Review

Author for correspondence:
Sarah E. Bush
e-mail: bush@biology.utah.edu

Anti-parasite behaviour of birds

Sarah E. Bush and Dale H. Clayton

Department of Biology, University of Utah, Salt Lake City, UT 84112, USA

SEB, 0000-0002-2913-4876; DHC, 0000-0003-1698-3542

Birds have many kinds of internal and external parasites, including viruses, bacteria and fungi, as well as protozoa, helminths and arthropods. Because parasites have negative effects on host fitness, selection favours the evolution of anti-parasite defences, many of which involve behaviour. We provide a brief review of anti-parasite behaviours in birds, divided into five major categories: (i) body maintenance, (ii) nest maintenance, (iii) avoidance of parasitized prey, (iv) migration and (v) tolerance. We evaluate the adaptive significance of the different behaviours and note cases in which additional research is particularly needed. We briefly consider the interaction of different behaviours, such as sunning and preening, and how behavioural defences may interact with other forms of defence, such as immune responses. We conclude by suggesting some general questions that need to be addressed concerning the nature of anti-parasite behaviour in birds.

This article is part of the Theo Murphy meeting issue 'Evolution of pathogen and parasite avoidance behaviours'.

1. Introduction

Birds have diverse mechanisms for defence against parasites and pathogens. These mechanisms include morphological adaptations, immunological responses and anti-parasite behaviour [1–3]. In this review, we summarize behavioural adaptations known or hypothesized to help birds avoid or combat parasites. We divide anti-parasite behaviour into five broad categories: body maintenance behaviour, nest maintenance behaviour, avoidance of parasitized prey, migration and tolerance. We do not cover parasite-mediated mate choice or other forms of sexual selection because these topics have been thoroughly treated in earlier reviews [1–9].

We adopt a broad, evolutionary definition of 'parasite' that includes organisms living internally or externally on birds and which reduce one or more components of host fitness, i.e. survival or reproductive success. Avian parasites include viruses, bacteria, fungi, protozoa, helminth worms, arthropods and brood parasites [1]. We do not include behavioural adaptations for combating brood parasites because this topic has also been thoroughly treated in recent reviews [10–12]. 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) or *abundance* (the number of individual parasites in a host, regardless of infestation). Thus, *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.* [13].

2. Body maintenance behaviour

The most important form of maintenance behaviour is grooming, which includes preening with the beak and scratching with the feet [14,15]. Other possible forms of maintenance are water bathing, dusting, sunning, heterospecific cleaning, anointing and cosmetic behaviour.
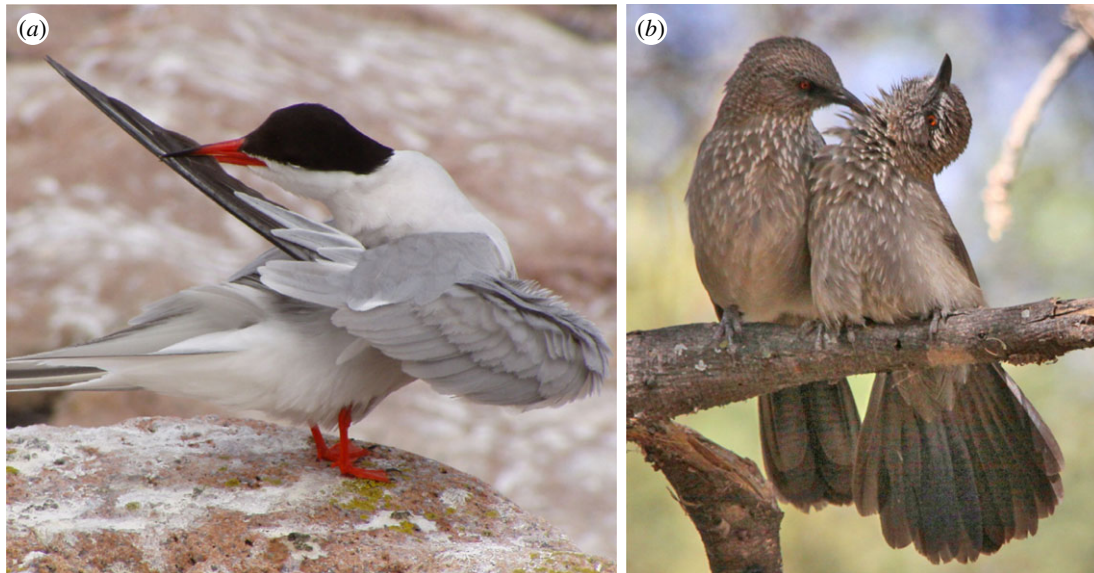
Figure 1. (a) Common tern self-preening (*Sterna hirundo*; USFWS, wikimedia.org). (b) Arrow-marked babblers allopreening (*Turdoides jardineii*; Derek Keats, wikimedia.org). (Online version in colour.)

(a) Preening

Preening occurs when birds pull feathers between the mandibles of the beak, or use the tips of the mandibles to nibble feathers (figure 1a). Preening has several functions: birds preen to straighten and clean their feathers and to 'zip' the barbules of flight feathers together. Preening also plays an important role in the control of external parasites. A comparative study suggested that birds visually inspect their plumage and remove conspicuously coloured ectoparasites during preening [16]. More recently, a study of preening in green herons (*Butorides virescens*) described how herons hold and examine their wings in a particular posture that backlights the feathers; this behaviour may facilitate the removal of cryptic ectoparasites [17]. Birds with long, unwieldy bills (e.g. toucans) appear to be less efficient at preening than those with relatively short bills; such birds compensate for inefficient preening by scratching relatively more [18].

The effectiveness of preening for removing ectoparasites has been shown experimentally. For example, experiments removing a portion (approx. 1 cm) of the upper mandible of the beak led to dramatic increases in the ectoparasite loads of domestic chickens [19–21]. Preening has been impaired less invasively using poultry 'bits', which are small C-shaped pieces of metal or plastic inserted between the upper and lower mandibles. Bits create a 1–3 mm mandibular gap that eliminates occlusion of the bill required for efficient preening [22]. Bitted pigeons experience dramatic increases in ectoparasites, such as feather lice [22–25] and blood-feeding flies [26].

Waite *et al.* [26] showed that pigeons with normal preening ability killed twice as many pigeon flies (*Pseudolynchia canariensis*) as birds with impaired preening. Preening could conceivably also help birds defend against the blood parasites vectored by flies. Surprisingly, however, an experimental test of this hypothesis failed to show such an effect [27]. Preening may also influence blood parasites by stimulating the movement of vectors between birds [28]; however, this hypothesis has not been tested.

Preening is an inducible defence. Waite *et al.* [26] found that captive pigeons infested with flies spend more than twice as much time preening (23.5%) as uninfested pigeons

(11.2%). Similarly, Villa *et al.* [29] found that captive pigeons with feather lice spend more time preening than pigeons without lice (19.5% versus 14.1%). When these infested pigeons were subsequently cleared of lice, they preened at the rate of birds with no lice; hence, preening is also a reversible defence. The study by Villa *et al.* [29] also showed that preening to remove feather lice is an innate behaviour that does not improve with practice.

Preening can be induced by the presence of other parasites, such as feather-degrading bacteria. Leclaire *et al.* [30] reduced feather bacteria on captive pigeons by spraying experimental birds with a chlorohexidine solution. The authors increased bacteria on another group of pigeons by spraying them with live bacterial cultures. Pigeons thus inoculated preened a third more than those without bacteria (approx. 22% versus 15% of time). However, as the authors of this paper themselves note, the difference in preening could have been influenced by the chemical treatment itself. The inducibility of preening may limit the energetic cost of preening when parasites are not present. It may also reduce negative side-effects, such as accidental ingestion of infectious viral particles [31]. Moreover, minimizing time spent preening would allow birds to devote more time to other behaviours, such as feeding, mating and anti-predator vigilance [32].

Although the beaks of birds are first and foremost adaptations for feeding, they are also adapted for ectoparasite control. Comparative studies indicate that the anti-parasite function of preening is influenced by the relative size of the beak's upper mandibular overhang (figure 2). Clayton & Walther [33] examined the morphology of 52 species of Peruvian birds representing 13 families. They found that the abundance of lice on birds was negatively correlated with the length of the bill overhang, suggesting that birds with longer overhangs are better at controlling lice by preening. Clayton *et al.* [22] tested this hypothesis experimentally by removing the 1–2 mm overhang from pigeons, which triggered a dramatic increase in the number of feather lice. When the overhang was allowed to grow back, the lice returned to normal population sizes. High-speed videography showed that, when preening, pigeons shift their lower mandible
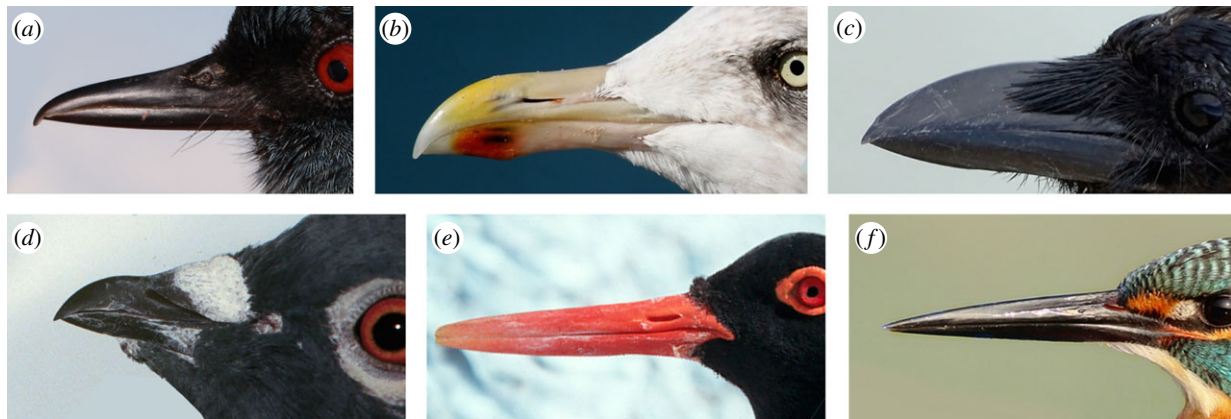
Figure 2. Most species of birds have a small mandibular overhang at the tip of their bill (a–d); however, some species of birds do not have an overhang (e,f). (a) Bluish flowerpiercer (*Diglossa caerulescens*; Andres Cuervo, wikimedia.org). (b) European herring gull (*Larus argentatus*; anonymous, maxpixel.com). (c) House crow (*Corvus splendens*; Picasa, pexels.com). (d) Rock pigeon (*Columba livia*; SEB); (e) African black oystercatcher (*Haematopus moquini*; Philip Hockey, wikimedia.org). (f) Common kingfisher (*Alcedo atthis*; Boris Smokrovic, unsplash.com). The overhang is often missing in cases where it would presumably interfere with feeding, as in the case of the oystercatcher and the kingfisher. (Online version in colour.)
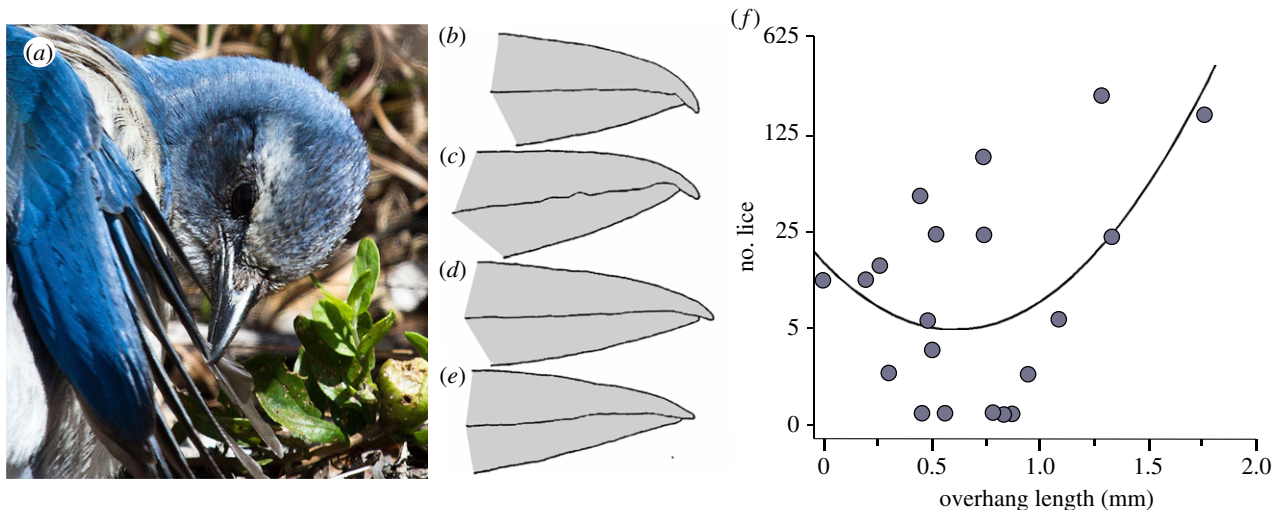
Figure 3. (a) Scrub jay preening with bill tips (photo by Bob Montanaro). (b–e) Four examples of scrub jay bills from the western USA, showing the range of morphological variation within the species (redrawn from [34]). (f) Intensity of feather lice in relation to overhang length of western scrub-jays (redrawn from [2]). Among 20 infested birds, those with intermediate overhangs had the fewest lice (quadratic regression $R^2 = 0.30$, $p < 0.05$). This relationship suggests that lice may exert stabilizing selection for intermediate overhang length, presumably because intermediate overhangs are better at controlling lice. (Online version in colour.)

forward, which creates a shearing force between the tip of the lower mandible and the upper mandibular overhang. Without this overhang, birds are unable to generate the force needed to crush tough, dorsoventrally compressed insects like lice [22].

Although the mandibular overhang is critical for controlling lice, it does not play a role in the control of all ectoparasites. For example, Waite *et al.* [26] showed that pigeons without overhangs are just as effective at controlling hippoboscid flies as pigeons with intact overhangs. Because the flies are much larger than lice, they can apparently be killed without the need for grinding between the upper mandibular overhang and the tip of the lower mandible.

Removal of the mandibular overhang had no impact on the feeding efficiency of pigeons [22], suggesting that the overhang is a specific adaptation for controlling lice and other small ectoparasites. With regard to overhang size, bigger is not necessarily better. Overhangs longer than approximately 1.5 mm break significantly more often than short overhangs [22]. Thus, overhang length may be under stabilizing selection

for intermediate length. Studies of other species of birds also suggest that ectoparasites may exert stabilizing selection on beak morphology. For example, overhang length in wild populations of western scrub-jays (*Aphelocoma californica*) appears to be under stabilizing selection for intermediate length; birds with relatively long overhangs, or relatively short overhangs, have more lice than those with intermediate overhangs (figure 3) [2,35].

Extreme overhangs, such as the hooked bills of raptors or parrots, are adaptations for feeding that presumably play little or no role in preening efficiency [33]. Interestingly, however, Bush *et al.* [36] noted that barn owls (*Tyto alba*) with longer beak hooks are infested with lice more often than owls with shorter hooks. It is not clear how to interpret this result.

Another adaptation that may improve the effectiveness of preening as a means of controlling ectoparasites is uropygial (preen) oil. Most birds have a nipple-like uropygial gland on their rump. They squeeze this protuberance with their bill during preening and spread the secreted oil throughout the
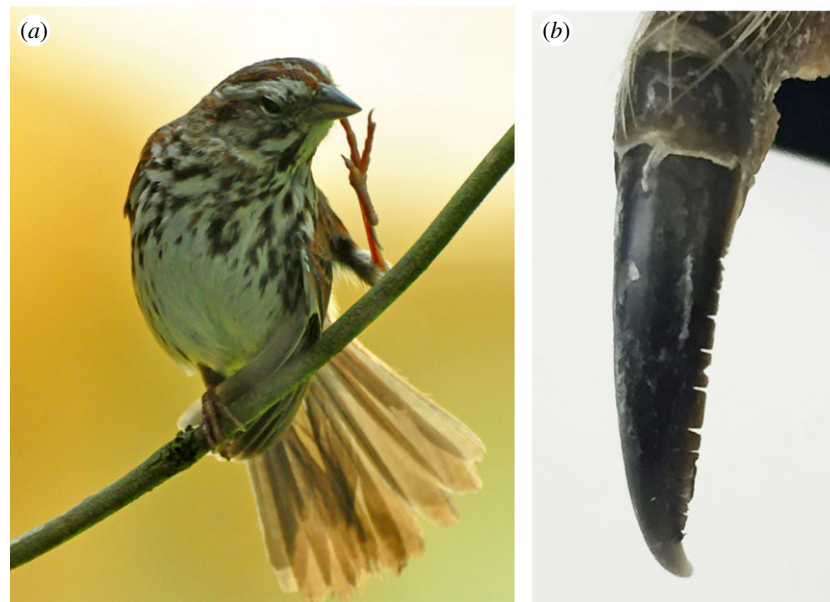
Figure 4. (*a*) Song sparrow scratching (*Melospiza melodia*; Berkeley T. Compton, wikimedia.org). (*b*) Pectinate claw of a barn owl (*T. alba*; SEB). (Online version in colour.)

plumage. Preen oil is known to help in waterproofing feathers. Preen oil may also contain symbiotic bacteria or sequestered toxins [37] that help kill ectoparasitic arthropods and feather degrading bacteria; however, the evidence for anti-parasite activity by preen oil is mixed (see reviews [2,38,39]).

Although preening is an effective means of combating ectoparasites, it has been co-opted as a transmission pathway by other parasites. Ectoparasites like lice and fleas are intermediate hosts of parasitic helminths [40–43]. These helminths are transmitted to avian hosts when the birds ingest ectoparasites during preening [42]. For example, filarioid nematodes (*Eulimdana* spp.) infecting marbled godwits (*Limosa fedoa*) and whimbrels (*Numenius phaeopus*), as well as tapeworms (*Hymenolepis microps*) infecting willow ptarmigans (*Lagopus lagopus*), can all be transmitted through the ingestion of infected feather lice [42–44]. Only a handful of studies have documented this mode of transmission; however, it is likely that other undiscovered parasites exploit this pathway.

(b) Allopreening

Mutual preening, or allopreening (figure 1*b*), may help control avian ectoparasites, just as allogrooming helps control mammalian ectoparasites [45]. Allopreening, which has been observed in more than 50 families of birds, reinforces pair bonds and hierarchies in social species [2,46]. Allopreening also appears to help control ectoparasites on the head and neck, i.e. regions that cannot be self-preened. The importance of allopreening in ectoparasite control was suggested by a field study of tick-infested eudyptid penguins [47]. Unmated penguins, which could only self-preen, had two to three times more ticks on their heads and necks than mated penguins, which engaged in regular allopreening. In another study, Radford & Du Plessis [48] suggested that allopreening in the green woodhoopoe (*Phoeniculus purpureus*) serves both social and parasite control functions. They found that allopreening of self-accessible body regions, such as the wings, back or breast, was influenced by group size and dominance status, indicating a social function. However, allopreening of the head and neck regions occurred at similar rates for dominant and subordinate individuals, suggesting a hygienic function.

More recently, Villa *et al.* [49] reported an inverse correlation between allopreening and feather lice in pigeons. Birds that allopreened less than 2% of the time had a mean of 25.2 lice, compared with a mean of 10.6 lice on birds that allopreened greater than 2% of the time. Generalized linear models in Villa *et al.* [49] show that the correlation between time spent preening and the number of lice per bird is stronger for allopreening than for self-preening. However, the authors claim that '…allopreening was about 17-fold more effective than self-preening' (third page) is misleading. The paper shows that allopreening is better than self-preening at *predicting* the number of lice on birds, not that it is necessarily more effective than self-preening. As discussed above, self-preening is very effective at controlling ectoparasites on regions that a bird can reach. Allopreening may also be effective at controlling ectoparasites on regions that a bird cannot reach, such as the head.

In summary, these studies suggest that allopreening plays a role in controlling ectoparasites. However, other variables, such as differences in overall condition, may influence the negative correlations observed between allopreening and ectoparasites. Thus, the importance of allopreening for ectoparasite control needs further testing.

(c) Scratching

Birds use their feet to scratch regions that cannot be self-preened, such as the head (figure 4*a*). Birds with a deformed or missing leg or foot have large numbers of lice and eggs restricted to their head and neck (which cannot be scratched while standing on the remaining good leg, [23]). Scratching is thought to damage and kill chicken fleas [41]. It may also compensate for inefficient preening in species of birds with unwieldy bills. Comparisons of closely related species show that long-billed species scratch more often than short-billed species. Indeed, long-billed species average 16.2% of their grooming time scratching, compared with only 2.3% of grooming time scratching in short-billed sister taxa [14].

Figure 5. (a) Ashy-crowned sparrow-lark dust bathing (*Eremopterix griseus*; Mymoom Moghul, wikimedia.org). (b) White-breasted nuthatch sunning (*Sitta carolinensis*; kenn3d.smugmug.com). (Online version in colour.)

Some birds have a pectinate claw that may improve the anti-parasite function of scratching. Pectinate claws occur in species from at least 17 families of birds representing 10 orders [2]. However, within most of these families, only some species have pectinate claws. The structure of the claw varies substantially among species, from scalloping to fine serrations, like those of the barn owl (*T. alba*) (figure 4b). The number of teeth on pectinate claws shows intraspecific variation. Individual barn owls with claws that have more teeth are less likely to be infested with lice than those with claws that have fewer teeth [36]. Although this correlation is intriguing, an experimental manipulation of the pectinate claw is needed to test the hypothesis that it plays a role in controlling lice and other ectoparasites.

(d) Water bathing

Rothschild & Clay [50] reported that 'Bathing in water and dust and the subsequent preening helps the bird to rid itself of parasites'. However, we are unaware of any evidence showing that water bathing has a detrimental effect on parasites. On the contrary, water bathing could have a positive effect, given that high humidity favours ectoparasites ranging from feather lice [51] to bacteria [52]. Moreover, avian influenza viruses in water are reported to concentrate on feathers coated with uropygial oil; thus, water bathing, followed by preening, may lead to the accidental ingestion of infectious viral particles [31]. Further work is clearly needed to test the role of water bathing, if any, in parasite control.

(e) Dusting

Birds representing at least a dozen orders perform dusting, in which fine dirt or sand is ruffled through the feathers [2] (figure 5a). This behaviour is thought to remove excess feather oil from the plumage [53,54]. It also combats lice through desiccation, either by killing the lice outright or by increasing their vulnerability to preening. Martin & Mullens [55] allowed chickens with lice to dust using sand, litter or kaolin (fine clay). Dusting with kaolin led to dramatic reductions in lice, but dusting with sand or litter had little effect. Similarly, dusting with sand has no effect on ectoparasitic mites [56].

(f) Sunning

Birds from at least 50 families perform sunning behaviour, in which birds adopt stereotypical postures in direct sunlight (figure 5b) [2,57]. Sunning birds pant and show other signs of heat stress [58–60]. Thus, sunning may be analogous to behavioural 'fever', in which ectotherms, such as lizards, kill pathogens and other parasites by basking in warm spots to increase their body temperature [61].

Sunning may kill ectoparasites by exposing them to ultra-violet (UV) irradiation, which can have toxic effects on insects [62]. Spider mites, which are 'parasites' of plants, avoid UVB radiation by positioning themselves on the shady underside of leaves [63]. Recently, Hori *et al.* [64] found that short-wavelength visible (blue) light is lethal to insect eggs, larvae and adults; however, they also noted that different species of insects vary in their ability to tolerate light exposure. Experiments investigating the susceptibility of avian ectoparasites to irradiation are needed.

Sunning may also kill ectoparasites by desiccating them. Two lines of evidence are consistent with this hypothesis. First, Moyer & Wagenbach [58] exposed lice on model black noddy (*Anous minutus*) wings to sunny versus shady microhabitats in Australia. The duration of exposure was typical of natural sunning bouts, and the temperature of the models was similar to that of sunning live noddies. Significantly more lice died in the sun than shade, suggesting that mere exposure to sun can kill lice, even when preening is not involved. Second, Blem & Blem [60] compared the rate of sunning by fumigated versus non-fumigated violet-green swallows (*Tachycinete thalassina*). Fumigated birds sunned less than controls, suggesting that the motivation to sun decreases when ectoparasites are not present.

Sunlight may also cause ectoparasites to move about on feathers, increasing their vulnerability to preening. Koop *et al.* [65] tested this hypothesis using live mourning doves (*Zenaida macroura*) that were experimentally infested with lice. Birds in direct sunlight did not preen more, nor did they have lower louse loads. However, the study was conducted during relatively cool weather and sunning behaviour was not very frequent (less than 1% of recorded behaviours). Given that sunning behaviour usually occurs on hot summer days [2,58], this experiment should be repeated at a different time of year.

(g) Heterospecific cleaning

Heterospecific cleaning occurs when one species removes ecto-parasites from another species [15]. Heterospecific cleaning of mammals by birds feeding on ectoparasites, such as ticks, is common [66,67]. Birds are seldom the 'clients' in such inter-actions [68]. Perhaps, the best known example where birds benefit involves nestlings of brood parasitic giant cowbirds (*Scaphidura oryzivora*) that reportedly remove parasitic botflies from foster species nest-mates [69]. However, this account, which has been questioned, requires independent confirmation [2,70]. Another example involves adult grayish baywings (*Agelaioides badius*) that remove *Philornis* larvae from their own nestlings, as well as from nestlings of brood parasitic cowbirds (*Molothrus rufoaxillaris*) [71].

Another intriguing example of heterospecific cleaning involved eastern screech owls (*Otus asio*) in nests containing blind snakes (*Leptotyphlops dulcis*) [72]. Scars on the snakes suggested that they were transported to the nest by adult owls, yet not eaten. The authors argued that growth rates of nestlings in nests with snakes were higher because the snakes fed on soft-bodied insect larvae that could have been harmful to the nestlings. However, an experimental test of this hypothesis is needed.

(h) Anointing behaviour

Another possible mechanism for combating lice and other ectoparasites is anointing behaviour, in which birds apply pungent materials to their feathers [73,74]. One of the most intriguing forms of anointing is 'active anting', in which birds crush and smear ants into their plumage, or 'passive anting', in which birds lie on ant mounds or trails and allow ants to crawl through their feathers [75,76]. Anting has been observed in more than 200 species of birds, most of them pas-serines. The fact that birds use ants that secrete formic acid or other pungent fluids suggests that the behaviour may kill or deter ectoparasites. However, there is very little actual evidence in support of this hypothesis [2,76].

An experimental test of anting in European starlings (*Stur-nus vulgaris*) found that starlings with access to wood ants (*Formica rufa*) engaged in anting behaviour, and had plumage that smelled strongly of formic acid, unlike (control) starlings that did not have access to ants [2]. However, there was no sig-nificant difference in the number of mites or lice on birds in anting versus non-anting treatments. Ehrlich *et al.* [77] suggested that anting may control harmful plumage bacteria or fungi; however, Revis & Waller [78] found that formic acid, in the concentrations present in formicine ants, did not have bactericidal or fungicidal effects.

In addition to ants, birds anoint themselves with a diverse array of other items that have anti-parasite properties including millipedes, caterpillars, beetles, plant materials and manufac-tured pesticides [2]. Clayton & Vernon [79] tested whether citrus kills lice. After observing a common grackle (*Quiscalus quiscula*) anointing its feathers with a lime fruit, the authors measured the effect of lime on pigeon lice *in vitro*. Lime juice had no effect, but exposure to vapour from lime rind was lethal. The rind contains D-limonene, a monoterpene that is toxic to cat fleas [80]. Citronella and other citrus components are also known to repel lice [81] and other ectoparasites [82].

Darwin's finches in the Galápagos Islands were recently observed treating their feathers with leaves of the endemic tree *Psidium galapageium*. Experiments *in vitro*, and with human subjects, showed that extracts from these leaves are effective at repelling both mosquitoes and *Philornis downsi* flies [83]. Experiments also showed that leaf extracts slowed the growth of *P. downsi* larvae, which are virulent parasites of Darwin's finches and other land birds in the Galápagos [84]. Despite these lines of evidence, however, no study has shown that birds actually use pungent substances—or ants—to control their parasites. Experiments are needed in which live birds are allowed to ant and their parasite loads are com-pared with control birds that are not allowed to ant. Unfortunately, such experiments are not easy to conduct.

(i) Cosmetic behaviour

At least 13 families of birds are known to apply 'cosmetic' sub-stances to their bodies [2,85], such as skin secretions [86], powder down [87,88] or soil [89,90]. In one of the best known examples, bearded vultures (*Gypaetus barbatus*) stain their plu-mage with soils that are rich in iron oxide. They either rub their plumage in dry red soil, or rub damp red soil into their plu-mage following a bath. Vultures spend up to an hour applying the soil [89]. The adaptive significance of this behav-iour remains unknown. One hypothesis is that it helps birds combat external parasites. However, Frey & Roth-Callies [91] found no significant difference in the survival of lice exposed to a suspension containing iron oxide versus water controls. Arlettaz *et al.* [92] suggested that iron oxides may have antibac-terial properties that help vultures control harmful bacteria on the carcasses they eat. However, Tributsch [90] recently pointed out that known bactericidal activities of iron oxides are photo-catalytic. Consequently, tests of the hypothesized role of this behaviour as a defence against parasites should be done in direct sunlight, rather than *in vitro*, because laboratory lighting may not trigger the predicted photocatalytic reactions [89–91].

3. Nest maintenance behaviour

Birds also have parasites that live primarily in their nests. Fleas, flies, true bugs and some mites spend portions of their life cycle in the nest material, moving temporarily onto nestlings and parents to feed [41]. These parasites can be deadly to nestlings or fledglings [93–95]. Birds show several anti-parasite behaviours that appear to help control nest-based parasites.

(a) Territoriality and colony size

Parasite transmission is often more efficient in dense host populations [96]. Indeed, parasitism is often viewed as a pri-mary cost of sociality [97]. In a recent meta-analysis, Rifkin *et al.* [97] found a positive association between group size and parasite risk, and the association was stronger for birds than for mammals. Antisocial behaviour, such as territoriality, may thus help protect birds against parasites [98]. Even in highly colonial species, such as cliff swallows (*Petrochelidon pyrrhonota*, formerly *Hirundo pyrrhonota*), nesting in small colonies may help protect against ectoparasites [99].

(b) Nest site avoidance

The most effective defence against nest parasites may be to avoid them in the first place. Several studies show that birds detect and avoid nesting (and roosting) sites with ectoparasites [15,99–104]. For example, Oppliger *et al.* [100] experimentally investigated the effects of the blood-feeding hen flea

(*Ceratophyllus gallinae*) on nest-site choice in the great tit (*Parus major*). When offered a choice between adjacent nest-boxes—one with fleas, the other without fleas—significantly more birds chose parasite-free boxes.

Cliff swallows show a similar preference for uninfested nests. Brown & Brown [99] noted that during the early spring, overwintering fleas (*Ceratophyllus celsus*) and swallow bugs (*Oeciacus vicarius*) congregate around the entrances of old swallow nests, where these parasites are better able to infest birds that venture too close. Cliff swallows frequently hover a few centimetres in front of old nests, rather than entering them. This behaviour allows birds to safely inspect the nest opening for ectoparasites [99].

A very different strategy is used by saltmarsh sparrows (*Ammodramus caudacutus*), which nest in areas prone to flooding. Up to 85% of nests get flooded [105]. While flooding can be lethal to nestlings, non-lethal flooding appears to reduce ectoparasites in the nest [106]. However, this pattern covaries with other factors, such as the type of nesting material used. Experimental manipulations are needed to test whether flooding itself reduces ectoparasites, and whether sparrows choose to build nests in areas subject to flooding for this specific reason.

Birds can also avoid ectoparasites on a short-term basis. For example, great tits delay reproduction to minimize infestations by hen fleas [107], which overwinter in the nest cavity. If a host does not use the cavity, the fleas leave in search of hosts elsewhere [108]. Thus, by delaying reproduction, birds reduce their exposure to parasites. In an experimental test of the delayed-reproduction hypothesis, Oppliger *et al.* [100] found that great tits whose nest-boxes were infested with fleas started laying eggs 11 days later than birds with uninfested nest-boxes.

(c) Nest sanitation

In some cases, birds perform nest 'sanitation' behaviour [15]. Female great tits and blue tits (*Cyanistes caeruleus* formerly *Parus caeruleus*) show this behaviour, which Christe *et al.* [109] 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 of flea-infested nests than uninfested nests [109]. Similarly, female blue tits spend more time in sanitation of nests infested with blowfly larvae or fleas [110,111], compared with uninfested nests. Cantarero *et al.* [112] experimentally manipulated nest parasitism by heating nests of pied flycatchers (*Ficedula hypoleuca*) to kill parasites. The frequency and intensity of nest sanitation behaviour was significantly lower in heated nests than unheated controls. Another form of nest sanitation is to clean out nests that have been used before. Male house wrens (*Troglodytes aedon*) remove old nest material from their nest-boxes prior to each reproductive bout. Pacejka *et al.* [113] showed that this behaviour reduces the abundance of mites (*Dermanyssus*) in the nest.

(d) Nest fumigation

Some species of birds incorporate fresh, green vegetation into their nests. This behaviour may have several functions [114], including the use of aromatic plants to fumigate the nest and control nest-based parasites [73,115,116]. An intriguing aspect of this behaviour is that birds selectively choose plants that contain volatile compounds. For example, the nesting habitat of blue tits in Corsica, France includes more than 200 species of plants, yet blue tits only use green vegetation from 10 aromatic species in their nests [114,117]. Similar preferences have been recorded in starlings [118] and raptors [114,119]. The quantity of green vegetation in the nest is negatively correlated with parasite abundance in some studies. For example, a survey of songbirds in Argentina found that botfly parasitism (*Philonis* sp.) was negatively correlated with the presence of green vegetation in the nest [120]. Similarly, a study of Bonelli's eagles (*Hieraaetus fasciatus*) showed that nests with a higher percentage of pine greenery had fewer blow fly larvae (*Protocalliphora*) and higher host reproductive success [121]. The results of these studies are intriguing, but more studies that experimentally manipulate green vegetation are needed. In one of the few experimental studies, Shutler & Campbell [122] added yarrow (*Achillea millefolium*) to the nests of tree swallows (*Tachycineta bicolor*), which reduced fleas in the nest by half, compared with control nests. Interestingly, however, the authors did not find that this reduction in parasites contributed to a change in nestling survival or fledgling success.

European starlings also insert vegetation in their nests. The vegetation dries out and is eventually broken up by nestling birds as they move about in the nest. This process releases volatiles into the air around the nest [123]. Starlings are known to incorporate species of plants with antibiotic and insecticidal properties that reduce the hatching success of parasitic lice (*Menacanthus* sp.) [118]. Wild carrot (*Daucus carota*) or fleabane (*Erigeron philadelphicus*) added to nests reduces the emergence of ectoparasitic mites (*Ornithonyssus sylviarum*) [124]. Indeed, the name 'fleabane' is derived from the fact that its flowers were said to repel and kill fleas and other insects in households [125].

Green vegetation may also help control parasites by stimulating the immune system of the host, which is known as the 'drug hypothesis' [114]. This hypothesis was proposed by Gwinner *et al.* [126] as a potential explanation for the enigmatic results of one of their experiments. Gwinner *et al.* [126] manipulated green vegetation in starling nests but found no difference in the number of ectoparasites (mites, lice and fleas) between experimental and control nests. Interestingly, however, the nestlings from nests with vegetation had significantly higher red blood cell counts and body masses than nestlings from nests without vegetation. The authors argued that the addition of vegetation stimulated the immune system of nestlings, which may have ameliorated detrimental effects of (blood-feeding) ectoparasites, even though it did not change parasite load, *per se*. Similarly, a study with blue tits showed that, in enlarged broods, nestling mass gain was positively affected by the addition of green vegetation [127]. However, there was no ultimate difference in the body mass of nestlings fledgling from nests with added vegetation compared to control nests. In yet another study, the experimental addition of yarrow to tree swallow nests did not stimulate immune function (e.g. leucocyte proliferation) in nestlings [122]. Tree swallows do not add greenery to their own nests; consequently, it is not clear whether the lack of support for the drug hypothesis in this study can be generalized to other species that do fumigate their own nests in the wild. The 'drug hypothesis' is relatively new and the results of relevant studies are conflicting. To critically evaluate the drug hypothesis, more studies are needed to determine if, and under what conditions, the addition of green vegetation stimulates immune function in nestlings.

In conclusion, these studies reveal a link between green vegetation and decreased ectoparasite load, and subsequent

nestling condition. However, there is no experimental evidence that fumigation of nests with green vegetation actually increases fledging success. Disentangling direct effects of green vegetation on parasites from indirect effects through stimulated immune responses requires carefully designed experiments in which green vegetation is manipulated in conjunction with measures of parasite load, immune responsiveness and host reproductive success [114].

Another plant product that has been used by humans to control arthropod pests of poultry and agricultural crops is the nicotine produced by tobacco [128]. Remarkably, house sparrows (Passer domesticus) and house finches (Carpodacus mexicanus) have learned to weave fibres of discarded cigarette butts into their nests, and nests with the highest density of fibres have the lowest density of mites [129,130]. This observation was followed by a series of experiments to test the anti-parasite function of this behaviour. Birds with experimentally elevated mite loads respond by weaving significantly more cigarette fibres into their nests, compared to control nests without mites, or with dead mites (Haemolaelaps sp.; Mesostigmata) [131]. However, nestlings and parents exposed to the fibres also have blood cells with significantly higher levels of genotoxicity (e.g. damaged DNA) than unexposed birds [130]. Thus, it is not yet clear if the incorporation of nicotine laden cigarette fibres into the nest has a net positive or negative effect on host fitness.

(e) Nest desertion

When all else fails, birds can simply abandon nests, rather than continuing to invest in offspring that may be doomed by parasites. Nest desertion is common in the face of brood parasites, such as cowbirds or cuckoos that lay eggs in the nests of foster species. Birds are also known to desert nests when ectoparasite loads are high [93,99,100,132–134]. For example, Duffy [133] showed that argasid ticks (Ornithodoros amblus) cause large-scale desertion of colonial seabird nesting colonies. In another study, whooping cranes (Grus americana), an endangered species being introduced to protected estuaries, abandoned nests in response to black flies in central Wisconsin [135]. Interestingly, sandhill cranes nesting under the same conditions were much less likely to desert their nests. Sandhill cranes, unlike whooping cranes, have nested in the area for thousands of years and frequently engage in higher levels of 'comfort behaviour', such as head rubbing and flicking, which is known to deter flies [136]. This behaviour begs the question: do birds often desert nests to cut reproductive losses, or do they desert nests mainly to escape irritation? Because short-lived species of birds have fewer breeding seasons in which to reproduce, such species should perhaps abandon nests less often than long-lived birds that will be able to attempt to breed again. Comparative and experimental studies are needed to investigate how lifespan affects the decision to desert nests.

4. Avoidance of parasitized prey

Birds may also have behavioural adaptations that allow them to avoid consuming intermediate hosts of parasites. Trophically transmitted parasites, such as gastrointestinal helminths, are known to manipulate the behaviour and morphology of their intermediate hosts (often arthropods and molluscs) to increase transmission to definitive hosts,

such as birds [137]. One such nematode parasite causes its intermediate host, an amphipod (Corophium volutator), to be most active when semipalmated sandpipers (Calidris pusilla) are foraging [138]. Another nematode that infests turtle ants (Cephalotes atratus) causes normally black ants to look like ripe red berries in order to attract frugivorous birds [139]. Although parasites are effective at manipulating intermediate hosts to assure transmission to bird hosts, there is evidence that birds may be able to avoid infested prey. For example, oystercatchers (Haematopus ostralegus) avoid eating the largest cockles, which are likely to be infested with parasitic helminths. Instead, oystercatchers appear to balance foraging efficiency and parasite avoidance by feeding on intermediate sized cockles [140]. Similarly, Stellar's eiders (Polysticta stelleri) seem to avoid eating infected amphipods unless they are starving [141]. The pervasiveness of anti-parasite foraging behaviour among birds should be heavily dependent on the cost of parasitism [142]. However, little is known about whether most trophically transmitted parasites actually reduce avian host fitness. A broader understanding of parasite avoidance in foraging birds would benefit from analysis of the fitness cost of trophically transmitted parasites, relative to the strength of avian avoidance behaviours.

5. Migration

Migration is an energetically costly behaviour that provides migrants access to rich, seasonal resources [143]. Recent studies argue that migration may also reduce the risk of infection by pathogens and parasites [144–146]. Migratory behaviour may reduce the cost of parasitism in several ways [146]. First, birds may be able to spatially and temporally escape from parasites by moving [144,147]. This strategy, known as 'migratory escape', may be particularly effective for birds that breed in dense populations that facilitate parasite transmission [148,149]. Second, 'migratory culling' occurs when parasitized individuals suffer high mortality during migration. Death of infected individuals during migration may lower the risk of infection for individuals that successfully migrate [147]. Third, 'migratory recovery' is yet another possible anti-parasite mechanism. Shaw & Binning [146] suggest that changes experienced by a host during migration may make it unsuitable for parasites. Changes in the internal environment of a bird as a consequence of starvation, dehydration or changing diets over the migratory route may reduce some internal parasites. Similarly, different temperatures, humidities, altitudes and oxygen levels may reduce parasites on the external surfaces of migrating birds. Thus, by migrating, infected hosts may eliminate or reduce parasites. To our knowledge, this hypothesis has not been tested using bird–parasite systems.

On the other hand, migration may actually increase susceptibility to parasites and pathogens. The physiological stress of migration could weaken host defences. Migrants may also suffer from greater exposure to parasites as they encounter parasites on both their breeding and wintering grounds, as well as along their migratory route [146]. Gregory [150] found a positive relationship between distance flown by migratory waterfowl and their parasite species richness. Similarly, Koprivnikar & Leung [151] compared the nematode species richness of migratory and non-migratory species in three orders of birds: Anseriformes (ducks, geese and swans), Accipitriformes (eagles, hawks and falcons) and Passeriformes: Turdidae

(thrushes). They found that, in all three orders, nematode species richness was two to three times higher in migratory than non-migratory species. A similar pattern has been shown for avian blood parasites (haematozoa). Figuerola & Green [152] reported that the generic and species richness of blood parasites infecting waterfowl was positively correlated with migration distance. By contrast, other studies show little or no correlation between migration distance and the prevalence or intensity of blood or helminth parasites [153–155].

Further research is needed to test the possible anti-parasite function of migratory behaviour. Studies on this topic may be especially important for wildlife management and conservation, as migratory patterns change in response to reduced habitat availability and climate change [156].

6. Tolerance

Another form of anti-parasite defence is tolerance, in which hosts compensate for parasite damage, rather than combating parasites directly. For example, hosts may be able to tolerate parasites by investing more energy in maintaining homeostasis or repairing damaged tissue in the face of parasitism [157,158]. Birds also appear to use tolerance as a strategy for defence against parasites. For example, Christe *et al.* [159] found that hen fleas (*C. gallinae*) reduce the size of great tit nestlings. However, they also found that nestlings in parasitized broods beg twice as much as nestlings in unparasitized nests. The parents respond to the increase in begging and increase their rate of provisioning by 50% [159]. Similarly, Tripet *et al.* [111] found that female blue tits (*Cyanistes caeruleus*) with nestlings in highly flea-infested nests provisioned nestlings at a rate three times greater than females with nestlings in nests with small numbers of fleas.

By contrast, Morrison & Johnson [160] found no increase in the provisioning of nestling house wrens that were heavily parasitized by fly larvae and mites. In this case, parasitized nestlings may have been too anaemic or weak to increase rates of begging to signal parents of the increased need for food. Cantarero *et al.* [112] found that pied flycatcher (*F. hypoleuca*) young in nests with high parasite loads begged more than young in nests with fewer parasites; in this case, however, there was no significant increase in parental provisioning. They speculated that parents were physiologically constrained and unable to increase provisioning to meet nestling demands, as shown in other studies with pied flycatchers [112,161].

Although tolerance may be a useful defence for some species of birds, it may actually increase the detrimental effects of parasites on other members of the bird community. For example, the invasive parasitic nest fly *P. downsi* has devastating effects on the nesting success of Darwin's finches [162]. Interestingly, however, Galápagos mockingbirds (*Mimus parvulus*), which are also hosts of *P. downsi*, are able to tolerate the fly [163]. Mockingbird nestlings in parasitized nests beg more and parents increase the rate of provisioning. By contrast, the medium ground finch (*Geospiza fortis*), which is a species of Darwin's finch that lives in the same habitat as the Galápagos mockingbird, is not tolerant of *P. downsi*. Parasitized medium ground finch nestlings do not beg more, and parental provisioning is not increased. Consequently, medium ground finches suffer high rates of nestling mortality in the face of the parasite [163]. Tolerant mockingbirds living in the same habitat as medium ground finches may be reservoir hosts that amplify the threat of *P. downsi* to finches [84].

7. Conclusion

We have provided a brief overview of how birds use behaviour to combat parasites. Unfortunately, much of the work remains observational in nature. The best approach for testing the adaptive function of a hypothesized anti-parasite behaviour is to manipulate the behaviour experimentally and measure the effect on parasite load. The effect of altered parasite load on host fitness should ideally also be measured because fitness is the 'currency' of adaptive evolution. Much of what we do know is from model systems (e.g. poultry and pigeons) because these species are well suited for experimental manipulations. It is likely that behavioural and morphological adaptations identified for parasite control in these systems are applicable to other birds; however, studies with other species are needed to assess the generality of results from the model systems.

In summary, the topic of anti-parasite behaviour in birds is poorly understood, as much of the available information merely forms a catalogue of behaviours that may matter for parasite control. Future advances in this field will require experimental manipulations that accurately determine the cause and effect of each of these purported anti-parasite behaviours. Once the adaptive bases of these behaviours are more firmly established, the condition dependency of behaviours can be more thoroughly assessed. For example, are behavioural defences 'primed', analogous to the immune system? Is early exposure to parasites important in the proper development of efficient anti-parasite behaviours? Are behavioural defences against parasites mainly constitutive or inducible? Is most anti-parasite behaviour energetically expensive and, if so, is it reversible?

Most research on anti-parasite behaviour tends to focus on single behaviours. Yet, work is also needed concerning how different behaviours interact. At least two major kinds of interactions are possible. First, different behaviours can complement one another, targeting different parasites and sites of infection. For example, preening controls parasites on the body, while scratching may help control parasites on the head. Allopreening may also help control parasites on the head. Are scratching and allopreening additive in their effects, or synergistic? How do behavioural and immunological defences interact? Does local inflammation (an acquired immune response) help direct preening to the sites of infestation on the body of the host? These and many other questions await answers.

These are exciting times for researchers interested in conducting experiments designed to answer long-standing questions regarding the adaptive significance of anti-parasite behaviour in birds.

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