

# Parasitic Diseases of Wild Birds

Edited by

Carter T. Atkinson  
Nancy J. Thomas  
D. Bruce Hunter

 **WILEY-BLACKWELL**

A John Wiley & Sons, Ltd., Publication

# Phthiraptera, the Chewing Lice

*Dale H. Clayton, Richard J. Adams, and Sarah E. Bush*

## INTRODUCTION

Chewing lice are small, wingless, dorsoventrally compressed insects that parasitize birds and some mammals. They range from  $\leq 1$  mm to about 10 mm in length. Avian chewing lice belong to one of two suborders: Amblycera, which occur on feathers and skin, or Ischnocera, which are more restricted to feathers. As a group, chewing lice are among the most host specific of all parasites with many species being found on only one genus or species of host. Some species of chewing lice are less specific, however, occurring on multiple host genera, families, or even orders. Most bird lice feed on feathers, dead skin, and skin products, which they appear to metabolize with the aid of endosymbiotic bacteria. Some species also feed on blood, and a few species of Amblycera feed exclusively on blood.

Chewing lice are normally found in small, subclinical infestations that are kept in check by regular host grooming, including preening with the bill and scratching with the feet. Because small numbers of lice have no apparent effect on the host, the conventional wisdom has been that chewing lice are relatively benign parasites. When present in large numbers, however, they can cause severe irritation and reduced host survival and reproductive success. They can also affect the host indirectly by serving as vectors of other parasites, including some species of filarial worms. The time and energy that birds must devote to preening to keep lice in check may also be costly. In this chapter we focus on the impact of lice on wild birds.

## SYNONYMS

Infestation with lice is technically known as pediculosis, although this term is not often used in reference to wild birds.

## HISTORY

Linnaeus included 23 species of chewing lice in his 10th edition of the *Systema Naturae* (Linnaeus 1758).

Price et al. (2003) provided a brief history of subsequent taxonomic work on chewing lice. Blood feeding by amblyceran chewing lice was documented as early as 1778, thus establishing the possibility that chewing lice might elicit allergic reactions, transmit pathogens, and leave cutaneous wounds that can fester (Price and Graham 1997; Prelezov et al. 2006). Although blood feeding by some species has been documented in detail (Derylo and Gogacz 1974), the extent of blood feeding by most species of Amblycera remains poorly understood. Ischnoceran chewing lice are recognized vectors of some filarial worms (Bartlett 1993) and cause thermoregulatory stress (Booth et al. 1993), reduced mating success (Clayton 1990), and reduced survival in wild birds (Clayton et al. 1999).

## HOST RANGE AND DISTRIBUTION

Many chewing lice are extremely host specific, but host specificity should never be assumed. The systematics of chewing lice has suffered greatly at the hands of taxonomists who describe new species on the basis of host associations, rather than on the basis of the lice themselves. This practice has made it necessary to synonymize hundreds of species over the years (Price et al. 2003).

Clayton et al. (2004) reviewed factors governing the host specificity of chewing lice, and the related phenomenon of host-parasite cospeciation. Cospeciation occurs when speciation in a host group is "mirrored" by parallel speciation in its parasites. Repeated bouts of cospeciation yield congruent host-parasite phylogenies. Page (2003) provided an overview of cospeciation, including many examples involving lice.

Nearly all species of birds that have been checked have lice. Since many avian hosts have yet to be examined, new species of lice and new host records undoubtedly await discovery, particularly in the tropics. A thoroughly revised comprehensive world checklist and biological overview of chewing lice was published

by Price et al. (2003). It includes a key to the 253 known genera of bird lice.

The first confirmed fossil louse was recently described from Eckfeld maar, Germany (Wappler et al. 2004). This fossil is approximately 44 million years old, and feathers preserved in its foregut confirm that it was a bird louse.

Louse diversity varies considerably among avian taxa, ranging from just one species per host, as in the case of the Ostrich (*Struthio camelus*), to more than 20 species per host, as in the case of some tinamous (Ward 1957). It is not clear what factors govern the diversity of lice among avian taxa. Host ecology and behavior may play a role. For example, birds which dive underwater have fewer genera of lice than their nondiving relatives (Felsö and Rózsa 2006). Host morphology may also play a role. Among species of birds, the abundance component of diversity is correlated with host body size and bill morphology (Clayton and Walther 2001).

Abiotic factors such as humidity can also influence louse distributions. Species of lice that acquire water from the air are susceptible to desiccation and death in arid environments (Rudolph 1983). Consequently, birds living in arid environments tend to have fewer lice than similar birds in humid environments (Moyer et al. 2002b). Other factors, such as latitude, do not appear to affect parasite richness or abundance (Clayton et al. 1992).

The geographic distribution of lice often corresponds to that of the host. However, some lice show a more restricted distribution, being abundant on certain host populations, but rare or absent on others. For example, the louse *Quadriceps ridgwayi* occurs on Australasian populations of the Eurasian Oystercatcher (*Haematopus ostralegus*), but is absent from this species in Africa and Eurasia (Clay 1976). In short, lice can exhibit geographic "specificity" that is nested within their host specificity.

Geographic specificity of lice can be helpful in elucidating the ecological history of the host. For example, there is little genetic structure among island populations of the endangered Galapagos Hawk (*Buteo galapagoensis*). However, the lice *Deegeriella regalis* and *Colpocephalum turbinatum* on hawks from different islands are genetically distinct, suggesting that the hawk populations on different islands are, in fact, isolated (Whiteman and Parker 2005).

In some cases geographic specificity may explain louse distributions better than the relatedness of their hosts. For example, lice from toucans (*Ramphastos* spp.) are more likely to be found on distantly related toucans in the same geographic region than on more closely related toucans in different regions (Weckstein 2004).

**Table 29.1.** Higher level classification of lice (Insecta: Phthiraptera).

Suborder	Family	Genera	Species
Amblycera	<b>Menoponidae</b>	<b>68</b>	<b>1,039</b>
	Boopidae*	8	55
	<b>Laemobothriidae</b>	<b>1</b>	<b>20</b>
	<b>Ricinidae</b>	<b>3</b>	<b>109</b>
	Gyropidae	9	93
	Trimenoponidae	6	18
Ischnocera	<b>Philopteridae</b> †	<b>138</b>	<b>2,698</b>
	Trichodectidae	19	362
Rhynchophthirina	Haematomyzidae	1	3
Anoplura	(16 families)	49	532

Families in boldface are found on birds; the others are found on mammals. Data were compiled from Price et al. (2003).

\*One genus (*Therodoxus*) occurs on birds (cassowaries).

†One genus (*Trichophilopterus*) occurs on mammals (lemurs).

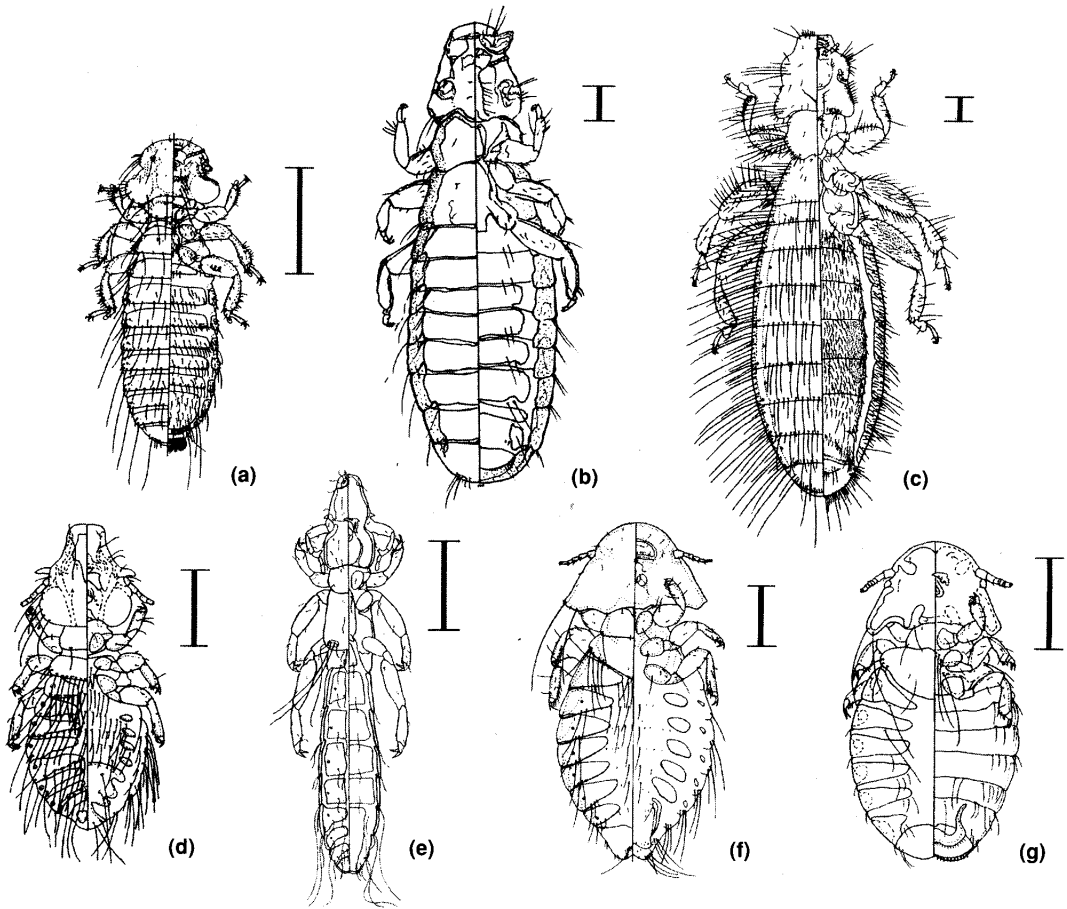
## ETIOLOGY

Chewing lice are members of the insect order Phthiraptera, which also contains the sucking lice (Table 29.1). Modern classifications divide Phthiraptera into four suborders, three of which comprise the chewing lice: Amblycera, Ischnocera, and Rhynchophthirina. Members of these three suborders all have mandibulate, chewing mouthparts. Most species of Amblycera and Ischnocera are parasites of birds, although about 12% of the species, along with the three species of Rhynchophthirina, are parasites of mammals. Members of the fourth suborder, Anoplura, all of which parasitize mammals, are known as sucking lice because they have piercing-sucking mouthparts. Durden (2001) provides an excellent review of the sucking lice, as well as taxa of chewing lice found on mammals.

Despite sharing mandibulate mouthparts, the three suborders of chewing lice are not the closest relatives to one another. Ischnocera and Anoplura share a more recent common ancestor than either suborder shares with Amblycera (Lyal 1985; Barker et al. 2002; Johnson and Whiting 2002). For this reason, modern workers classify all lice in the single order Phthiraptera, rather than following the traditional classification in which the chewing lice are placed in one order (Mallophaga), with sucking lice in another order (Anoplura). Recent molecular and morphological evidence (Johnson et al. 2004; Yoshizawa and Johnson 2006) also confirms the hypothesis that Phthiraptera is polyphyletic (Lyal 1985). The sister group of Amblycera is actually Liposcelidae, a family of nonparasitic bark/book lice in the order Pscoptera.

The two suborders of lice on birds, Amblycera and Ischnocera, are relatively easy to distinguish. Roughly 30% of all species of bird lice belong to the suborder Amblycera. Members of this suborder feed on blood and feathers, have maxillary palps, and concealed antennae with four segments (Figures 29.1a–29.1c). The majority of species of bird lice (70%) belong to the suborder Ischnocera and feed primarily on feathers and dead skin that are metabolized with the aid of endosymbiotic bacteria (Fukatsu et al. 2007). Members of

the Ischnocera lack maxillary palps and have protruding 3–5 segmented antennae (Figures 29.1d–29.1g). The Amblycera are more mobile than the Ischnocera and will make short forays away from the host and abandon a dead host to search for a new one. In contrast, the Ischnocera, which are often called “feather lice,” are so specialized for life on feathers that many species are not even capable of moving from feathers onto the skin of the host (e.g., Clayton et al. 1999).



**Figure 29.1.** Representatives of the six families of avian chewing lice (see Table 29.1). Dorsal morphology to left of midlines, ventral morphology to right. M, male, F, female. Scale bars = 0.5 mm. (a) *Colpocephalum holzenthali* (Amblycera: Menoponidae), F, host: Barred Forest-Falcon (*Micrastur ruficollis*); (b) *Ricinus* sp. (Amblycera: Ricinidae), F, host: passeriformes spp; (c) *Laemobothrion maximum* (Amblycera: Laemobothriidae), F, host: *Buteo* sp.; (d) *Philopterus* sp. (Ischnocera: Philopteridae), M, host: passeriformes spp.; (e) *Columbicola columbae* (Ischnocera: Philopteridae) M, host: Rock Pigeon (*Columba livia*); (f) *Goniodes australis* (Ischnocera: Gonioididae), F, host: Malleefowl (*Leipoa ocellata*); (g) *Heptapsogaster* sp. (Ischnocera: Heptapsogasteridae), F, host: Tinamiformes spp. (a) Redrawn from Clayton and Price (1989); (b) redrawn from Ledger (1980); (c) redrawn from Nelson and Price (1965); (d) redrawn from Price and Hellenthal (1998); (e) by the second author; (f) redrawn from Emerson and Price (1986); (g) by the second author.

Ecologically speaking, bird lice can be divided into five categories based on overall morphology and how they escape host preening: (1) agile Amblycera that run quickly across the skin or feathers (Figure 29.1a); (2) very large Amblycera that slip sideways between the feathers (Figures 29.1b, c); (3) sluggish, triangular-headed Ischnocera that avoid preening by dwelling mainly on the head and neck (Figure 29.1d); (4) elongate Ischnocera that hide between the barbs of wing and tail feathers (Figure 29.1e); and (5) sluggish Ischnocera that burrow into the lush, downy regions of neck and abdominal feathers (Figures 29.1f, g). Although some species cannot be placed into one of these categories, this scheme illustrates the principal adaptive zones occupied by bird lice.

### EPIZOOTIOLOGY

Chewing lice are obligate, permanent parasites that complete their entire life cycle on the body of the host. This cycle consists of the egg, three nymphal instars, and the adult stage. The eggs incubate for 4 to 10 days, depending on the species, and each nymphal instar requires 3–12 days for completion (Marshall 1981). Most adult lice are thought to live about a month, with females producing about one egg per day, for a total of 12–20 eggs.

Transmission of chewing lice among hosts often requires physical contact between birds, such as between mates and parents and their offspring in the nest (Hillgarth 1996; Tompkins et al. 1996). However, ischnoceran lice are also capable of moving between hosts by phoresis or “hitchhiking” on hippoboscids (Keirans 1975). Phoresis can be common. For example, lice were attached to 44% of 156 hippoboscids that were removed from European Starlings (*Sturnus vulgaris*) (Corbet 1956). Because hippoboscids are not generally as host specific as lice, phoresis may help explain why some lice have a wide range of taxonomically diverse avian hosts (Clayton et al. 2004; Harbison et al. in press). Although phoresis is common among the Ischnocera, it is rare among the Amblycera because members of this suborder appear to be morphologically incapable of attaching to flies (Keirans 1975).

### CLINICAL SIGNS, PATHOLOGY, AND PATHOGENESIS

When present in large numbers, amblyceran lice can cause extensive feather and skin damage, leading to dermatitis, puritis (itching), insomnia, and excessive preening and scratching. Although ectoparasites that feed solely on blood can cause anemia in their hosts, this has seldom been reported in the case of avian

lice, perhaps because so few species feed exclusively on blood (Marshall 1981; Price and Graham 1997). Poultry lice cause reductions in food consumption, body mass, and egg production as a result of irritation (Nelson et al. 1977; Arends 1997; Prelezov et al. 2006). For example, infestations of the chicken head louse, *Cuclotogaster heterographus*, cause severe restlessness and debility (Kim et al. 1973) and sometimes kill chicks outright (Loomis 1978). Grooming rates of chickens infested with the louse *Menacanthus stramineus* also increase significantly (Brown 1974). Despite their potential effects, poultry lice are considered a relatively minor problem in modern operations because they are relatively easy to control.

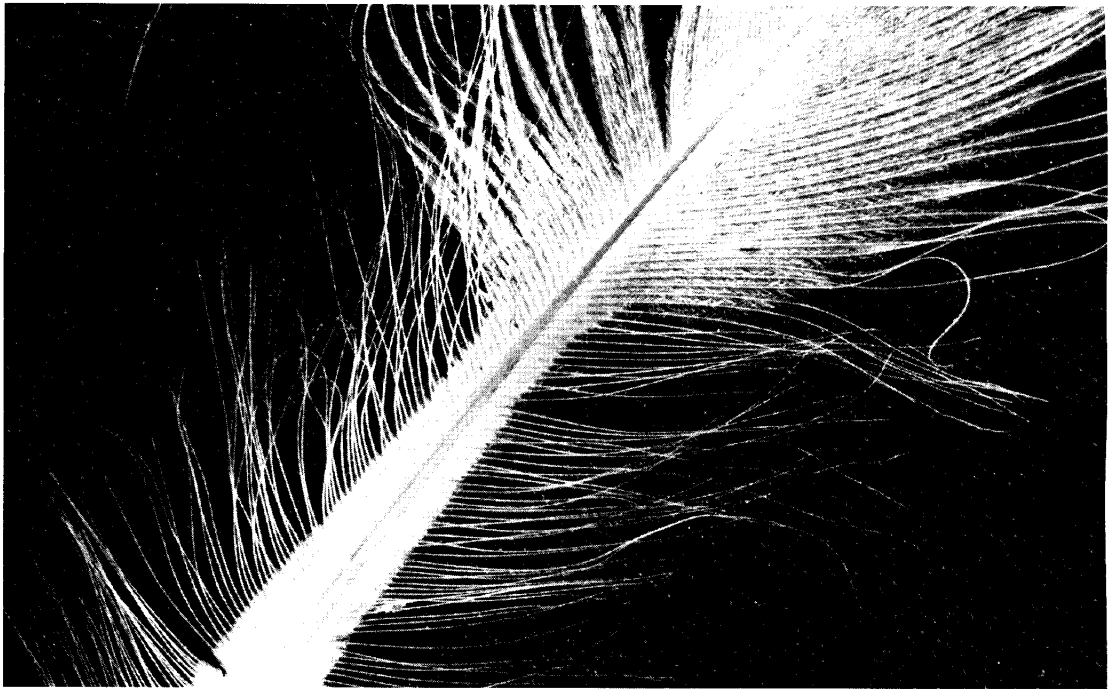
Lice also have negative effects on wild birds. Severe hemorrhagic ulcerative stomatitis and death has been documented in juvenile American White Pelicans (*Pelecanus erythrorhynchos*) infested with the menoponid louse, *Piagetiella peralis*, a species that lives within the pouch of these hosts (Samuel et al. 1982; Dik 2006). Although it is not clear whether lice were the principal cause of death, they clearly contributed to poor condition in heavily infested young pelicans.

One of the most thorough case studies of the impact of lice on wild birds involves free-ranging Rock Pigeons (*Columba livia*). Populations of the ischnoceran lice *Columbicola columbae* and *Campanulotes compar* increase dramatically on pigeons with naturally or experimentally impaired preening ability (Clayton et al. 2005). These two species feed on abdominal contour feathers (Figure 29.2) and reduce the density of the plumage. This leads to an increase in thermal conductance and a corresponding increase in the metabolic rates of their avian hosts to maintain normal core body temperatures (Figure 29.3). Metabolic rates increase by an average of 8.5% and heavily infested birds need to draw on fat reserves to keep up with these energetic costs, leading to a chronic decline in body mass over several months (Booth et al. 1993). The end result, not surprisingly, is a significant drop in survival during the winter months (Clayton et al. 1999). The impact of feather lice on energetics may also be responsible for a significant drop in the rate of male courtship display, and thus the ability of heavily infested males to attract mates (Figure 29.3) (Clayton 1990).

Studies of several other bird species have also demonstrated reductions in the potential attractiveness of lousy males to females (Clayton 1991b). For example, Barn Swallows (*Hirundo rustica*) with high louse loads have songs of shorter duration than swallows with few lice (Garamszegi et al. 2005). Adult male Satin Bowerbirds (*Ptilonorhynchus violaceus*) with the most attractive bowers had low infestations of the louse *Myrsidea ptilinorhynchi* when they were juveniles (Borgia et al. 2004).



(a)

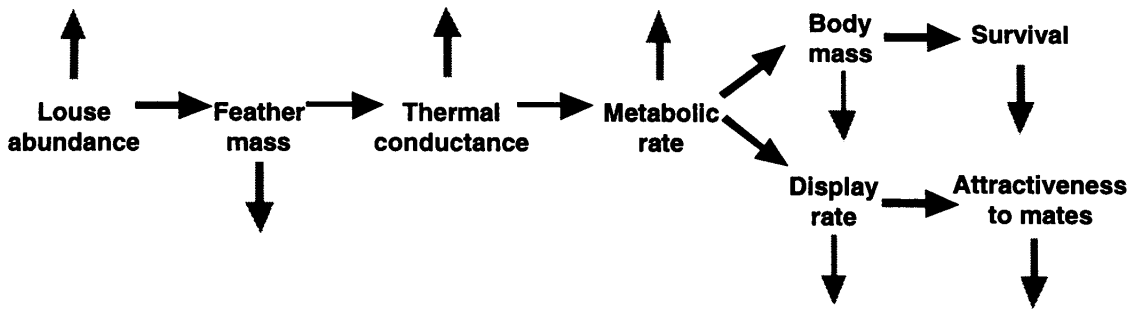


(b)

**Figure 29.2.** Damage to Rock Pigeon (*Columba livia*) feathers by feeding lice (*Columbicola columbae* and *Campanulotes compar*). (a) Abdominal contour feathers with (left to right) no damage, average damage and severe damage. The basal downy region and barbules of the basal and medial regions have been consumed (reprinted with permission from the *American Zoologist* (Clayton 1990)). (b) Magnified view of severe damage showing where barbules have been removed by lice. Neither the barbs, nor the rachis itself (=shaft) are damaged, probably because they are too large for the lice to sever with their mandibles. Reprinted with permission from Oxford University Press (Clayton 1991a).

Feather damage from chewing lice can have other consequences. The menoponid louse, *Hirundoecus* (= *Machaerilaemus*) *malleus*, chews holes in the tail feathers of Barn Swallows (Kose et al. 1999). These holes may increase feather breakage as well as per-

meability of the feathers to air, thus altering aerodynamic efficiency (Bonser 2001). Barn Swallows with many holes flap more frequently than other swallows (Barbosa et al. 2002), presumably incurring an energetic cost. The holes also increase the potential



**Figure 29.3.** Consequences of experimentally increasing the abundance of chewing lice on Rock Pigeons (*Columba livia*) (combined results of Clayton 1990; Booth et al. 1993; and Clayton et al. 1999). See the text for discussion.

costliness of long tails, which appear to function as sexually selected “handicaps” signaling freedom from parasites (Kose et al. 1999). In another study, Cliff Swallows (*Petrochelidon pyrrhonota*) infested with lice, fleas, and bugs had significantly lower long-term survivorship relative to fumigated, parasite-free controls (Brown et al. 1995), although it was not possible to assess what fraction, if any, of the survival effect could be attributed specifically to lice, fleas, or bugs.

The time and energy required for efficient grooming to control lice may also be costly. Both numbers of lice and their species richness can influence grooming rates and the amount of time devoted to these activities (Brown 1974; Cotgreave and Clayton 1994). More time devoted to grooming may mean less time available for other activities, such as foraging and defense of territories. Increased grooming can also reduce vigilance and increase the risk of being killed by a predator (Redpath 1988).

Chewing lice can also have indirect effects on the host by acting as vectors or intermediate hosts of other parasites (Table 29.2). For example, the amblyceran louse *Trinoton anserium* transmits the common heartworm, *Sarconema eurycera*, to swans when the louse takes a bloodmeal (Seegar et al. 1976; Cohen et al. 1991; Chapter 26), while ischnoceran lice that serve as intermediate hosts for other filarid nematodes transmit these worms when they are ingested during preening (Bartlett 1993). Viruses and bacteria have also been isolated from chewing lice (Table 29.2), but it is not clear whether lice play a role in their transmission. Saxena et al. (1985) provided a detailed review of chewing lice as intermediate hosts and vectors.

## DIAGNOSIS

In principle, lice are easy to detect because their life cycle is restricted to the body of the host. In practice,

however, some lice are small and can be difficult to see. Some species are also restricted to microhabitats that are difficult to examine, such as the interior of quill feathers. Even lice that are normally found on the surface of feathers can be hidden in the shafts of developing pin-feathers during molt (Moyer et al. 2002a).

Methods for collecting and quantifying lice and other avian ectoparasites were reviewed by Clayton and Walther (1997). The five most commonly used methods for quantifying lice include body washing and post-mortem ruffling for dead birds, and dust ruffling, visual examination, and the use of fumigation chambers for live birds (Clayton and Drown 2001). The authors provided a decision tree for choosing among these five methods.

Louse nits (eggs) are usually white and are sometimes easier to detect than lice themselves. Although they are small (usually  $\leq 1$  mm in length), unhatched eggs can be obvious because they glisten in reflected light and are often laid in clusters. Hatched eggs remain attached to the feathers and are grayish and flattened in appearance. Many species of lice deposit their eggs in regions that are relatively protected from host grooming, such as the gular region (throat), vent region, or between the barbs of feathers (Nelson and Murray 1971). Most species of lice attach their eggs to the base of feathers. Representative photographs and diagnostic drawings of eggs can be found in Balter (1968), Foster (1969), Nelson and Murray (1971), Marshall (1981), and Cohen et al. (1991).

## HOST DEFENSE AND IMMUNITY

Birds combat lice using a variety of defenses. The simplest defense is to avoid infection. This may be the principal advantage birds gain from choosing louse-free individuals as mates (Clayton 1991b). The most important defense of infested birds against lice is preening.

**Table 29.2.** Parasites and pathogens isolated from bird lice.

Bird host	Louse	Parasite/pathogen	Source
Charadriiformes			
Marbled Godwit ( <i>Limosa fedoa</i> )	<i>Actornithophilus limosae</i> <sup>*</sup> <i>Carduiceps clayae</i> <sup>†</sup>	<sup>‡</sup> <i>Eulimdana wongae</i> <sup>‡</sup> <i>Eulimdana wongae</i> <sup>‡</sup>	Bartlett (1993) Bartlett (1993)
Charadriiformes			
Whimbrel ( <i>Numenius phaeopus</i> )	<i>Austromenopon phaeopodis</i> <sup>*</sup> <i>Luniceps numenii</i> <sup>†</sup>	<i>Eulimdana baina</i> <sup>‡</sup> <i>Eulimdana baina</i> <sup>‡</sup>	Bartlett (1993) Bartlett (1993)
Apodiformes			
African Swift ( <i>Apus barbatus</i> )	<i>Dennyus hirundinis</i> <sup>*</sup>	<i>Filaria cypseli</i> <sup>‡</sup>	Dutton (1905)
Gruiformes			
American Coot ( <i>Fulica americana</i> )	<i>Pseudomenopon pilosum</i> <sup>*</sup>	<i>Pelecitus fulicaeatrae</i> <sup>‡</sup>	Bartlett and Anderson (1987)
Podicipediformes			
Red-necked Grebe ( <i>Podiceps grisegena</i> )	<i>Pseudomenopon</i> sp. <sup>*</sup>	<i>Pelecitus fulicaeatrae</i> <sup>‡</sup>	Bartlett and Anderson (1987)
Anseriformes			
Mute Swan ( <i>Cygnus olor</i> )	<i>Trinoton anserinum</i> <sup>*</sup>	<i>Sarconema eurycera</i> <sup>‡</sup>	Seegar et al. (1976); Cohen et al. (1991)
Tundra swan ( <i>Cygnus columbianus</i> )			
Galliformes			
Red Junglefowl ( <i>Gallus gallus</i> )	<i>Eomenacanthus stramineus</i> (= <i>Menacanthus</i> ) <sup>*</sup>	<i>Escherichia coli</i> <sup>§</sup> Eastern equine <sup>¶</sup> Encephalitis <i>Pasteurella multocida</i> <sup>§</sup> <i>Salmonella gallinarum</i> <sup>§</sup> <i>Streptococcus equinus</i> <sup>§</sup>	Derylo and Jarosz (1972) Howitt et al. (1948) Derylo (1970) Derylo (1975) Derylo and Jarosz (1972)
	<i>Menopon gallinae</i> <sup>*</sup>	<i>Escherichia coli</i> <sup>§</sup> <i>Ornithosis bedsoniae</i> <sup>§</sup> (= <i>Chlamydochila</i> ) <i>Pasteurella multocida</i> <sup>§</sup> <i>Streptococcus equinus</i> <sup>§</sup>	Derylo and Jarosz (1972) Eddie et al. (1962) Derylo (1970) Derylo and Jarosz (1972)

\* Amblycera.

† Ischnocera.

‡ Helminth.

§ Bacteria.

¶ Virus.

Wild birds with bill deformities can have enormous louse populations because they are not able to preen efficiently (reviewed by Pomeroy 1962 and Clayton 1991a). Experimental manipulations of the bill confirm that efficient self-preening is critical for controlling louse populations (Brown 1972; Clayton et al. 2005). Similarly, natural "experiments" confirm that scratching with the feet is critical for controlling louse populations on regions that cannot be preened. Birds that cannot scratch because of leg injuries sometimes have

large numbers of lice and nits on the head and neck, but not on regions that the bird can still preen (Clayton 1991a). Allopreening, in which one bird preens another, may also play a role in louse control, although this possibility has not been tested carefully. Other behaviors that may help control lice include dusting, sunning, anting, and "fumigation" of nests with aromatic green vegetation (Hart 1997). Additional research is needed to determine the importance of these behaviors in louse control.



Feather chemistry is also important in defense against lice. The feathers and skin of several species of birds in the genus *Pitohui* contain the neurotoxin found in the skin of poison dart frogs (Dumbacher et al. 1992). When given a choice between these feathers and nontoxic control feathers, lice have higher mortality and avoid feeding or resting on the toxic feathers (Dumbacher 1999). A more common feather compound, the pigment melanin, makes feathers more resistant to mechanical abrasion (Bonser 1995). There is some evidence that lice on Barn Swallows avoid feeding on heavily melanized feathers (Kose et al. 1999), although a diet rich in melanin had no effect on lice of Rock Pigeons (Bush et al. 2006).

The avian immune system also provides another probable defense against lice that feed on blood or living tissue (Wikel 1996). Some early studies reported inverse correlations between avian "immunocompetence" and size of louse populations (Saino et al. 1995; Eens et al. 2000; Blanco et al. 2001). A recent comparative study by Møller and Rózsa (2005) reported a positive correlation between the number of genera of amblyceran lice on different species of altricial birds, and the T-cell-mediated immune responsiveness of nestlings of those species. The authors argued that the positive correlation reflects greater specialization of lice on species with strong immune responses. In contrast, there was no correlation between ischnoceran lice and immune responsiveness by the same species. This result makes sense because feather-feeding lice should be invisible to the immune system. More recently, Whiteman et al. (2005) found an inverse correlation between natural antibody (NAb) levels and the abundance of amblyceran lice (*Colpocephalum turbinatum*) on Galapagos Hawks. In contrast (but in parallel to Møller and Rózsa's (2005) results), the hawks showed no correlation between immunity and ischnoceran lice (*Degeeriella regalis*).

Although the results of these studies are intriguing, they should be interpreted with caution. Assessing immunocompetence on the basis of simple assays of immune function is risky. A decline in one component of the immune system can be offset by up-regulation of other components (innate, cell-mediated, or humoral), or by up-regulation of other aspects of the same component (Salvante 2006; Owen and Clayton 2007). Future studies need to explore the relationship between integrated immune responsiveness and lice, preferably in an experimental context.

### TREATMENT AND CONTROL

Jackson (1985) reviewed the use of pesticides for controlling ectoparasites on wild birds in nestboxes. The safest choice is probably pyrethrum dust or spray,

a "fast knock-down, slow killing" insecticide with no side effects on birds or mammals. Pyrethrum is a biodegradable derivative of chrysanthemums that breaks down within hours or days in the environment. Its kill rate is not 100%, so most commercial products use a combination of pyrethrin, a derivative of pyrethrum, and the synergist piperonyl butoxide. A 1.0% concentration of this mixture kills lice effectively, with no side effects on host nestlings or adults (Clayton and Tompkins 1995).

### PUBLIC HEALTH CONCERNS

Bird lice are of little concern to humans because they cannot survive or reproduce off the body of the avian host. Although some bird lice can bite when infested birds are handled, they do not transmit human pathogens. Arthropods from ledge nesting birds occasionally enter dwellings through ventilation ducts or windows and take blood meals from people; however, such reports usually involve nest mites, not lice.

### DOMESTIC ANIMAL HEALTH CONCERNS

Lice are considered a relatively minor problem in modern poultry operations because they are relatively easy to control (Williams 1992). However, they can still be a major problem for poultry kept under traditional conditions, particularly when birds are crowded or in poor health. Arends (1997) and Price and Graham (1997) review the impact of lice on poultry and other domestic birds, and provide details concerning the control of lice on domestic birds. The host specificity of lice on wild birds means that they pose little threat to domesticated birds.

### WILDLIFE POPULATION IMPACTS AND MANAGEMENT IMPLICATIONS

Wildlife managers should be aware that lice can have negative effects on wild birds under certain conditions (e.g., Samuel et al. 1982; Cohen et al. 1991). Although healthy hosts normally keep their louse populations in check, lice can quickly increase on debilitated hosts. This can lead to blood loss, feather damage, irritation, and possible transmission of endoparasites and pathogens (Table 29.2), with effects on individual hosts or entire breeding populations (Samuel et al. 1982). Overcrowding of birds should be avoided because it facilitates transmission of lice, with a subsequent increase in average louse load (Clayton 1991a). For this reason, highly social birds are probably more at risk than solitary birds. Increases in lice can be either a cause or consequence of poor host health, depending on the situation. Although direct effects of lice are usually correlated with the number of lice present, their

indirect effects as vectors of other pathogens may be density independent.

## LITERATURE CITED

- Arends, J. J. 1997. External parasites and poultry pests. In *Diseases of Poultry*, B. W. Calnek (ed.). Iowa State University Press, Ames, 1080 pp.
- Balter, R. S. 1968. The microtopography of avian lice eggs. *Medical and Biological Illustration* 18:166–179.
- Barbosa, A., S. Merino, F. de Lope, and A. P. Møller. 2002. Effects of feather lice on flight behavior of male Barn Swallows (*Hirundo rustica*). *The Auk* 119:213–216.
- Barker, S. C., M. Whiting, K. P. Johnson, and A. Murrell. 2002. Phylogeny of the lice (Insecta, Phthiraptera) inferred from small subunit rRNA. *Zoologica Scripta* 32:407–414.
- Bartlett, C. M. 1993. Lice (Amblycera and Ischnocera) as vectors of *Eulimdana* spp. (Nematoda: Filarioidea) in charadriiform birds and the necessity of short reproductive periods in adult worms. *Journal of Parasitology* 79:85–91.
- Bartlett, C. M., and R. C. Anderson. 1987. *Pelecitus fulicaeatrae* (Nematoda, Filarioidea) of coots (Gruiformes) and grebes (Podicipediformes)—skin inhabiting microfilariae and development in Mallophaga. *Canadian Journal of Zoology* 65:2803–2812.
- Blanco, G., J. De La Puente, M. Corroto, A. Baz, and J. Colas. 2001. Condition-dependent immune defence in the Magpie: How important is ectoparasitism? *Biological Journal of the Linnean Society* 72:279–286.
- Bonser, R. H. C. 1995. Melanin and the abrasion resistance of feathers. *Condor* 97:590–591.
- Bonser, R. H. C. 2001. Mites on birds. *Trends in Ecology and Evolution* 16:18–19.
- Booth, D. T., D. H. Clayton, and B. A. Block. 1993. Experimental demonstration of the energetic cost of parasitism in free-range hosts. *Proceedings of the Royal Society of London, B* 253:125–129.
- Borgia, G., M. Egeeth, J. A. Uy, and G. L. Patricelli. 2004. Juvenile infection and male display: testing the bright male hypothesis across individual life histories. *Behavioral Ecology* 15:722–728.
- Brown, N. S. 1972. The effect of host beak condition on the size of *Menacanthus stramineus* populations of domestic chickens. *Poultry Science* 51:162–164.
- Brown, N. S. 1974. The effect of louse infestation, wet feathers, and relative humidity on the grooming behavior of the domestic chicken. *Poultry Science* 53:1717–1719.
- Brown, C. R., M. B. Brown, and B. Rannala. 1995. Ectoparasites reduce long-term survivorship of their avian host. *Proceedings of the Royal Society of London, B* 262:313–319.
- Bush, S. E., B. R. Moyer, D. Kim, J. Lever, and D. H. Clayton. 2006. Is melanin a defense against feather-feeding lice? *The Auk* 123:153–161.
- Clay, T. 1976. Geographical distribution of the avian lice (Phthiraptera): a review. *Journal of the Bombay Natural History Society* 71:536–547.
- Clayton, D. H. 1990. Mate choice in experimentally parasitized Rock Doves: Lousy males lose. *American Zoologist* 30:251–262.
- Clayton, D. H. 1991a. Coevolution of avian grooming and ectoparasite avoidance. In *Bird-Parasite Interactions: Ecology, Evolution, and Behaviour*, J. E. Loye and M. Zuk (eds.). Oxford University Press, Oxford, pp. 258–289.
- Clayton, D. H. 1991b. The influence of parasites on host sexual selection. *Parasitology Today* 7:329–334.
- Clayton, D. H., and D. M. Drown. 2001. Critical evaluation of five methods for quantifying chewing lice (Insecta: Phthiraptera). *Journal of Parasitology* 87:1291–1300.
- Clayton, D. H., and R. D. Price. 1989. *Colpocephalum holxenthalii* n. sp. (Mallophaga: Menoponidae) from the Barred Forest-falcon *Micrastur ruficollis* (Falconidae) in Peru. *Journal of Parasitology* 75:505–507.
- Clayton, D. H., and D. M. Tompkins. 1995. Comparative effects of mites and lice on the reproductive success of Rock Doves (*Columba livia*). *Parasitology* 110:195–206.
- Clayton, D. H., and B. A. Walther. 1997. Collection and quantification of arthropod parasites of birds. In *Host-Parasite Evolution: General Principles and Avian Models*, D. H. Clayton and J. Moore (eds.). Oxford University Press, Oxford, pp. 419–440.
- Clayton, D. H., and B. A. Walther. 2001. Influence of host ecology and morphology on the diversity of Neotropical bird lice. *Oikos* 94:455–467.
- Clayton, D. H., R. D. Gregory, and R. D. Price 1992. Comparative ecology of neotropical bird lice. *Journal of Animal Ecology* 61:781–795.
- Clayton, D. H., P. L. M. Lee, D. M. Tompkins, and E. D. Brodie III. 1999. Reciprocal natural selection on host-parasite phenotypes. *American Naturalist* 154:261–270.
- Clayton, D. H., S. E. Bush, and K. P. Johnson. 2004. Ecology of congruence: Past meets present. *Systematic Biology* 53:165–173.
- Clayton, D. H., B. R. Moyer, S. E. Bush, D. W. Gardiner, B. B. Rhodes, T. G. Jones, and F. Goller. 2005. Adaptive significance of avian beak morphology for

- ectoparasite control. *Proceedings of the Royal Society, B* 272:811–817.
- Cohen, S., M. T. Greenwood, and J. A. Fowler. 1991. The louse *Trinoton anserium* (Amblycera: Phthiraptera); an intermediate host of *Sarconema eurycerca* (Filarioidea: Nematoda), a heatworm of swans. *Medical and Veterinary Entomology* 5:101–110.
- Corbet, G. B. 1956. The life-history and host relations of a hippoboscid fly *Ornithomyia fringillina* Curtis. *Journal of Animal Ecology* 25:402–420.
- Cotgreave, P., and D. H. Clayton. 1994. Comparative analysis of time spent grooming by birds in relation to parasite load. *Behaviour* 131:171–187.
- Derylo, A. 1970. Mallophage as a reservoir of *Pasteurella multocida*. *Acta Parasitologica Polonica* 17:301–313.
- Derylo, A. 1975. Badania nad Szkodliwoscia gospodarza wszolow (Mallophaga) V. proba ustalenia roli Wszolow *Eomenacanthus stramineus* (Nitzsch) W przenoszeniu Tyfusu U kur. *Wiadomosci Parazytologiczne* 21:61–68.
- Derylo, A., and E. Gogacz. 1974. Attempts to determine blood amount taken from hens by bird lice (*Eomenacanthus stramineus* Nitzsch) by using radioactive chromium as a labelling factor. *Bulletin of the Veterinary Institute Pulawy* 18:50–51.
- Derylo, A., and J. Jarosz. 1972. Mikroflora jelitowa niektórych wszolow hematofogicznych. *Wiadomosci Parazytologiczne* 18:113–119.
- Dik, B. 2006. Erosive stomatitis in a White Pelican (*Pelecanus onocrotalus*) caused by *Piagetiella titan* (Mallophaga: Menoponidae). *Journal of Veterinary Medicine, B* 53:153–154.
- Dumbacher, J. P. 1999. Evolution of toxicity in Pitohuis: I. Effects of homobatrachotoxin on chewing lice (order Phthiraptera). *The Auk* 116:957–963.
- Dumbacher, J. P., B. M. Beehler, T. F. Spande, H. M. Garraffo, and J. W. Daly. 1992. Homobatrachotoxin in the genus *Pitohui*: chemical defense in birds? *Science* 258:799–801.
- Durden, L. A. 2001. Lice (Phthiraptera). In *Parasitic Diseases of Wild Mammals*, W. M. Samuel, M. J. Pybus, and A. A. Kocan (eds.). Iowa State University Press, Ames, IA, pp. 3–17.
- Dutton, J. E. 1905. The intermediary host of *Filaria cypseli* (Annett, Dutton, Elliot). The filaria of the African Swift, *Cypselus affinis*. *Journal of Tropical Medicine* 8:108.
- Eddie, B., K. F. Meyer, F. L. Lambrecht, and D. P. Furman. 1962. Isolation of *Ornithosis bedsoniae* from mites collected in turkey quarters and from chicken lice. *Journal of Infectious Diseases* 110:231–237.
- Eens, M., E. V. Duyse, and L. Berghman. 2000. Shield characteristics are testosterone dependent in both male and female Moorhens. *Hormones and Behavior* 37:126–134.
- Emerson, K. C., and R. D. Price. 1986. Two new species of Mallophaga (Phloopteridae) from the Mallee Fowl (Galliformes: Megapodiidae) in Australia. *Journal of Medical Entomology* 23:353–355.
- Felső, B., and L. Rózsa. 2006. Reduced taxonomic richness of lice (Insecta: Phthiraptera) in diving birds. *Journal of Parasitology* 92:867–869.
- Foster, M. S. 1969. The eggs of three species of Mallophaga and their significance in ecological studies. *Journal of Parasitology* 55:453–456.
- Fukatsu, T., R. Koga, W. A. Smith, K. Tanaka, N. Nikoh, K. Sasaki-Fukatsu, K. Yoshizawa, C. Dale, and D. H. Clayton. 2007. Bacterial endosymbiont of the slender pigeon louse *Columbicola columbae* allied to endosymbionts of grain weevils and tsetse flies. *Applied and Environmental Microbiology* 73:6660–6668.
- Garamszegi, L. Z., D. Heylen, A. P. Møller, M. Eens, and F. de Lope. 2005. Age-dependent health status and song characteristics in the Barn Swallow. *Behavioral Ecology* 16:580–591.
- Harbison, C. W., S. E. Bush, J. R. Molenke, and D. H. Clayton. In press. Comparative transmission dynamics of competing parasite species. *Ecology*
- Hart, B. L. 1997. Behavioural defence. In *Host-Parasite Evolution: General Principles and Avian Models*, D. H. Clayton and J. Moore (eds.). Oxford University Press, Oxford, pp. 59–77.
- Hillgarth, N. 1996. Ectoparasite transfer during mating in Ring-necked Pheasants *Phasianus colchicus*. *Journal of Avian Biology* 27:260–262.
- Howitt, B. F., H. R. Dodge, L. K. Bishop, and R. H. Gorrie. 1948. Virus of Eastern Equine Encephalomyelitis isolated from chicken mites (*Dermanyssus gallinae*) and chicken lice (*Eomenacanthus stramineus*). *Proceedings of the Society of Experimental Biology and Medicine* 68:622–625.
- Jackson, J. A. 1985. On the control of parasites in nest boxes and the use of pesticides near birds. *Sialia* 7:17–25.
- Johnson, K. P., and M. F. Whiting. 2002. Multiple genes and the monophyly of Ischnocera (Insecta: Phthiraptera). *Molecular Phylogenetics and Evolution* 22:101–110.
- Johnson, K. P., K. Yoshizawa, and V. S. Smith. 2004. Multiple origins of parasitism in lice. *Proceedings of the Royal Society of London, B* 271:1771–1776.
- Keirans, J. E. 1975. A review of the phoretic relationship between Mallophaga (Phthiraptera: Insecta) and Hippoboscidae (Diptera: Insecta). *Journal of Medical Entomology* 12:71–76.

- Kim, K. C., K. C. Emerson, and R. D. Price. 1973. Lice. In *Parasites of Laboratory Animals*, R. J. Flynn (ed.). Iowa State University Press, Ames, pp. 376–397.
- Kose, M., R. Mand, and A. P. Møller. 1999. Sexual selection for white tail spots in the Barn Swallow in relation to habitat choice by feather lice. *Animal Behaviour* 58:1201–1205.
- Ledger, J. A. 1980. The arthropod parasites of vertebrates in Africa south of the Sahara: Phthiraptera. *Publications of the South Africa Institute for Medical Research* 56:1–327.
- Linnaeus, C. 1758. *Systema Naturae*. Editio Decima, Reformata. Impensis Direct, L. Salvii, Holmiae. I:[chewing lice:610–614].
- Loomis, E. C. 1978. External parasites. In *Diseases of Poultry*, 7th ed. Iowa State University Press, Ames, pp. 667–704.
- Lyal, C. H. C. 1985. Phylogeny and classification of the Psocodea, with particular reference to the lice (Psocodea: Phthiraptera). *Systematic Entomology* 10:145–165.
- Marshall, A. G. 1981. *The Ecology of Ectoparasitic Insects*. Academic Press, London, 459 pp.
- Møller, A. P., and L. Rózsa. 2005. Parasite biodiversity and host defenses: chewing lice and immune response of their avian hosts. *Oecologia* 142:169–176.
- Moyer, B. R., D. W. Gardiner, and D. H. Clayton. 2002a. Impact of feather molt on ectoparasites: looks can be deceiving. *Oecologia* 131:203–210.
- Moyer, B. R., D. M. Drown, and D. H. Clayton. 2002b. Low humidity reduces ectoparasite pressure: implications for host life history evolution. *Oikos* 97:223–228.
- Nelson, B. C., and M. D. Murray. 1971. The distribution of Mallophaga on the domestic pigeon (*Columba livia*). *International Journal for Parasitology* 1:21–29.
- Nelson, R. C., and R. D. Price. 1965. The *Laemobothrion* (Mallophaga: Laemobothriidae) of the Falconiformes. *Journal of Medical Entomology* 2:249–257.
- Nelson, W. A., J. F. Bell, C. M. Clifford, and J. E. Keirans. 1977. Review Article: Interaction of ectoparasites and their hosts. *Journal of Medical Entomology* 13:389–428.
- Owen, J. P., and D. H. Clayton. 2007. Where are the parasites in the PHA response? *Trends in Ecology and Evolution* 22:228–229.
- Page, R. D. M. (ed). 2003. *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*. University of Chicago Press, Chicago, 378 pp.
- Pomeroy, D. E. 1962. Birds with abnormal bills. *British Birds* 55:49–72.
- Prelezov, P. N., N. I. Groseva, and D. I. Goundaheva. 2006. Pathomorphological changes in the tissues of chickens experimentally infected with biting lice (Insecta: Phthiraptera). *Veterinarski Archiv* 76:207–215.
- Price, M. A., and O. H. Graham. 1997. Chewing and Sucking Lice as Parasites of Mammals and Birds. U.S. Department of Agriculture, Technical Bulletin No. 1849, 309 pp.
- Price, R. D., and R. A. Hellenthal. 1998. Taxonomy of *Philopterus* (Phthiraptera: Philopteridae) from the Corvidae (Passeriformes), with descriptions of nine new species. *Entomological Society of America* 91:782–799.
- Price, R. D., R. A. Hellenthal, R. L. Palma, K. P. Johnson, and D. H. Clayton. 2003. *The Chewing Lice: World Checklist and Biological Overview*. Illinois Natural History Survey, Spec. Publ. 24.
- Redpath, S. 1988. Vigilance levels in preening Dunlin *Caladris alpina*. *Ibis* 130:555–557.
- Rudolph, D. 1983. The water-vapour uptake system of the Phthiraptera. *Journal of Insect Physiology* 29:15–25.
- Saino, N., A. P. Møller, and A. M. Bolzern. 1995. Testosterone effects on the immune system and parasite infestations in the Barn Swallow (*Hirundo rustica*): an experimental test of the immunocompetence hypothesis. *Behavioral Ecology* 6:397–404.
- Salvante, K. G. 2006. Techniques for studying integrated immune function in birds. *The Auk* 123:575–586.
- Samuel, W. M., E. S. Williams, and A. B. Rippin. 1982. Infestations of *Piagetiella peralis* (Mallophaga: Menoponidae) on juvenile White Pelicans. *Canadian Journal of Zoology* 60:951–953.
- Saxena, A. K., G. P. Agarwal, S. Chandra, and O. P. Singh. 1985. Pathogenic involvement of Mallophaga. *Zeitschrift fuer Angewandte Entomologie* 99:294–301 (In English).
- Seegar, W. S., E. L. Schiller, W. J. L. Sladen, and M. Trpis. 1976. A mallophaga, *Trinton anserium*, as a cyclodevelopmental vector for a heartworm parasite of waterfowl. *Science* 194:739–741.
- Tompkins, D. M., T. Jones, and D. H. Clayton. 1996. Effect of vertically transmitted ectoparasites on the reproductive success of swifts (*Apus apus*). *Functional Ecology* 10:733–740.
- Wappler, T., V. S. Smith, and R. C. Dalgleish. 2004. Scratching an ancient itch: an Eocene bird louse fossil. *Proceedings of the Royal Society of London*, B.271(Suppl.):S255–S258.
- Ward, R. A. 1957. A study of the host distribution and some relationships of biting lice (Mallophaga) parasitic on birds of the order Tinamiformes. Part II.

- Annals of the Entomological Society of America* 50:452–459.
- Weckstein, J. D. 2004. Biogeography explains cophylogenetic patterns in Toucan chewing lice. *Systematic Biology* 53:154–164.
- Whiteman, N. K., K. D. Matson, J. L. Bollmer, and P. G. Parker. 2005. Disease ecology in the Galapagos Hawk (*Buteo galapagoensis*): host genetic diversity, parasite load and natural antibodies. *Proceedings of the Royal Society, B* 273:797–804.
- Whiteman, N. K., and P. G. Parker. 2005. Using parasites to infer host population history: a new rationale for parasite conservation. *Animal Conservation* 8:175–181.
- Wikel, S. K. (ed). 1996. *The Immunology of Host-Ectoparasitic Arthropod Relationships*. CAB International, Wallingford, Oxon, 331 pp.
- Williams, R. E. 1992. *External Parasites of Poultry*. Purdue University Cooperative Extension Service, West Lafayette, IN.
- Yoshizawa, K., and K. P. Johnson. 2006. Morphology of male genitalia in lice and their relatives and phylogenetic implications. *Systematic Entomology* 31:350–361.