

Mites and birds: diversity, parasitism and coevolution

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Bird–ectoparasite associations have provided many influential examples of parasite-mediated evolution and ecology^{1–5}. Among these studies, mites, lice and fleas are the most frequently studied parasites. Although the diets and life histories of insect parasites, such as lice and fleas, are relatively consistent within each taxon, those of mites are not so easily pigeon-holed. Mites are an ancient, taxonomically diverse group of arachnids that exhibit astonishing flexibility in their life histories (Box 1). Unlike lice and fleas, they have evolved parasitism (Box 2) on many phylogenetically independent occasions⁶. Their small bodies allow them to exploit habitats too cramped and food sources too meagre for insects, and their life cycles are often many times more rapid⁷. Relationships between mites and birds are also surprisingly diverse. Although some mites are detrimental, others are benign or might even be beneficial to their avian hosts⁶ (Box 2). Perhaps because of this great ecological diversity, studies on seemingly similar bird–mite systems often return conflicting or even contradictory results. Here, we provide a primer on bird associated mites, summarize how they have been used to test hypotheses about host life history, sexual selection, immunocompetence and cospeciation, and highlight important areas for future study.

Diversity of bird–mite relationships

At least 2500 species of mites from 40 families are closely associated with birds, occupying all conceivable habitats on the bodies and nests of their hosts (Box 1, Table 1). No avian taxon is free from a mite associate, because even those that lack feather mites, such as penguins, are attacked by ticks⁸. Bird mites can be divided into those that dwell primarily in, or near, the nest and those that reside mainly on the body of the host.

The best studied nest-dwelling mites are blood feeders from the genera *Dermanyssus* and *Ornithonyssus* (Fig. 1). Although they are commonly termed ‘fowl mites’, their natural hosts are more likely to be small passerines rather than domestic poultry (F. Radovsky, pers. commun.) (Table 1). Depending on the exact species involved, adults of these blood feeders live in the nest or on the hosts, but nymphal stages are primarily nestbound and only visit hosts when they need to feed⁹. These mites have short generation times⁷ and can rapidly build-up huge populations;

Ectoparasites play important roles in the lives of birds. Among these parasites, mites offer unique potential because of their extraordinary ecological and evolutionary diversity. However, the basic biology of most mites is poorly understood, and misleading extrapolations are sometimes made from better studied systems involving lice and fleas. Most importantly, not all bird-associated mites are parasitic; indeed, recent research suggests that some might even be beneficial. Here, we summarize what is known about the diversity of bird–mite relationships, and highlight how mites provide an ideal tool for the study of host life histories, sexual selection, immunocompetence and cospeciation.

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for example, half a million northern fowl mites have been extracted from a single nest¹⁰. Ticks can also be temporary nest parasites. Soft ticks visit the host at night, feed for a few minutes and then retreat to a refuge in, or near, the nest¹¹ (Fig. 2). Hard ticks tend not to be so nestbound and will attack birds as they brush against vegetation during foraging or resting. However, not all nest mites are parasitic. Relatives of human-associated ‘dust mites’ feed on the dermal detritus that sifts down into the nest material. Other nest dwelling mites prey on blood-sucking mites^{12,13}, and thus might act as mutualists (Table 1).

The skin, respiratory passages and feathers of birds all provide habitats for mites (Table 1; Box 2). In some groups, adult mites are nonparasitic scavengers in the nest and deutonymphs (a juvenile stage) are subcutaneous parasites. In other groups, both adults and nymphs burrow into the skin, causing dermal nodules and ‘scaly-leg’, in which the skin of the leg swells and becomes encrusted. Most other groups of skin-associated mites (e.g. ticks and chiggers) are only temporarily attached to the epidermis by their mouthparts.

Among the mites that dwell in the respiratory tract, the most transient are hummingbird-flower mites, which feed on nectar and pollen, and use the nostrils of hummingbirds as travelling chambers for trips between flowers. Although they are not parasitic, these mites compete with hummingbirds for nectar¹⁴. Other respiratory mites directly harm the host. For example, the parasitic canary lung mite has recently invaded the respiratory tract of the Gouldian finch (*Erythrura gouldiae*)⁹ and could be contributing to the decline of this species.

Feathers provide a habitat for the greatest diversity of bird-associated mites, some of which live on feather surfaces (plumicoles), while others live inside the quills (syringicoles) (Table 1) (Figs 3,4). Feather mites have received much taxonomic study¹⁵, but surprisingly little is understood about their basic biology. Most of our knowledge comes from a series of monographs by the Russian worker V.B. Dubinin¹⁶. Although one might expect that, like feather lice, feather mites consume feathers, the food of plumicolous feather mites consists mainly of uropygial-gland oil (predominantly waxes and fatty acids¹⁷), and scurf, pollen and fungi that adhere to the feather barbs^{6,16}. Feather particles have rarely been observed in the guts of plumicolous feather mites, their mouth parts are designed

less for chewing than for scraping, and feathers on which mites are found show little evidence of having been nibbled¹⁶. However, many syringicolous feather mites eat the medulla (pith) of the quill^{15,16} and could thus weaken the feathers.

Host life history

Although not all mites associated with birds are parasitic, some species do have a strong influence on their hosts' life history. The most compelling evidence for the effects of mites on birds comes from controlled laboratory studies on domestic fowl^{18,19}, but such work is limited in its taxonomic scope. Among field studies, those that involve manipulation of mite load provide better evidence than those based on correlational observations. Although there have been several manipulative studies of nest-associated mites^{2,3,10,13,20}, to our knowledge all studies of feather mites are correlative. Nevertheless, we present the results of this research because ultimately all experiments are instigated by original correlative observations. We hope that the ambiguities apparent in these observations of feather mites will encourage researchers to take the next essential experimental step.

Condition and survival

Nest mites, ticks and other taxa that feed on living tissues adversely affect the health of their hosts in many ways (Table 2), from inducing anaemia to causing death through asphyxiation. Some mites even secrete noxious substances that can disable their avian hosts. For example, feeding by the tick *Argas wakleri* induces 'fowl paralysis' in chickens. The paralysis, which can be fatal, is caused by a protein in the tick's saliva that appears to interfere with cellular transport mechanisms²¹.

Evidence for negative effects of feather-dwelling mites is more equivocal. Although many researchers have described plumicolous feather mites as parasites^{22–24}, other studies indicate that they are more likely to be commensals (Box 2) or even mutualists^{25,26}. Indeed, of the approximately 2000 species of plumicolous feather mites, only two taxa are known to harm their hosts by inducing depluming (Table 2). In both cases, the hosts are domesticated and are restricted in their normal flight activities. Evidence from wild populations is contradictory. Thompson *et al.*²³ found that high loads of feather mites on house finches (*Carpodacus mexicanus*) were associated with pox lesions and poor feather quality after moult. Similarly, Harper²⁴ found a negative correlation between feather mite load, body condition and plumage brightness in several species of passerines. By contrast, Blanco *et al.*²⁵ observed that red-billed coughts (*Pyrhcorax pyrrhcorax*) with high numbers of feather mites were in better condition than those with lighter loads. They suggest that these mites might benefit the birds, perhaps by controlling the growth of fungi or bacteria. It is clear that manipulative studies, such as those used to test the relationship between feather-chewing lice and their hosts⁵, are vital to resolve this conflict.

Reproductive success

Blood-feeding nest mites can reduce the reproductive success of their hosts by slowing development or even killing chicks (Table 2). For example, recent experimental work has shown that high densities of nest mites are associated with low haematocrit and small body size in pied flycatchers (*Ficedula hypoleuca*)^{27,28}, and low hatching success and postfledging survival in rock doves (*Columba livia*)³ and barn swallows (*Hirundo rustica*)²⁹. By contrast, however,

Box 1. What are mites?

Mites are chelicerate arthropods in the class Arachnida, subclass Acari. There are approximately 45 000 named species of mites but their true diversity is probably greater than one million species⁶. Morphologically, mites are minute (from 80 µm to a maximum of 3 cm for fully engorged ticks), are octopod as nymphs and adults, are hexapod as larvae, and have only a single body tagma composed of a fused cephalothorax and abdomen. The full complement of life history stages includes egg, larva, protonymph, deutonymph, tritonymph and adult; however, many species have a truncated life history, whereas a few (e.g. argasid ticks) have additional nymphal instars.

Of the three orders of mites – Opilioacariformes, Parasitiformes and Acariformes – the latter two are the most diverse and contain many bird-associated taxa. There are three suborders within the Parasitiformes: Holothyrida, Ixodida and Mesostigmata. Holothyridans have no known associations with birds, but the Ixodida (ticks) and Mesostigmata include many species of temporary and permanent avian symbiotes (note that the phrase 'mites and ticks' implies that these groups are co-equal; however, ticks are simply one small – ca. 800 spp. – group of mites). Within the Acariformes, the greatest diversity of avian associates occurs within the suborder Sarcotiformes, which includes feather mites, skin mites and nest-dwelling dust mites, all of which are placed within the infraorder Astigmata. Of the other two acariform groups, the suborder Trombidiformes (also known as Prostigmata) has a more modest array of bird symbiotes, whereas the suborder Endeostigmata has none. References to the taxonomy and ecology of mites can be found in Walter and Proctor⁶.

Box 2. Glossary

Symbiosis: a general term referring to a close physical relationship between members of two species, in which individuals of one species live near, on or in those of the other species. Symbiosis does not imply mutualism.

Host: the larger-bodied member in a symbiotic relationship.

Mutualism: a symbiosis in which the relationship benefits both members.

Parasitism: a symbiosis in which one member (the parasite) benefits through the use of resources gathered by the other member (the host); the parasite does not need to kill the host to gain this benefit, but the host does suffer some negative effects.

Commensalism: a symbiosis in which one member benefits from the relationship, but the other neither gains nor loses.

Phoresy: a symbiosis in which the smaller-bodied member uses the host primarily for transport.

Darolová *et al.*³⁰ observed a positive association between the percentage of penduline tit (*Remiz pendulinus*) nestlings that survived to fledging and the number of haematophagous mites in the nest. The authors suggest that nestling health determines mite load rather than vice versa. Other researchers have found no relationship between nest–parasite density and nesting success^{13,31}. Merino and Potti³² suggest that variable effects of nest parasites are, in part, a result of stochastic climatic factors, such as temperature and rainfall. New work is urgently required to establish why the effects of nest mites on host reproductive success are so variable across studies.

Mites as vectors of disease

As well as having direct effects upon their hosts, haematophagous mites can transmit viral, rickettsial and protozoan diseases among birds^{9,21}. Obvious candidates for vectors are haematophagous mites that feed repeatedly on many hosts. For example, the red fowl mite, *Dermanyssus gallinae*, is a vector of equine encephalitis virus among poultry¹⁹. Mites can also spread disease even if each mite bites only a single host. This is because some disease-causing pathogens, such as avian borreliosis, can be passed vertically from a female mite to her offspring (transovarial transmission)³³. However, the realized role of mites as vectors of disease in wild populations of birds remains to be investigated.

Table 1. Diversity of mites associated with birds^{a,b}

Suborder or infraorder (see Box 1)	Family, representative genera or species and common names	Habitat	Relationship and diet ^c
Ixodida	Ixodidae (<i>Ixodes</i> and <i>Amblyomma</i> – ‘hard ticks’)	On skin	Parasitic (feed on blood); also prey for birds that feed on ticks (e.g. oxpeckers)
	Argasidae (<i>Argas</i> and <i>Ornithodoros</i> – ‘soft ticks’)	On skin and near and/or in nests	Parasitic (feed on blood); also prey for tick-eating birds
Mesostigmata	Ascidae (<i>Proctolaelaps</i> and <i>Rhinoseius</i> – ‘hummingbird-flower’ mites)	In nostrils of hummingbirds	Phoretic (mites hitch rides from flower to flower)
	Dermanyssidae (<i>Dermanyssus gallinae</i> – ‘red fowl’ mite)	In nests and on skin	Parasitic (feed on blood)
	Laelapidae (<i>Androlaelaps</i> and <i>Haemogamasus</i>)	In nests and on skin	Obligately or facultatively parasitic (feed on the blood of nestlings), or potential mutualists (predatory on blood-feeding mites)
	Macronyssidae (<i>Ornithonyssus sylviarum</i> – ‘northern fowl’ mite; <i>Ornithonyssus bursa</i> – ‘tropical fowl’ mite)	On skin and in nests	Parasitic (feed on blood)
	Rhinonyssidae (<i>Sternostoma tracheacolum</i> – ‘canary lung’ mite)	In nasal passages and tracheal tissues	Parasitic (feeds on blood)
Astigmata	Acaridae (<i>Acarus</i>)	In nests	Commensal (feed on detritus)
	Analgoidea, Freyanoidea and Pterolichoidea (contain ~25 families of feather-dwelling mites) ^d	On or in feathers	Commensal to mildly parasitic, possibly mutualistic (feed on feather oils or pith in calamus)
	Cytoditidae (<i>Cytonyssus</i> and <i>Cytodites</i>)	Peritoneum, nasal passages, lungs and air sacs	Parasitic? (feed on host tissues?)
	Epidermoptidae (<i>Epidermoptes</i> and <i>Microlichus</i>)	Epi- and subcutaneously	Parasitic? (feed on host tissues?)
	Hypodectidae (<i>Hypodectes</i>)	Subcutaneous as deutonymphs and nest-dwelling in other stages	Parasitic as deutonymphs (absorb nutrients from host tissues), commensal in nest otherwise
	Knemidocoptidae (<i>Knemidocoptes</i>)	Subcutaneous in skin of body, face and legs; rarely in feathers	Parasitic (feed on host tissues, eat pith of quill)
	Laminosioptidae (<i>Laminosioptes</i>)	Subcutaneous	Parasitic? (feed on host tissues?)
	Pyroglyphidae (<i>Dermatophagoides</i> – ‘dust mites’)	In nests and on skin and feathers	Commensal (feed on skin flakes and fungus)
Turbinoptidae (<i>Turbinoptes</i>)	Nasal passages	Parasitic? (feed on host tissues?)	
Trombidiformes (Prostigmata)	Cheyletidae (<i>Cheyletus</i> and <i>Cheletonella</i>)	In nests, on skin and on and/or in feathers of hosts	Mutualistic and facultatively parasitic (?) (feed on other symbiotes and possibly on host skin)
	Cheyletiellidae (<i>Bakericheyla</i> and <i>Ornithocheyla</i>)	On skin of hosts	Parasitic (feed on skin of host)
	Cloacaridae (<i>Pneumophagus</i>)	In lungs	Parasitic? (feed on host tissues?)
	Ereynetidae (<i>Boydala</i>)	Nasal mucosae	Parasitic (feed on blood)
	Harpyrhynchidae (<i>Harpyrhynchus</i>)	In skin and feathers	Parasitic? (feed on host tissues?)
	Syringophilidae (<i>Syringophiloides</i>)	In quills of feathers	Parasitic (feed on host fluids by piercing through quill)
	Trombiculidae (<i>Neoschöngastia</i> – ‘chiggers’) and Lueuwenhoekidae (<i>Apolonia</i> – ‘chiggers’)	On skin of hosts	Parasitic (feed on liquefied tissues)

^aData from Refs 6,9,15.

^bNot all members of a listed family are necessarily avian symbiotes.

^cKey: ? = diet and relationship uncertain.

^dClassification of feather mites according to Gaud and Atyeo¹⁵.

Host sexual selection

Parasites affect a host’s mating success by reducing its probability of being chosen as a mate, either on the basis of ‘good genes’ or via direct effects (e.g. parental care or parasite transfer). Most studies of the role of mites in determining avian mating success have involved blood-feeding mites. Møller’s² manipulative experiments on the interaction between tropical fowl mites and barn swallows have revealed evidence supporting the good genes hypoth-

esis: males with extravagant sexual ornaments produce offspring with low mite loads, males with few mites are more likely to attract mates, high mite loads reduce song output, males from heavily parasitized nests develop more asymmetrical sexual ornaments, and, most importantly, host resistance to mites appears heritable. Similarly, Darolová *et al.*³⁰ observed a negative relationship between the width of the sexually selected ‘mask’ of male penduline tits and levels of blood-feeding mites in their nests. However, some

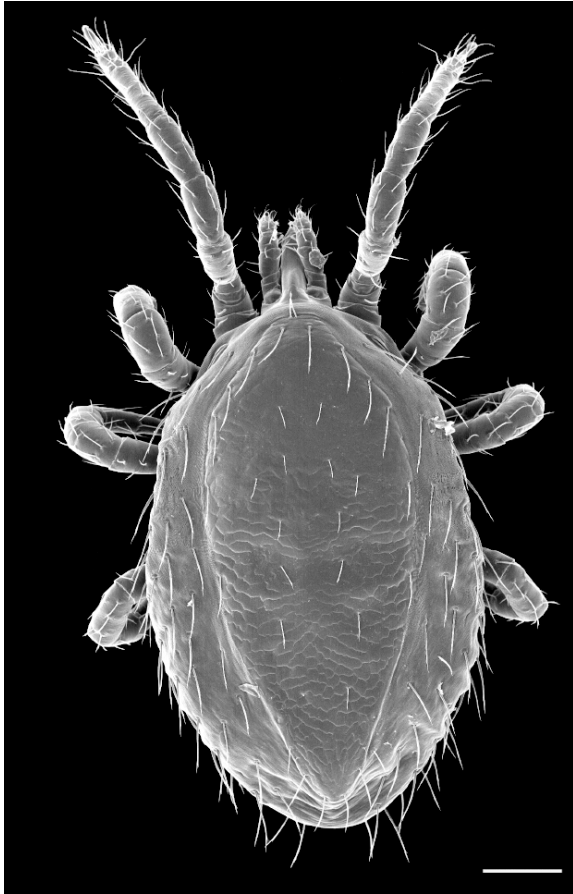


Fig. 1. Scanning electron micrograph of a female *Ornithonyssus bursa* (Mesostigmata: Macronyssidae), a common nest parasite of passerines. Scale bar = 100 μm . Micrograph reproduced, with permission, from Dave Walter, University of Queensland.

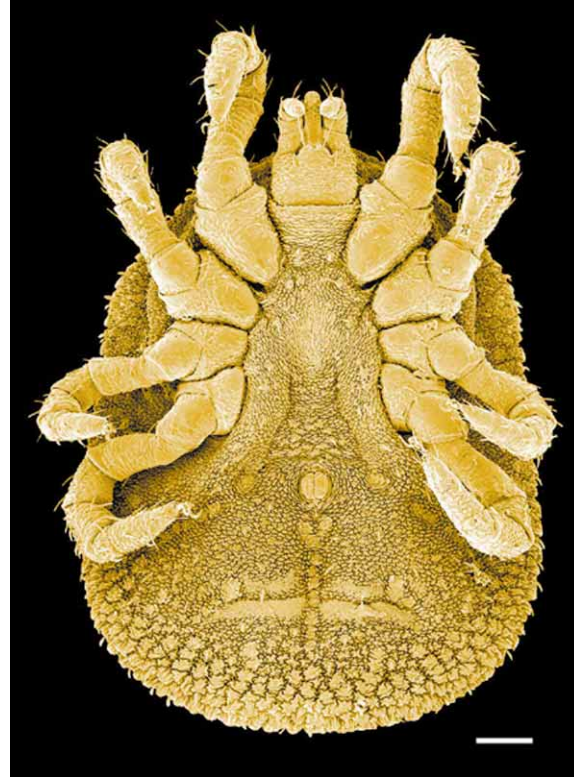


Fig. 2. Scanning electron micrograph of a nymphal soft tick (Ixodida: Argasidae). Scale bar = 100 μm . Micrograph reproduced, with permission, from Dave Walter, University of Queensland.

studies report no relationship between haematophagous mite load and the ability to perform sexual displays³⁴, and others have found high mite loads to be correlated with brighter plumage³⁵. Again, it is not known why different studies return such conflicting results.

There have been few studies of feather mites and sexual characters in birds. Thompson *et al.*²³ found that male house finches with few, or no, feather mites before their moult increased in rank of plumage brightness after moult, whereas heavily laden males decreased in rank. Conversely, Blanco *et al.*²⁶ found no relationship between feather mite load and intensity of carotenoid pigment in male linnets (*Carduelis cannabina*). Once again, our understanding of feather mites lags well behind that of insect ectoparasites, where recent studies suggest that some sexual ornaments are designed specifically to reveal damage from lice³⁶. We know of no manipulative studies of the role of feather mites in host sexual selection.

Behavioural and physiological immunocompetence

Transmission of mites between birds

For most mite species, transmission between hosts occurs through physical contact between mite-bearing individuals and their offspring, mates or members of communal roosts. Undoubtedly, this is the primary route of transmission for plumicolous feather mites, which die within 3–10 days after removal from the host¹⁶ and are too morphologically specialized to walk well on nonfeather surfaces. However, ticks and nest mites are able to walk from host to

host, and transfer rates are probably higher in species that nest communally^{3,11}. Some skin mites move between hosts by hitching rides on hippoboscid flies¹⁵. Theory predicts that parasites transmitted horizontally, such as many nest mites, should be more virulent than vertically transmitted parasites. Although this has been tested across taxonomically disparate parasites (feather lice versus nest mites³), it would be valuable to make this comparison between more closely related parasites (e.g. syringophilid quill mites versus chiggers).

Behavioural avoidance of mites

Barclay³⁷ and Møller² found that barn swallows avoid using old nests containing haematophagous mites. By contrast, male house wrens (*Troglodytes aedon*) prefer nest boxes containing old nests, but remove most of the nesting material



Fig. 3. Scanning electron micrograph of a pair of feather mites *in copula* (Astigmata: Pterolichidae), collected from a pale-headed rosella (Psittacidae: *Platyercus eximius*); the male is on the right. Scale bar = 100 μm . Micrograph reproduced, with permission, from Dave Walter, University of Queensland.

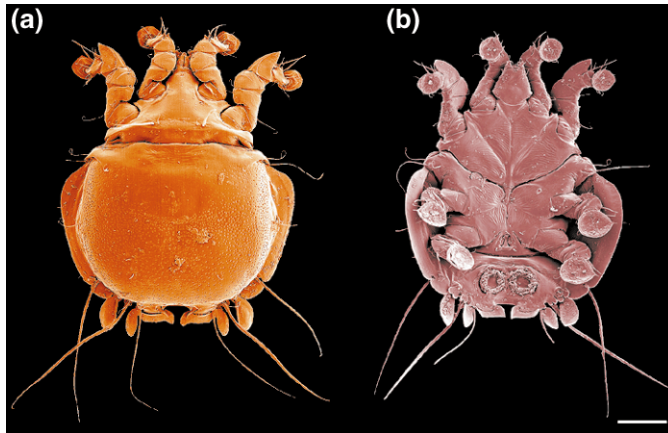


Fig. 4. Dorsal (a) and ventral (b) views of a male feather mite (Astigmata: Freyanidae) showing the sucker-like ventral setae used to hold the female during copulation. Scale bar = 100 μ m. Micrograph reproduced, with permission, from Dave Walter, University of Queensland.

before laying begins¹³, thus significantly reducing the number of nest mites. Many species of birds incorporate sprigs of aromatic foliage in their nest material that could act as antiarthropod fumigants¹⁰. Clark¹⁰ found that starling nests lined with a North American herb averaged 11 000 northern fowl mites at the end of the breeding period, whereas nests without the herb contained approximately 500 000 mites. Recently, however, Gwinner *et al.*²⁰ repeated the study using plants typically included by starlings in Europe and found no reduction in numbers of red fowl mites.

Both auto- and allopreening remove ectoparasites. Birds with impaired grooming ability often⁵, but not always²⁵, have higher arthropod loads. Brooke⁸ found that penguins that were preened by their mates were much less likely to bear ticks than were unmated penguins. Host behaviours such as sunbathing and anting (in which a bird picks up ants and rubs them through its feathers) might also help rid birds of ectoparasites¹⁶; however, evidence that anting reduces louse and mite loads is weak at best³⁸.

Table 2. Effects of mites on their hosts^a

Action of mite on host	Host	Mite	Refs
Damage integument (skin or feathers)	Wild and domestic birds	Skin mites (Knemidocoptidae)	9
	Poultry	Skin mite (<i>Laminosioptes cysticola</i>)	9
	Galliform birds	Skin mite (<i>Epidermoptes bilobatus</i>)	9
	Parrots	Syringicolous feather mites (<i>Cystoidosoma</i>)	6
	'Birds'	Syringicolous feather mites (<i>Syringobia</i>)	16
Induce depluming	Budgerigars (<i>Melopsittacus undulatus</i>)	Plumicolous feather mite (<i>Dubininia melopsittaci</i>)	15
	Domestic chickens	Plumicolous feather mites (<i>Megninia</i>)	15
	Poultry, pheasants and geese	Skin mites (<i>Knemidocoptes</i>)	9
Increase feather asymmetry	Barn swallows (<i>Hirundo rustica</i>)	Tropical fowl mite (<i>Ornithonyssus bursa</i>)	2
Transmit disease	Poultry	Soft tick (<i>Argas persicus</i>)	9
	Domestic chickens	Red fowl mite (<i>Dermanyssus gallinae</i>)	19
Induce paralysis	Poultry	Soft ticks (<i>Argas</i> spp.)	9
Reduce fecundity (for female hosts)	Domestic chickens	Red fowl mite (<i>Dermanyssus gallinae</i>) and northern fowl mite (<i>Ornithonyssus sylviarum</i>)	9
Reduce virility (for male hosts)	Domestic chickens	Northern fowl mite (<i>Ornithonyssus sylviarum</i>)	6
Cause nest abandonment	Colonial birds	Ticks (Ixodida)	11
	Rock doves (<i>Columba livia</i>)	Red fowl mite (<i>Dermanyssus gallinae</i>)	3
Compete for food	Hummingbirds	Hummingbird-flower mite (<i>Proctolaelaps kirmsei</i>)	14
Reduce growth rate or survival (in juvenile hosts)	Rock doves	Red fowl mite (<i>Dermanyssus gallinae</i>)	3
	Cattle egrets (<i>Ardeola ibis</i>)	Soft tick (<i>Argas robertsi</i>)	46
	Pied flycatchers (<i>Ficedula hypoleuca</i>)	Fowl mite (<i>Dermanyssus gallinoides</i>)	27
Reduce haematocrit	Pied flycatchers	Fowl mite (<i>Dermanyssus gallinoides</i>)	28
	Poultry	Soft tick (<i>Argas persicus</i>)	9
	Starling (<i>Sturnus vulgaris</i>)	Red fowl mite (<i>Dermanyssus gallinae</i>)	20
Affect sexual size-dimorphism	Pied flycatchers (<i>Ficedula hypoleuca</i>)	Fowl mite (<i>Dermanyssus gallinoides</i>)	27
Feed on nest parasites (possible mutualism)	House wren (<i>Troglodytes aedon</i>)	Laelapid mite (<i>Androlaelaps casalis</i>)	13
	Tree swallow (<i>Tachycineta bicolor</i>) and house wren (<i>Troglodytes aedon</i>)	Cheyletid mite (<i>Chelotomorpha lepidopterorum</i>)	12
Eat feather-inhabiting fungi (possible mutualism)	Red-billed chough (<i>Pyrrhocorax pyrrhocorax</i>)	Plumicolous feather mite (<i>Gabucinia delibata</i>)	25

^aThis list is not exhaustive.

Immunological arms race

Vertebrate immune responses to parasitic mites are best understood in mammal–tick systems, where immunity is acquired through a combination of cell- and humoral-mediated responses³⁹. Cell-mediated responses cause inflammation at the site of the bite, which prevents the mite from obtaining a blood meal. Humoral responses involve antibodies that bind with proteins in the mite's saliva and prevent it from feeding effectively, or that inhibit nutrient absorption in the mite's gut. However, mites are not passive targets for host immune defences. Mammal-associated ticks have developed an impressive array of mechanisms to overcome host immunity⁴⁰, including substances in the saliva that act as anticoagulants and prevent inflammation responses.

Immunological studies of bird–mite systems are less common, but have parallels with those for mammal–tick interactions. DeVaney and Augustine¹⁸ found that domestic hens developed a humoral antibody after several days of being infested with tropical fowl mites, and that the appearance of the antibody was correlated with a reduction in population growth rate of the mites. Gwinner *et al.*²⁰ used a field test to show that starlings in nests with high loads of red fowl mites had a greater immune response when injected with a foreign protein than did those from nests with low mite loads, thus suggesting that the nestlings' immune systems were 'primed' to withstand the effects of mite feeding. Another recent study found that the presence of ticks increased the concentration of immunoglobulins in the blood of nestling sand martins (*Riparia riparia*)⁴¹.

Cospeciation

Bird–mite systems represent an underexploited resource for those interested in the evolution of symbiosis (Box 2). In contrast to lice and fleas, whose evolutionary origins are unclear, most lineages of bird-associated mites have extant free-living relatives. Likewise, a range of dependence on the host (e.g. nest-dwelling predators, occasional feeders at wounds and obligate blood feeders) can be observed in closely related groups of symbiotic mites⁶, making them ideal subjects for comparative studies. Despite this, there are virtually no studies of coadaptation or cospeciation in mites and birds.

A high degree of host specificity is a prerequisite for cospeciation. Many taxa of feather mites are strongly host specific, and are thus probable candidates for cospeciation between host and symbiote (Box 3). Reasons for this specificity include morphological adaptation by mites to the feather structure of their host^{15,16,42}, host-specific uropygial secretions¹⁷ and the need for close contact between hosts for transfer. However, rigorous tests of cospeciation between birds and feather mites are rare. Dabert and Ehrnsberger⁴³ constructed a cladogram of all 17 species of the mite family Ptiloxenidae and compared it with a phylogenetic tree of the avian host taxa. Although the topology of the mite tree was congruent with that of the birds, these mites were absent from several taxa nested within the host tree. As has recently been shown for lice⁴⁴, this might be an example of 'missing the boat', that is mites failed to colonize the ancestors of some lineages. Alternatively, extinction might have played a role in their uneven distribution across host taxa.

Future directions

Despite a growing body of research on the effects of mites on birds, results show a surprising degree of conflict. Even for ticks and nest mites, which have been the objects of many well-designed studies, evidence for damage to host health or reproductive fitness is often equivocal. For feather

Box 3. Patterns in diversity and host specificity of feather mites

A single species of bird might host between two and 25 species of feather mites¹⁵. How do so many species of symbiotes share a single habitat? Feather structure varies within an individual bird, and when different species of feather mites share a host, they each occupy a limited area of the plumage^{16,42}. It is probable that the diversity of plumage structure plays a role in determining the total number of feather mite species hosted by a bird; however, no comparative analysis has yet explored this idea.

With the exception of penguins (Sphenisciformes) and some ratites (rheas, emus and cassowaries), all major groups of birds possess their own feather mite fauna^{6,15,42}. For example, the mite family Crypturoptidae is composed of nine genera restricted to the Tinamiformes (tinamous) and the family Eustathiidae has 18 genera found only on Apodiformes (swifts and hummingbirds). However, not all feather mite taxa show this degree of specialization. Members of the family Xolalgidae are associated with 16 orders of birds ranging from grebes to woodpeckers¹⁵, and the feather mite *Proctophylodes ampelidis* has been collected from 27 species of small passerines¹⁶. There are even a few examples of mites 'jumping' from one host taxon to a phylogenetically distant one¹⁵. Physical association between different bird species could encourage such transfers. Although European cuckoos (*Cuculus canorus*) do not acquire their hosts' mites¹⁵, African diederic cuckoos (*Chrysococcyx caprius*) do retain feather mites and lice typical of their ploceid weaver foster parents⁴⁷. Perhaps, as has recently been shown for feather lice experimentally transferred to different hosts⁴⁵, feather structure of diederic cuckoos and weavers is similar enough to allow mites to inhabit the plumage of both hosts.

mites, the lack of consensus among researchers is even more striking. Some of this conflict could arise from methodological differences. First, ornithologists should exchange correlation based studies for manipulative ones, in which experimental defaunation of hosts or nests is employed^{3,29}. Second, many studies correlating current parasite load with host plumage are flawed because feathers develop under previous, not current, mite loads²³. Third, given the uncertainties of the 'hand in the nest' and the 'wing held to light' methods of mite counting (Box 4), a more rigorous approach towards enumeration is required. Fourth, ornithologists need to clearly identify mite species. Taxonomic vagueness makes comparison between studies difficult and can result in the inclusion of mutualistic predatory mites with counts of blood-feeding nest mites.

Box 4. Methods of collecting and enumerating bird-associated mites

Appendix C in Clayton and Moore⁴ provides a summary of mite collection methods. Nest mites can be extracted live from nest material using Berlese or Tullgren funnels¹³, or dead using kerosene- or heptane-flotation⁴⁸. Determining the number and identity of nest mites *in situ* is a much more difficult task. Some researchers place a white card (or their hand) into a nest and count the mites that swarm on it³⁷, but it is important to calculate the relationship between that number and the density of mites in the nest based on Tullgren extraction²⁹. Ticks are especially unlikely to respond to a 'hand-test' (M. Shaw, pers. commun.). Likewise, if one is counting the number of mites or scabs on nestlings as an indication of nest load^{3,20}, one should quantify the relationship between the two.

Many authors have estimated feather mite density by holding a bird's wing or tail up to a light and counting the dark specks^{23–25}. This method is problematic because the cast skins of feather mites often remain firmly attached to the feather (H. Proctor, pers. observ.) and might be mistaken for living mites. The apparent mite load also varies during the day¹⁶. Inspection with a hand lens or a portable dissecting microscope will result in greater precision. Behnke *et al.*⁴⁹ examined the relationship between mite load as estimated by the unaided eye and that determined using a microscope, and found that the strength of the correlation depended on the species of bird. Plucking a few feathers from the wings will provide a fair estimate of incidence and will also allow identification of mite taxa. Dusting living birds with a pesticidal powder and ruffling the feathers over a collecting tray can also provide specimens⁵⁰.

Another hindrance to consensus is our ignorance of basic physiological and ecological features of bird-mite systems. Do haematophagous mites transmit diseases in natural avian populations? Can immunological defences be passed from mother to chicks? Are feather mites commensals, mutualists or parasites? Why are some mites host specific and others indiscriminating⁴⁵? What are the selective factors behind the evolution of parasitism? As field-based immunological techniques²⁰ and new mite phylogenies⁴³ become available, we urge more ecologists to use the diverse interactions between birds and mites to test the generality of theory derived from other host-symbiote systems.

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References

1 Loye, J.E. and Zuk, M., eds (1991) *Bird-Parasite Interactions: Ecology, Evolution and Behaviour*, Oxford University Press

2 Møller, A.P. (1994) *Sexual Selection and the Barn Swallow*, Oxford University Press

3 Clayton, D.H. and Tompkins, D.M. (1995) Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*). *Parasitology* 110, 195–206

4 Clayton, D.H. and Moore, J., eds (1997) *Host-Parasite Evolution: General Principles and Avian Models*, Oxford University Press

5 Clayton, D.H. *et al.* (1999) Reciprocal natural selection on host-parasite phenotypes. *Am. Nat.* 154, 261–270

6 Walter, D.E. and Proctor, H.C. (1999) *Mites: Ecology, Evolution and Behaviour*, CAB International

7 Richner, H. and Heeb, P. (1995) Are clutch and brood size patterns in birds shaped by ectoparasites? *Oikos* 73, 435–441

8 Brooke, M. de L. (1985) The effect of allopreening on tick burdens of molting eudyptid penguins. *Auk* 102, 893–895

9 Kettle, D.S. (1995) *Medical and Veterinary Entomology* (2nd edn), CAB International

10 Clark, L. (1991) The nest protection hypothesis: the adaptive use of plant secondary compounds by European starlings. In *Bird-Parasite Interactions: Ecology, Evolution and Behaviour* (Loye, J.E. and Zuk, M., eds), pp. 205–221, Oxford University Press

11 Chapman, B.R. and George, J.E. (1991) The effects of ectoparasites on cliff swallow growth and survival. In *Bird-Parasite Interactions: Ecology, Evolution and Behaviour* (Loye, J.E. and Zuk, M., eds), pp. 69–92, Oxford University Press

12 Burt, E.H., Jr, *et al.* (1991) Occurrence and demography of mites of tree swallow, house wren, and eastern bluebird nests. In *Bird-Parasite Interactions: Ecology, Evolution and Behaviour* (Loye, J.E. and Zuk, M., eds), pp. 104–122, Oxford University Press

13 Pacejka, A.J. *et al.* (1998) Do potentially virulent mites affect house wren (*Troglodytes aedon*) reproductive success? *Ecology* 79, 1797–1806

14 Colwell, R.K. (1995) Effects of nectar consumption by the hummingbird flower mite *Proctolaelaps kirmsei* on nectar availability in *Hamelia patens*. *Biotropica* 27, 206–217

15 Gaud, J. and Atyeo, W.T. (1996) Feather mites of the world (Acarina, Astigmata): the supraspecific taxa. *Ann. Zool. Wetenschappen* 277, 1–193

16 Dubinin, V.B. (1951) Feather mites (Analgesoidea) Part I. Introduction to their study. *Fauna SSSR Paukoobraznye* 6, 1–363

17 Jacob, J. and Ziswiler, V. (1982) The uropygial gland. In *Avian Biology VI* (Farner, D.S. *et al.*, eds), pp. 199–324, Academic Press

18 DeVaney, J.A. and Augustine, P.C. (1988) Correlation of estimated and actual northern fowl mite populations with the evolution of specific antibody to a low molecular weight polypeptide in sera of infested hens. *Poultry Sci.* 67, 549–556

19 Durden, L.A. *et al.* (1993) Laboratory transmission of equine encephalomyelitis virus to chickens by chicken mites (Acari: Dermanyssidae). *J. Med. Entomol.* 30, 281–285.

20 Gwinner, H. *et al.* (2000) Green plants in starling nests: effects on nestlings. *Anim. Behav.* 59, 301–309

21 Sonenshine, D.E. (1993) *Biology of Ticks* (Vol. 2). Oxford University Press

22 Poulin, R. (1991) Group-living and infestation by ectoparasites in passerines. *Condor* 93, 418–423

23 Thompson, C.W. *et al.* (1997) High parasite load in house finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. *Am. Nat.* 149, 270–294

24 Harper, D.G.C. (1999) Feather mites, pectoral muscle condition, wing length and plumage coloration of passerines. *Anim. Behav.* 58, 553–562

25 Blanco, G. *et al.* (1997) Feather mites on group-living red-billed choughs: a non-parasitic interaction? *J. Avian Biol.* 28, 197–206

26 Blanco, G. *et al.* (1999) Showiness, non-parasitic symbionts, and nutritional condition in a passerine bird. *Ann. Zool. Fenn.* 36, 83–91

27 Potti, J. and Merino, S. (1996) Parasites and the ontogeny of sexual size dimorphism in a passerine bird. *Proc. R. Soc. London Ser. B* 263, 9–12

28 Potti, J. *et al.* (1999) Environmental and genetic variation in the haematocrit of fledgling pied flycatchers *Ficedula hypoleuca*. *Oecologia* 120, 1–8

29 Møller, A.P. (1990) Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. *Ecology* 71, 2345–2357

30 Darolová, A. *et al.* (1997) The effect of ectoparasite nest load on the breeding biology of the penduline tit *Remiz pendulinus*. *Ibis* 139, 115–120

31 Rendell, W.B. and Verbeek, N.A.M. (1996) Old nest material in nestboxes of tree swallows: effects on reproductive success. *Condor* 98, 142–152

32 Merino, S. and Potti, J. (1996) Weather dependent effects of nest ectoparasites on their bird hosts. *Ecography* 19, 107–113

33 Bowman, D.D. (1995) *Parasitology for Veterinarians* (6th edn), W.B. Saunders

34 Soler, M. *et al.* (1999) Weight-lifting and health status in the black wheatear. *Behav. Ecol.* 10, 281–286

35 Weatherhead, P.J. *et al.* (1993) Parasite faunas, testosterone and secondary sexual traits in male red-winged blackbirds. *Behav. Ecol. Sociobiol.* 33, 13–23

36 Kose, M. and Møller, A.P. (1999) Sexual selection, feather breakage and parasites: the importance of white spots in the tail of the barn swallow (*Hirundo rustica*). *Behav. Ecol. Sociobiol.* 45, 430–436

37 Barclay, R.M.R. (1988) Variation in the costs, benefits, and frequency of nest reuse by barn swallows (*Hirundo rustica*). *Auk* 105, 53–60

38 Clayton, D.H. and Wolfe, N.D. (1993) The adaptive significance of self-medication. *Trends Ecol. Evol.* 8, 60–63

39 Wikel, S.K. (1996) Host immunity to ticks. *Annu. Rev. Entomol.* 41, 1–22

40 Wikel, S.K. and Bergman, D. (1997) Tick-host immunology: significant advances and challenging opportunities. *Parasitol. Today* 13, 383–389

41 Szep, T. and Møller, A.P. (1999) Cost of parasitism and host immune defence in the sand martin *Riparia riparia*: a role for parent-offspring conflict? *Oecologia* 119, 9–15

42 Dabert, J. and Mironov, S.V. (1999) Origin and evolution of feather mites (Astigmata). *Exp. Appl. Acarol.* 23, 437–454

43 Dabert, J. and Ehrnsberger, R. (1998) Phylogeny of the feather mite family Ptiloxenidae Gaud, 1982 (Acari: Pterolichoidea). In *Arthropod Biology: Biosystematics and Ecology Series 14* (Ebermann, E., ed.), pp. 145–178, Austrian Academy of Sciences

44 Paterson, A.M. *et al.* (1999) How frequently do avian lice miss the boat? Implications for coevolutionary studies. *Syst. Biol.* 48, 214–223

45 Timms, R. and Read, A.F. (1999) What makes a specialist special? *Trends Ecol. Evol.* 14, 333–334

46 McKilligan, N.G. (1996) Field experiments on the effect of ticks on breeding success and chick health of cattle egrets. *Aust. J. Ecol.* 21, 442–449

47 Lindholm, A.K. *et al.* (1998) Persistence of passerine ectoparasites on the diderik cuckoo *Chrysococcyx caprius*. *J. Zool. London* 244, 145–153

48 Walter, D.E. *et al.* (1987) A heptane flotation method for recovering microarthropods from semiarid soils, with comparison to the Merchant-Crossley high-gradient extraction method and estimates of microarthropod biomass. *Pedobiologia* 30, 221–232

49 Behnke, J. *et al.* (1999) Semi-quantitative assessment of wing feather mite (Acarina) infestations on passerine birds from Portugal: evaluation of the criteria for accurate quantification of mite burdens. *J. Zool. London* 248, 337–347

50 Walther, B.A. and Clayton, D.H. (1997) Dust-ruffling: a simple method for quantifying ectoparasite loads of live birds. *J. Field Ornith.* 68, 509–518