, 1991). The authors showed that this louse feeds more on white than dark regions of the tail, resulting in more extensive damage to white regions. Interestingly, this damage may be used as a cue by female swallows for detecting and avoiding lousy males as mates. The results of these studies are consistent with the hypothesis that melanin discourages feeding by lice. However, a direct test of this hypothesis has yet to be conducted.

Further tests of the role of feather toughness as a defence against ectoparasites are needed. It should be relatively easy to test the influence of feather pigments on the feeding and population ecology of ectoparasites. It is intriguing to speculate on the generality of possible relationships between feather-feeding ectoparasites and the plumage colours of birds. For example, how widespread is parasite-indicative plumage, such as the white tail spots of barn swallows, that reveal louse damage to discriminating mates? Are some species of birds black because they are parasitised by more species of feather-feeding ectoparasites than are white species? Are other features of feather structure, including pigments other than melanin, important in preventing ectoparasite damage? These and other questions relevant to feather toughness have received little attention.

FEATHER TOXICITY

Somewhat more attention has been devoted to the possibility that the toxic feathers or skin (Dumbacher & Pruett-Jones, 1996) of some birds may protect them against ectoparasites. For example, the feathers and skin of several species in the genus Pitohui contain homobatrachotoxin, the neurotoxin found in the skin of poison dart frogs (Dumbacher et al., 1992). Although this toxin probably plays some role in deterring predators of Pitohui, recent evidence suggests that it deters ectoparasites also (Mouritsen & Madsen, 1994; Poulsen, 1994; Dumbacher, 1999). Dumbacher (1999) conducted a series of Petri dish trials in which he exposed feather lice from a variety of bird species to Pitohui feathers and the feathers of non-toxic birds. He found that, given a choice, lice avoided feeding or resting on Pitohui feathers. Furthermore, lice on Pitohui feathers showed higher mortality than lice on non-toxic feathers. Since homobatrachotoxin affects a wide range of invertebrates (Dumbacher, 1999), it may deter a range of ectoparasites.

Body maintenance behaviour

Avian body maintenance includes grooming, dusting, sunning, and anting (Cotgreave & Clayton, 1994). Grooming behaviour, defined as preening and scratching combined
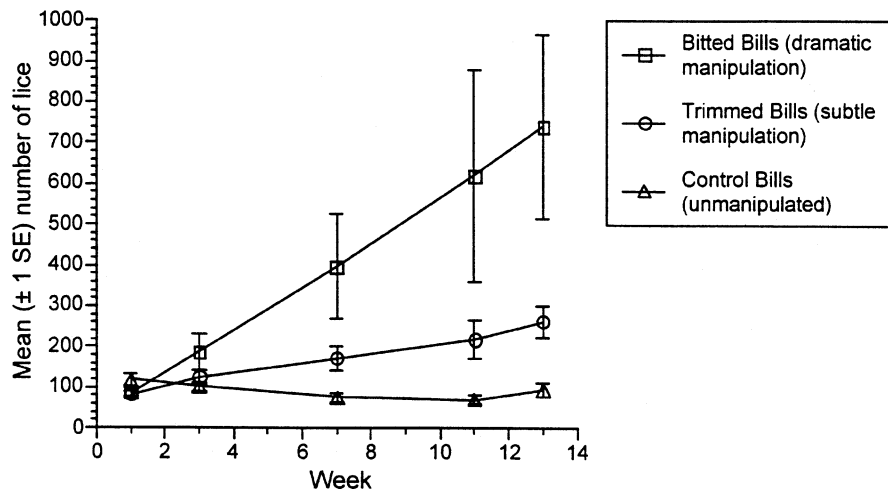
Figure 18.2. Change-over time in the number of lice on feral pigeons with bitted bills (n = 18), the bill overhang trimmed (n = 19), or unmanipulated bills (n = 18). Birds with bitted bills were fitted with small, C-shaped pieces of plastic that are inserted between the mandibles and crimped slightly in the nostrils to prevent dislodging, but without piercing the tissue. Bits create a 1.0–3.0 mm gap between the mandibles that impairs preening, resulting in direct increases in louse load (Clayton, 1990; Clayton, 1991; Booth *et al.*, 1993; Clayton & Tompkins, 1995; Clayton *et al.*, 1999). Although bits interfere with preening, they do not interfere with feeding since feral pigeons feed on grain that is easy to pick up, despite the mandibular gap created by bits. In an experimental test for possible side effects of bits, Clayton & Tompkins (1995) found that bits did not significantly alter the body mass or reproductive success of (parasite-free) feral pigeons. Birds with trimmed bills had the 1–2 mm maxillary overhang removed. This procedure is harmless to the bird and was repeated each week because the overhang grows back rapidly, much like a fingernail. Birds with control bills were not manipulated.

Lice were estimated using regression models that predict the total population size ($r^2 = 0.82$) from timed visual counts of lice on various body regions (Clayton, 1991). A comparison of the (log-transformed) number of lice on bitted, trimmed, and control birds over the course of the experiment revealed a significant effect of treatment on the change in louse population size (ANOVA, $F_{(2,52)} = 31.4$, $P < 0.0001$). Lice increased significantly faster on bitted and trimmed birds than on controls (Tukey HSD, $P < 0.05$). Furthermore, lice increased significantly faster on bitted birds than on trimmed birds (Tukey HSD, $P < 0.05$).

The effect of bill treatment on lice was not due to a difference in the amount of preening: time devoted to preening during the experiment did not differ significantly among treatments (repeated measures ANOVA: treatment, $F_{(2,52)} = 1.0$, $P = 0.39$; time, $F_{(1,52)} = 14.3$, $P < 0.001$; time × treatment, $F_{(2,52)} = 0.3$, $P = 0.74$). The effect of bill treatment on lice was the result of an apparent difference in the efficiency of preening. This experiment confirms earlier work showing that efficient preening is critical for controlling lice (see text). It further shows that the maxillary overhang is an important component of efficient preening. However, the more rapid increase in lice on bitted birds than on trimmed birds indicates that the overhang is not the only component of efficient preening. Bitting prevents contact of the upper and lower mandibles along their entire lengths, which is a more dramatic manipulation than merely trimming the maxillary overhang.

(Clayton & Cotgreave, 1994), is critical for defence against ectoparasites (Marshall, 1981; Hart, 1997). Preening is of two types: self-preening and allopreening – the latter when one individual preens another. Dusting, sunning, and anting may also play a role in ectoparasite defence, but have received less attention than grooming, as outlined below. Other behavioural defences, such as fly-repelling behaviour, are important for defence against ephemeral parasites (reviewed by Lehane, 1991; Hart, 1997).

GROOMING: SELF-PREENING

A substantial body of work shows that preening is a major defence against ectoparasites,

and that bill morphology is an important component of preening efficiency. Numerous anecdotal reports document that wild birds with deformed bills have elevated ectoparasite loads (Rothschild & Clay, 1952; Ash, 1960; Pomeroy, 1962; Ledger, 1969; Marshall, 1981). Controlled experiments, in which bill morphology was dramatically manipulated (reviewed by Clayton, 1991; Hart, 1997), triggered rapid increases in ectoparasite load. The results of these studies clearly show the importance of preening, and normal bill morphology, for controlling ectoparasites.

Recent work demonstrates that even subtle features of bill morphology are critical for controlling ectoparasites. A comparative analysis of 52 species of neotropical birds revealed a significant negative correlation between length of the maxillary overhang of the bill and the mean number of lice on a given species (Clayton & Walther, 2001). The maxillary overhang is the distal portion of the upper mandible (maxilla) that curves over the lower mandible. The negative correlation between length of the overhang and louse load suggests that the overhang is important for controlling lice during preening. This functional hypothesis was tested through a series of manipulative experiments in which the 1–2 mm overhang was trimmed from feral pigeons (*Columba livia*) (Moyer *et al.*, *in press*). Removal of this small overhang caused louse load to triple in just three months (*Figure 18.2*). Preening is a complex behaviour in which the bill is used in a variety of ways (Simmons, 1985a). Different components of bill morphology may be important to different aspects of preening. Unfortunately, preening behaviour has not been studied in detail for many species of birds.

A major conclusion from these studies is that the evolution of bill morphology is probably influenced by the need for efficient preening, in addition to the more generally recognised need for efficient foraging. Indeed, preening and foraging could conceivably represent opposing selective forces shaping bill morphology. To date, avian biologists have focused almost exclusively on bills as tools for feeding. However, the critical importance of efficient preening for ectoparasite control suggests that the adaptive radiation of bill morphology may need to be re-interpreted with both preening and feeding firmly in mind.

GROOMING: ALLOPREENING

Allopreening may help to reduce ectoparasite loads, particularly on the head and neck, which are difficult or impossible to self-preen, and which are the sites of most allopreening (Harrison, 1965). Allopreening is a widespread behaviour which has been observed in many species and higher taxa of birds (Harrison, 1965). It is most common between courting individuals, mates, and between parents and their offspring. Harrison (1965) argued that allopreening serves mainly a social function, such as re-inforcement of pair bonds, and is of little or no importance for ectoparasite control. However, several more recent studies have implicated allopreening in the removal of ectoparasites (Fraga, 1984; Brooke, 1985; Murray, 1990; Wernham-Calladine, 1995).

For example, in a study of breeding penguins, Brooke (1985) showed that allopreening (paired) individuals had significantly fewer ticks than unpaired individuals, which could only self-preen. Unfortunately, Brooke was unable to control for possible co-variates of tick load, such as genetic resistance. Such resistance, if present, could have been responsible for the low tick loads of some individuals, as well as for their ability to attract mates (see 'mate choice' above). This would lead to

a spurious (inverse) correlation between tick load and allopreening. A more rigorous test of the role of allopreening requires analysis of co-variation between allopreening and parasite load (c.f. Mooring, 1995), or experimental manipulation of allopreening and its subsequent effect on ectoparasites.

GROOMING: SCRATCHING

Although the role of allopreening remains unclear, scratching with the feet definitely controls ectoparasites on inaccessible regions, such as the head. Birds with a deformed or missing leg often have large numbers of ectoparasites (and their eggs) concentrated around the head and neck (Clayton, 1991). The obvious explanation is that, although a bird can preen itself while standing on one leg, it is unable to scratch itself. Head-scratching is known to kill or damage fleas on chickens (Suter, 1964, cited in Marshall, 1981, p. 107).

Some birds may use scratching as compensation for the absence of other methods of ectoparasite control. The unpaired penguins in Brooke's (1985) study spent significantly more time scratching than did the paired individuals with access to allopreening. Scratching may also compensate for inefficient preening in species of birds with unwieldy bills. In a phylogenetically-controlled comparative study, Clayton & Cotgreave (1994) reported that long-billed species average 16.2% of their grooming time scratching, compared to only 2.3% in short-billed species. In a series of paired taxonomic comparisons, long-billed species scratched significantly more than related short-billed taxa (Clayton & Cotgreave, 1994).

The efficiency of scratching for ectoparasite control may be enhanced by the presence of a pectinate claw on the middle toenail (Brewer, 1839; Brauner, 1953; Clay, 1957). A recent survey documented this curious feature in dozens of species of birds from 17 families representing eight orders (Moyer *et al.*, *in press*). The serrations on some pectinate claws are similar to the teeth of combs designed to rid humans of head lice, suggesting that the claw may help in removing lice and other ectoparasites during scratching. This hypothesis, which has not been tested, could be explored by comparing the ectoparasite loads of birds with trimmed claws to those with untrimmed controls.

Although experimental data do not exist, a recent comparative study tested Clay's (1957) assertion that bird species with pectinate claws have fewer species of head lice than clawless species. In a series of paired taxonomic comparisons, Moyer *et al.* (*in press*) found no significant difference in the number of species of head lice on birds with and without claws. However, it is unclear an inverse correlation between claw presence and parasite species richness should be expected anyway. If parasite richness decreases on birds that evolve pectinate claws, then selection maintaining the claw will be relaxed, leading to disappearance of the structure (assuming it is costly to maintain). Thus, the results of the comparative analysis of Moyer *et al.* (*in press*) should not be viewed as a conclusive test of the hypothesis that pectinate claws help to control ectoparasites.

DUSTING

Many species of birds (*Table 18.1*) engage in dusting, a behaviour in which they

Table 18.1. Examples of birds known to dust (compiled from Simmons, 1985b; with Latin names where given). Classification based on Howard & Moore (1991).

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	Sparrow (*Passer, Petronia, Montifringilla*)
Sandgrouse	GRALLINIDAE
	Chough (*Corcorax*)

'ruffle' fine earth or sand through the plumage (Simmons, 1985b). Several authors have suggested that dusting may help control ectoparasites through dislodgement (Hoyle, 1938), abrasion of the cuticle leading to desiccation (Murray, 1990; Hendricks & Hendricks, 1995), plugging of the spiracles leading to poor respiration, or by reducing feather lipids upon which some ectoparasites feed (Borchelt & Duncan, 1974). Dusting is known to remove excess feather oil that can lead to matting of the plumage (Healy & Thomas, 1973; Borchelt & Duncan, 1974; van Liere, 1992), but no direct test of the impact of dusting on ectoparasites has been carried out.

SUNNING

Sunning, a behaviour in which birds expose themselves to solar radiation while adopting a stereotyped posture, has been recorded for over 170 species in nearly 50 families (Kennedy, 1969; Simmons, 1986). Sunning may control ectoparasites by killing them directly through overheating (Moyer & Wagenbach, 1995), or indirectly by increasing their vulnerability to preening as they try to escape the heat (Simmons, 1986). Sunning also appears to be an adaptation for conserving energy, since birds

sun in cool temperatures to warm themselves and reduce metabolic expenditure (Morton, 1967; Ohmart and Lasiewski, 1971; Simmons 1986). However, sunning birds often show signs of heat stress, such as panting (Simmons, 1986). Black noddies (*Anous minutus*) sun more frequently in periods of high, rather than low, temperature (Moyer & Wagenbach, 1995). Blem & Blem (1993) observed swallows "panting markedly", while sunning on substrates in excess of 50°C.

No direct test of the impact of sunning on ectoparasites has been carried out. However, two recent studies provide evidence that is consistent with the ectoparasite control hypothesis. Blem & Blem (1993) compared the rate of sunning in swallows that were fumigated to remove ectoparasites, with the rate of sunning by non-fumigated controls. They found that fumigated birds sunned less frequently than controls (Blem & Blem, 1993), suggesting that the need for sunning decreases with a reduction in ectoparasite load. Moyer & Wagenbach (1995) exposed model black noddy wings to sun and shade. The duration of exposure was typical of a sunning bout, and the temperature of model wings did not exceed that of sunning noddies. The mortality of feather lice placed on model wings in the sun was higher than that of lice placed on wings in the shade, suggesting that sunning may help noddies combat lice. Additional research is needed to test the impact of sunning on the ectoparasites of live birds. Since birds sun readily in captivity (Simmons, 1986), it should be possible to use captive birds for rigorous tests of the impact of sunning on ectoparasites.

ANTING

Another oft mentioned defence against parasites is 'anting' behaviour, in which birds crush and rub ants on their feathers (active anting), or allow ants to crawl through the plumage (passive anting). The fact that birds ant exclusively with ants that secrete acid or other pungent fluids suggests that anting may kill or deter ectoparasites. Although anting has been observed in over 200 bird species, its function remains controversial (Simmons, 1986; Clayton & Wolfe, 1993; Hart, 1997). At present, no study has provided convincing evidence that anting combats ectoparasites.

Birds also 'ant' with items such as fruit peel, flowers, mothballs, and other substances, many of which have anti-parasite properties (Clark *et al.*, 1990). After observing a common grackle (*Quiscalus quiscula*) anting with a hemisphere of lime, Clayton & Vernon (1993) showed that lime oil vapour rapidly kills feather lice in Petri dishes. The impact of anting with such substances on ectoparasites has not been tested *in situ*.

Nest maintenance behaviour

An important component of ectoparasite defence is a suite of behaviours that control parasites in nests, such as nest 'sanitation'. For example, male house wrens (*Troglodytes aedon*) remove old nest material from their nest cavities prior to each nesting bout. Pacejka *et al.* (1996) showed that removal of the old material dramatically reduces the number of parasitic mites in the nest cavity (*Figure 18.3*). The authors argued that this reduction delays mite population growth, allowing young birds to leave the nest before mites reach a detrimental level.

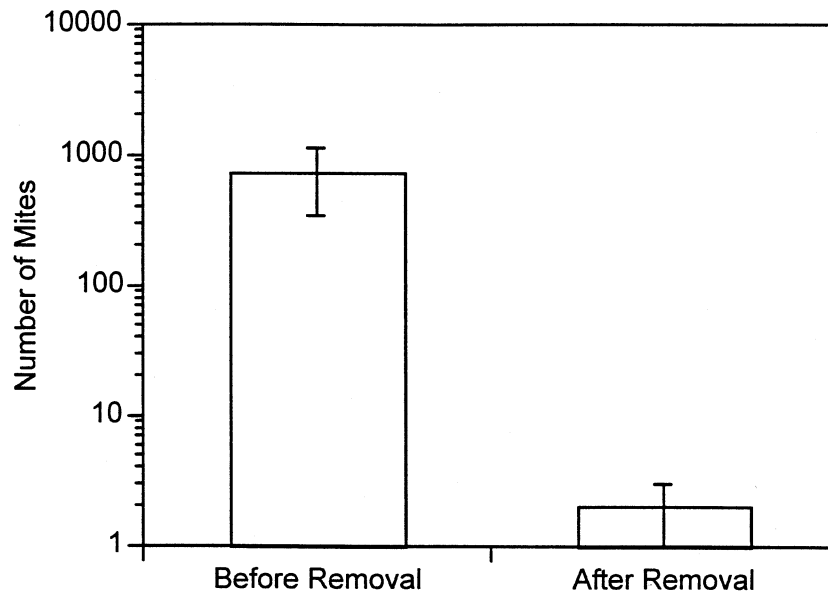The hole-nesting great tit (*Parus major*) also engages in a form of nest sanitation.

Figure 18.3. Mean (± 1 s.e.) number of mites in house wren nest boxes sampled before (n = 6 boxes) and after (n = 6) the male wren removed nest material remaining from the previous breeding season. Redrawn from Pacejka *et al.* (1996).
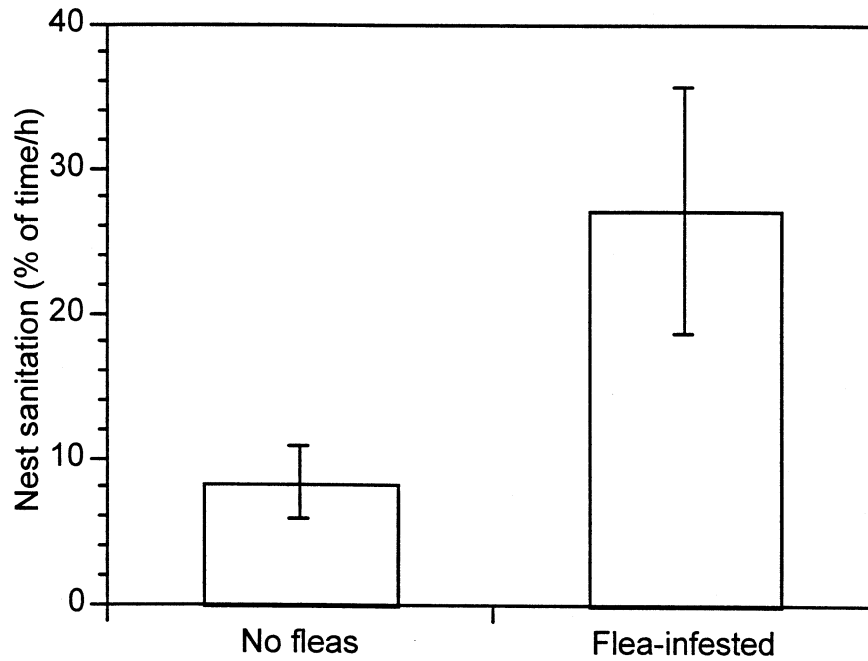

Figure 18.4. Mean (± 95% CI) percentage of a night hour taken up by nest sanitation behaviour for female great tits in nests without fleas (n = 15) and with fleas (n = 14). Redrawn from Christe *et al.* (1996).

Christe *et al.* (1996) described it as "a period of active search with the head dug into the nest material." Although the precise effect of this behaviour is unclear, the authors showed that females devote significantly more time to sanitation in flea-infested nests than in uninfested nests (*Figure 18.4*). The increased sanitation behaviour in infested nests comes at the expense of sleep, suggesting that the behaviour is costly to the birds (Christe *et al.*, 1996).

Another behaviour demonstrated to control nest parasites is the insertion of green vegetation into nests (reviewed by Clark, 1991; Clayton & Wolfe, 1993; Dumbacher & Pruett-Jones, 1996; Hart, 1997). Clark & Mason (1985) showed that European starlings (*Sturnus vulgaris*) select species of plants that contain volatile chemicals with antibacterial, insecticidal, or miticidal properties. The same authors later showed that nests containing such herbs have lower infestations of blood-sucking mites (Clark & Mason, 1988). More recent research suggests that the addition of herbs to the nest does not necessarily serve to reduce ectoparasite loads, but may help nestlings cope with the detrimental effects of the ectoparasites. Gwinner *et al.* (2000) manipulated green vegetation in 148 starling nests. They found no difference in the ectoparasite loads (mites, lice, fleas) of nests with and without the herbs starlings normally choose to insert. However, nestlings from nests with herbs had higher red blood cell counts and body masses than nestlings from nests without herbs. Gwinner *et al.* (2000) argued that herbs may stimulate the immune system of nestlings such that they can better deal with the detrimental effects of blood-feeding ectoparasites.

Plants apparently may not be the only biological control agents used by birds to control parasites in the nest. Eastern screech owls (*Otus asio*) deposit live blind snakes (*Leptotyphlops dulcis*) in their nests. Gehlbach & Baldridge (1987) found that nestlings from nests with live snakes grew significantly faster than nestlings from nests without snakes. Since the snakes consume soft-bodied insect larvae from the nests, the authors suggested that the snakes might reduce larval parasitism on owl nestlings. But, as the presence of snakes was not experimentally manipulated in this study, there may be other factors that co-vary with the presence of snakes (e.g. hunting ability of parents) that might contribute to the difference in nestling growth rate.

While owls may exploit snakes to reduce nest ectoparasites, oropendolas and caciques reportedly exploit cowbirds (Smith, 1968). Smith claimed that adult oropendola and cacique tolerate brood parasitism by cowbirds when bot fly parasitism is likely, because cowbird nestlings preen the host nestlings of their bot fly larvae. Presumably owing to this attention, host broods with cowbirds produced more nestlings than broods without cowbirds (Smith, 1968). The use of snakes and cowbirds to control nest ectoparasites are intriguing accounts that warrant further study and replication.

Conclusions

In this chapter, we have attempted to review some of the ways in which birds combat ectoparasites. Most of the research in this area has tended to focus on how single defences combat single types of ectoparasites. Future research should address how birds use suites of defences to control ectoparasites. This approach is important because individual defences can interact in at least two fundamental ways. First,

defences can be complementary. They could target different types of ectoparasites, or ectoparasites on different host body regions. For example, we have mentioned that preening can control ectoparasites on the wing, while scratching can control ectoparasites on the head.

Second, defences can interact synergistically – where their combined effect is greater than the sum of their individual effects. One example regards the possible synergistic interaction of preening and sunning. In the case of a single defence, an ectoparasite can exploit a refuge to escape that defence. For instance, some wing lice are dorsoventrally flattened so that they can slide between the barbs of flight feathers and escape the preening bill. Sunning, however, heats the flight feathers such that lice flee the interbarb refuge and move down the feather towards the body (B. R. Moyer, *unpublished*). Thus, lice may not have a refuge from preening in the presence of sunning, and their mortality may increase synergistically. In short, in addition to conducting needed tests of additional candidate defences (e.g. feather toughness and dusting), future research should address how defences interact.

An intriguing pattern arising from the basic research on avian defences is that different birds employ rather different suites of defences. Several factors might help to explain the variation in how different birds combat ectoparasites. First, the nature and intensity of selection by ectoparasites varies among different birds. Second, environmental and phylogenetic constraints may influence the defences available to different birds. Third, ectoparasite defence is just one component of avian life history demands; accordingly, the optimum defensive strategy will depend on a bird's life history trade-offs.

Ectoparasite populations and communities vary greatly among different birds, and may thereby influence defensive strategies. As we discussed earlier (under 'habitat choice'), ectoparasite loads can vary by more than an order of magnitude in different environments. This variation may cause variation in the intensity of selection for defence among birds. Just as the size of an ectoparasite population can vary, so can the diversity of the ectoparasite community. For instance, a single species of tinamou can be infested by a dozen species of lice, while ostriches are only ever infested by one species (Marshall, 1981). The optimum defensive strategy against a single ectoparasite is likely to differ from that against a diverse community of ectoparasites. Cotgreave & Clayton (1994) found that bird species infested with more species of lice devoted more time to maintenance behaviour than bird species with fewer species of lice.

Even if ectoparasite pressure is uniform among birds, environmental and phylogenetic constraints can limit the defences available to different birds. Some defences may not be effective in some habitats. For example, dusting may not be an option in a marshy habitat. Similarly, insertion of green vegetation in nests may not be an option on barren oceanic islands. The phylogenetic history of a bird can also place constraints on defence. For example, scratching as a means of controlling ectoparasites appears to be constrained by foot morphology; species belonging to web-footed families scratch very little, regardless of other factors (Clayton & Cotgreave, 1994)

Parasite defence is just one of many life history demands. Birds must balance limited resources among competing life history traits, forcing trade-offs. Accordingly, variation in parasite defence might be governed partly by variation in other life

history parameters. For instance, we have described how having a specialized bill for feeding can influence parasite defence. Birds with unwieldy bills compensate for inefficient preening by scratching more. The composition of grooming behaviour is thus dictated partly by constraints related to foraging ecology. Likewise, as we discussed earlier, the evolution of bill morphology is probably influenced by the need for efficient preening, in addition to the more generally recognised need for efficient foraging. To what extent do foraging, breeding strategy, migration, and other life history components influence the composition of ectoparasite defence in different bird species (see Piersma, 1997)?

Just as variation in general life history demands may help to explain variation in ectoparasite defence, the converse is also true. We may be better able to understand variation in general life history traits by understanding how the demands for ectoparasite defence vary among different bird taxa. A species living in an environment with few ectoparasites should be released, to some extent, from constraints imposed by ectoparasite defence on other life history traits.

In conclusion, birds have a variety of defences against ectoparasites. For a more complete understanding of how birds combat ectoparasites, future research should investigate how these different defences interact, and why the composition of the defensive arsenal differs among bird taxa. This variation might be explained by considering how avian defences are influenced by 1) parasite communities, 2) environmental and phylogenetic constraints on the host, and 3) broader life history trade-offs. An appreciation of variation in ectoparasite pressure and the consequent investment in avian defence may also shed reciprocal light on other parameters influencing the evolution of avian life histories.

Acknowledgements

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