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Chapter 17  

**Biodiversity of Ectoparasites: Lice (Phthiraptera) and Fleas (Siphonaptera)**  

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**Summary**

This chapter addresses the two insect orders in which all known species are ectoparasites. The sucking and chewing lice (Phthiraptera) are hemimetabolous insects that spend their entire lives on the bodies of their hosts. Fleas (Siphonaptera), on the other hand, are holometabolous. The diversity of these ectoparasites is limited by the diversity of the birds and mammals available as hosts. Determining the community diversity of lice and fleas is essential to understanding ecological structure and interactions, yet offers a number of challenges to the ectoparasitologist. The chapter explores medical and veterinary importance of lice and fleas. They are more likely to be considered detrimental parasites, perhaps even a threat to conservation efforts by their very presence or by the disease agents they transmit. Perez-Osorio emphasized the importance of a more objective approach to conservation strategies by abandoning overemphasis on charismatic fauna and setting priorities in ecological management of wider biodiversity issues.

When most people see a bird or mammal, they don’t look beneath the feathers or hair of that animal to see what is hidden. They see the animal at its face value, and seldom appreciate the diversity of life before them. The animal is typically a mobile menagerie, infested by external parasites and their body laden with internal parasites and pathogens.  

Insects in all their enormous diversity are known for their ability to make use of a variety of resources available in their environment. It should be no surprise that many groups of insects have capitalized on the resources associated with terrestrial vertebrates, notably birds and mammals. The construction and utilization of nests may, in fact, have led to the first dependent relationships of these insects, future ectoparasites, with their hosts. Insect ectoparasites include those species where one or more life stages live in close association with their host(s), which have specialized morphological adaptations to this association, and which gain nutrition and/or accommodation from their host(s) (Marshall 1981). This implies there is some inherent cost to the host, but this is not always clearly defined. Under this definition, “micropredators” such as...
mosquitoes, black flies, no-see-ums and tabanids are not included. These insects may rely upon their hosts as a source of food, but direct contact with their hosts is limited mostly to the acquisition of blood. Ectoparasites exhibit a much closer relationship with their hosts, living in close proximity or even on the body of their host.

To take some liberties with the estimate of Marshall (1981) there are more than 125,000 described species of insect ectoparasites. Insects in at least seven orders (three hemimetabolous, four holometabolous) include some ectoparasites. In the Dermaptera and Hemiptera, there are at least four families: Arexeniidae and Hemimeridae, and Cimicidae and Polycetenidae, respectively. In the Lepidoptera (a small number of species of Pyralidae which feed on algae on the hair of their sloth hosts), Coleoptera (Leioididae, Leptinidae, Platypsyllidae, some species of Staphylinidae, Languriidae and Scarabaeidae, though the exact relationship with their hosts are debatable, perhaps occurring as commensals or ectosymbionts) and Diptera (Carnidae, Mystacinobiidae, Hippoboscidae, Nycteribiidae, and Streblidae), there are at least 12 families. The reader is referred to Marshall (1981) for an excellent overview of the ecology of these groups. For the remainder of this chapter, I shall address the two insect orders in which all known species are ectoparasites. The sucking and chewing lice (Phthiraptera) are hemimetabolous insects which spend their entire lives on the bodies of their hosts. To become accidentally dislodged from their host means almost certain death. Fleas (Siphonaptera), on the other hand, are holometabolous. With a few exceptions, the larvae are associated with the nest of their host, while adults have sucking mouthparts and are blood-feeders on their host.

**Phthiraptera – The Parasitic Lice**

The first encounter with parasitic lice for most people likely involves a personal infestation as a child with the human head louse, *Pediculus humanus capitis* de Geer. For some, this entails great emotional trauma and disgust, while for many, just something that happens in the course of growing up. Most lice are rather small, innocuous and difficult to see on the living host. Veterinarians, hunters, and, of course, ectoparasitologists are most likely to encounter the greatest diversity of these interesting species on a routine basis.

Lice range in size from less than 0.5 mm (*Microptthirus uncinatus* (Ferris) which infests flying squirrels), to greater than a centimetre, in the case of the monstrous louse, *Laemobothrion vulturis* (Fabricius), which infests eagles. They are hemimetabolous, wingless, and somewhat dorso-ventrally flattened, with three juvenile instars (nymphs) leading up to the adult stage. Females cement their eggs to hairs or feathers (Fig. 1) of their hosts, and hatching nymphs immediately move across the surface of the body and its outgrowths to find a suitable location to feed and continue development.

The parasitic lice are generally divided into four groups or suborders within the order Phthiraptera (more recently, Psocodea, in part): Anoplura, Rhynchophthirina, Amblycera and Ischnocera (564, 3, 1516, and 3156 species each, respectively, Table 1). The phylogeny of the order and the relationships to the book lice and bark lice (Psocoptera) are somewhat unclear (Murrell and
Barker 2005; Trautwein et al. 2012) and further research will no doubt resolve some of the issues of apparent paraphyly. Endosymbiotic bacteria are present in most lice examined so far. It is likely these bacteria played an essential role in the evolutionary steps from bark lice to ectoparasitic lice, but the exact role of these endosymbionts is not always certain (Perotti et al. 2009).

The Anoplura are all blood-feeders, usually referred to as sucking lice. They infest only placental mammals, piercing the skin with specially developed stylet-like mouthparts, feeding directly from small blood vessels (solenophagy). The mouthparts are withdrawn into the head capsule unless the louse is feeding. Sucking lice possess bacterial symbionts which are found in special structures (mycetomes) along the gut. These symbionts are essential for survival of the louse, because they produce vitamins required for growth and development, but which are in short supply in host blood (Boyd and Reed 2012). Blood, of course, is also essential for egg development. Eggs are cemented by the female to host hair follicles. The eggs, or nits, are oval-shaped, often with surface ornamentation, and an operculum (Fig. 2). The hatching nymph pops the top off the egg along the operculum and takes up its parasitic life on the host.

The strongly developed tibio-tarsal claws are immediately obvious features of sucking lice (Fig. 3). If a louse loses intimate contact with its host, it is likely to die. Therefore these claws provide a vital means of attachment, to prevent removal during host grooming and an efficient means to travel among the hairs of the host. The curved tarsal claw is clamped around a hair follicle against a projecting spur from the tibia and anchors the louse in place. The size and shape of the claws may account to some degree of host specificity and even site specificity upon the host. For example, the human head louse has relatively small tarsal claws, well suited to fine head hair, whereas the human crab louse (Pthirus pubis (Linnaeus)) has enormously developed tarsal claws and inhabits parts of the body where the hair is much coarser.

The chewing lice (Rhynchophthirina, Amblycera and Ischnocera) infest both mammals and birds. There are three species of Rhynchophthirina which are found on elephants, desert warthog and Red River hog, respectively. The majority of species of Amblycera infest birds, but there are three smaller families (Boopiidae, Gyropidae and Trimenoponidae) whose members infest mammals. Among the Ischnocera, the Philopteridae all infest birds, while the Trichodectidae are all ectoparasites of mammals. However, they all share chewing mouthparts (Fig. 4), though somewhat reduced in the rhynchophthirines. These lice face the same problem as the sucking lice in having to remain on the body of their host, and for those chewing lice which infest birds, they are not only assaulted by the grooming activities of their host, but must deal with the risks presented by flight. While the chewing lice have much smaller claws than the sucking lice, they use their chewing mouthparts to maintain a grasp on hair and feathers. Some Amblycera move through the feathers very rapidly to avoid grooming activity, facilitated by their small tarsal claws and backward-directed hairs and spines (Fig. 5). More rotund, slow-moving species of Ischnocera (e.g., Craspedorrhynchus, Strigiphilus) occupy regions of the body which are more difficult for the host to reach during grooming, where they cling to the feathers by their mandibles. In contrast,
some ischnocerans (e.g., *Columbicola*) are long and slender and can escape the grooming actions of the host’s beak by taking refuge between the feather barbs.

Chewing mandibles in some species, especially in the Ischnocera, are used to shear short pieces of feather barbs which are fed into the crop. Other chewing lice use their mandibles to scrape feather or skin surfaces, and the Ricinidae use their mandibles to obtain blood and fluids from their hosts. Some species of the amblyceran genus, *Actornithophilus*, use their mandibles to chew a hole and gain entrance into the shafts of larger feathers on the wings and tail. There has not been a great deal of work on nutrition in chewing lice, but symbiotic bacteria are present in mycetocytes of Philopteridae, presumably to assist in breakdown of feather particles which are very hard to digest (Boyd and Reed 2012).

The antennae of chewing lice are covered with chemosensory and tactile sense organs. Amblyceran lice have short, clubbed antennae which lie in a groove along the sides of the head. In contrast, the antennae of the Rhynchophthirina and Ischnocera are filamentous and are easily seen sticking out from the side of the head. However, the antennae in males of some philopterids (e.g., *Haffneria*, *Ornithobius*, *Pectinopygus*) and trichodectids (e.g., *Thomomydoecus*, *Neotrichodectes*) are grossly modified (Fig. 6). During copulation in these species, the male lies beneath the female and the antennae flip upwards and grasp the body of the female, holding it in place. The antennae of no amblycerans are so modified, though in *Piagetiella peralis* (Leidy), the male positions itself over the dorsal surface of a female and surrounds her body with its enlarged legs, not only during copulation, but prior to copulation in what appears to be a mate-guarding stance. Species in the genus *Piagetiella* are unusual among chewing lice in living part of their life cycle inside the pouch of pelicans (Fig. 7) and cormorants. Females still cement their eggs to the feathers on the body, so they must leave the pouch after mating to do so.

Lice are permanent ectoparasites on their hosts; if any stage is lost from the host, its chances of survival are very slim. Therefore, their life cycles are entirely dependent upon the conditions that occur on the body of their hosts, as they live among the hair follicles and feathers. Changes in intensity of infestation are typically the result of interactions with changing environmental conditions (temperature, relative humidity, host molt) or host response, either a physical response which involves more intense or more efficient grooming, a behavioral response (close contact with conspecifics, especially offspring or siblings), or a physiological response associated with host condition (hibernation, reproductive status, immune competency). Of course, these interactions are not mutually exclusive and louse populations may increase or decrease in response to a variety of dynamic changes in their environment. No parasitic lice are known to enter diapause during any stage of their development, so they must be able to cope with adverse conditions by some means, or they are extirpated from an individual host or even from wide areas of potential host distribution. Seasonal dynamics in louse populations have been most intensively studied in species which infest domestic livestock, but there are sufficient studies to make some broad generalizations.

It is important to recognize that the distribution of lice among a host population is typically aggregated, exhibiting a strong negative binomial distribution. This is most pronounced in
populations where prevalence of infestation (proportion of hosts infested) is not extremely high. In such cases, many or perhaps even most hosts are uninfested, while a small number of hosts might carry the greater proportion of the entire louse population. Galloway (2012) collected 208,842 sucking lice (*Haemodipsus setoni* Ewing) from 58 adult eastern cottontail rabbits, but 166,249 (almost 80%) of those lice infested one rabbit. Because of the aggregated distribution of lice and the variety of factors that may affect louse populations, when studying wild host populations, it is sometimes necessary to have large sample sizes, over a long period of time. Patterns in population growth and fluctuation are more easily studied if animals are artificially infested and kept in captivity under uniform environmental conditions.

Numbers of chewing and sucking lice which infest cattle, horses, sheep and swine tend to reach their maxima during winter and spring. In temperate regions, winter may impose considerable stress on these animals, and it is the time of year when the hair coat is heaviest. Once animals molt in spring, the hair coat is thinner, ambient temperature for the lice may increase and relative humidity decreases. Lice also become more vulnerable to grooming by their hosts and may be adversely affected by exposure to rainfall.

Members of the sucking louse family Echinophthiriidae are all ectoparasites of pinnipeds (one exception, *Latagophthirus rauschi* Kim and Emerson, infests river otters (Price *et al.* 2003)). The seasonal breeding cycle and individual behavior of the hosts affect the seasonal abundance of the lice, since the lice are able to reproduce only when their hosts are ashore. Lice depend on a consistent source of peripheral blood to feed and produce eggs. When seals are ashore, they need to cool their body, exchanging excess heat through peripheral blood flow, especially in the flippers and tail, ideal to support an increase in louse populations. Consequently, lice are typically more abundant on pups and mature females during the breeding season when they spend a greater amount of time ashore (Murray *et al.* 1965). *Antarctophthirus microchir* (Trouessart & Neumann) was more abundant on the chest and belly of pups, perhaps to avoid high temperatures elsewhere on the body (Aznar *et al.* 2009). They also predicted this louse had time to complete only two generations each year while pups were ashore, before heading off to sea, a severe temporal constraint on louse population growth.

Some species of chewing lice (*Ricinus* spp.) seem to reach their greatest abundance on their hosts at about the time of host reproduction (Ash 1960; Rheinwald 1968), or perhaps relative to seasonal molts (Baum 1968). In a long-term study, Galloway and Lamb (2015a) investigated the seasonal patterns in intensity of infestation among four species of chewing lice infesting the rock pigeon. Populations of *Campanulotes compar* (Burmeister) and *Columbicola columbae* (Linnaeus) were lowest in the spring and gradually reached their peaks in the fall; *Coloceras tovornikae* Tendeiro had two peaks in abundance, one in the spring and one at the end of summer. Populations of *Hohorstiella lata* (Piaget), the species encountered least often reached their greatest numbers in winter. Clearly species living on the same host can exhibit distinctly different seasonal cycles.
There are too few studies on seasonal dynamics of lice, especially on hosts in tropical and subtropical latitudes. Long-term studies in particular will provide critical information about relationships of lice with their hosts.

Siphonaptera – Fleas

Adult fleas are extraordinary insects, specialized as ectoparasites of mammals and birds. There are approximately 2183 described species (Table 2). Fleas probably diverged from their mecopteroid ancestors about 95 million years ago, the Macropsyllidae being the earliest lineage (Zhu et al. 2015). Remaining flea lineages probably arose within a period of about 15 million years, beginning about 83 million years ago, radiating along with the appearance of placental mammals (Zhu et al. 2015). All are wingless, laterally flattened, and the exoskeleton is heavily sclerotized and darkly pigmented, especially in those species that may spend considerable time off the host. For those fleas that spend most of their time in the nest of the host, the exoskeleton is much more weakly sclerotized, and pale yellow.

The body is covered with backward-directed spines and setae which facilitate smooth, rapid movement through the hair of the host. These spines are sometimes large and in many species, are the most conspicuous external features. These ctenidia often occur in distinct rows, on the gena, the pronotum, and in some genera (e.g., Stenoponia), on terga of the abdomen. The genal ctenidia, if present, are found in a row along the ventral margin of the head, and numbers can vary from two small, overlapping spines on each side, to many. In some of the genera that infest bats (e.g., Myodopsylla), the genal ctenidia consist of broad, flat, and plate-like spines. The Stephanocircidae includes some species with the most spectacular development of the head and ctenidial spines (Fig. 8). Fleas in this family are called crown-of-thorn or helmet fleas, adorned with circles of spines, giving these fleas an otherworldly appearance. The pronotal ctenidium also varies in number of spines and arrangement. Fleas infesting insectivores, such as shrews, typically have fewer spines than fleas which infest rodents, while bird fleas (e.g., Ceratophyllus spp., which incidentally have no genal ctenidium) may have a greater number of closely allied spines, often more than 25. Stenoponia spp. are rather unusual in bearing a ctenidium on the first tergum of the first abdominal segment. Many genera of fleas (e.g., Pulex, Anomiopsyllus) have no ctenidial combs at all (Fig. 9).

The eyes are well developed in those species which routinely find themselves loose in the environment, searching for a host. Fleas confined to the nest and for which host location is less of a challenge, typically have no eyes at all. The antennae lie in shallow grooves on either side of the head. Males also have a groove along the dorsal margin of the head, and prehensile antennae, on the inner margins of which there are numerous specialized setae. During mating, males position themselves ventrally and behind the female and gradually move forward, allowing the keel-like ventral margin of the female abdomen to be guided along through the groove on the top of the male’s head. When the female is in an appropriate position, the prehensile antennae of the male (Fig. 9) are flipped up and grasp either side of the first abdominal sternum of the female, holding it in place while allowing the complex genitalia (Fig. 10) to align for copulation. In some
species, mating pairs may be so closely applied that on casual examination to appear as one flea. In mated females, spermatozoa are stored in a structure called the spermatheca. Most species of fleas have one, but some (e.g., *Hystrichopsylla* spp.) have two (Fig. 11).

The legs, too, are laterally flattened and specialized to accommodate movement over the body of the host. Most are armed with stout setae, especially on the tibiae and tarsal segments. The tarsal claws are bi-lobed and adapted to cling to individual hair follicles. This is never more apparent than when you have a sample of fleas in ethanol, along with a lot of hair. To remove each flea takes patience, because the tarsal claws ensnare the hairs and can become a frustrating tangle. The hind legs, in particular, are longer and are important in the well-known prodigious ability of fleas to jump. The hind legs act as levers to direct the energy released from pads of resilin located in the metathorax and pleural arch of the flea. A flea loads up the resilin pad by compressing this highly elastic protein and then locking the legs in place. When the energy is suddenly released from the resilin pads, the hind legs are extended explosively, and the flea is launched into the air, legs akimbo. The tarsal claws can snag onto a single hair, and the flea thereby gains access to the host. In some nest fleas (e.g., *Ceratophyllum arcuegens* Holland), the pleural arch is reduced or absent, and these fleas are unable to jump.

Adults of all species of fleas feed exclusively on blood. For this reason, they are closely tied to their host, for without blood, they inevitably starve to death. Hence the degree of association with their host is an interesting one. Most fleas are temporary ectoparasites. Adults of these species may spend most of their time in the nest, and visit the body of the host only when they go there to feed. Some of these temporary ectoparasites are commonly found on the host when it leaves the nest, and they may remain on the host until it returns to the nest. At that time, they jump off and remain in the nest material to lay eggs until their appetite for blood returns. This strategy makes some sense when we consider the risk associated with living on the body of a host that is sensitive not only to the bite of the flea, but also to its presence as it moves through the hair and feathers. This attention can attract the grooming activity of the host, potentially with dire consequences for the flea despite its array of morphological adaptations that make it difficult for the host to capture and remove it. However, some fleas spend much more time on the host, maintaining their ability to move about on the body of their host, but seldom leaving the host. The cat flea, *Ctenocephalides felis* (Bouché), is one of the best known examples of this level of host association. Infested hosts shed eggs laid by the infesting fleas, and their hair can become encrusted with fecal pellets from the fleas. The alakurt, *Vermipsylla alakurt* Schimkewitsch, is another spectacular example of a semipermanent ectoparasite that infests ungulates, often causing severe stress to their hosts during winter. There are also fleas which become permanently attached once they locate a host. The stick-tight flea, for example, *Echidnophaga gallinacea* (Westwood), infests many species of birds and mammals, where it is found about the eyes, ears and face, attached by its extremely long, serrated mouthparts (Fig. 12). The tungid fleas are an example of extreme adaptation as permanent ectoparasites. The adult females penetrate the skin of the host (Fig. 13), including humans, where they undergo secondary growth of cuticle (neosomy) and become greatly enlarged, a process rarely encountered among insects (though also seen in adult alakurts). The female tungid becomes a reproductive machine that releases thousands of eggs.
through the opening in the skin (Barnes and Radovsky 1969), and eventually dies never having left the host.

Most fleas have panoistic ovarioles (ovarioles without specialized nurse cells) and females produce eggs throughout their reproductive life, as long as a source of blood is available. There are fleas, *Hystrichopsylla* and *Stenoponia* for example, in which females have polytrophic meroistic ovarioles, where nurse cells are enclosed within the follicle. The eggs are oval in shape with a relatively thin chorion. The chorion may be variously sculptured, and distinctive, with a distinct micropyle and aeropyles on one end, but eggs of few species have been described (Linley *et al.* 1994; Ezquiaga and Lareschi 2012). Eggs typically hatch in a short time, and are not known to enter a dormant state to survive adverse conditions. The legless larva hatches from the egg by cutting its way through the chorion using an egg tooth. The egg tooth is borne on an egg-burster plate, on the dorsal surface at the back of the head. The egg tooth is variable in shape from knife-like, to spine-like and may even be retractable once hatching is complete. Most species have three larval instars, though two instars have been noted in tungids, and Larsen (1995) has described four instars in *Ceratophyllus (Monopsyllus) sciuorum* (Schrank). In addition to being legless, the larvae are usually white or cream-colored, with three thoracic and ten abdominal segments. The last abdominal segment is modified by the presence of two anal struts (Pilgrim 1991) (Fig. 14), which are used in locomotion, and it is surprising to see how quickly flea larvae can move about in the environment. Larvae of most species are confined to the nests of their hosts where they feed on organic debris, including the fecal pellets of adult fleas. The food and feeding behavior of flea larvae are poorly studied, and from the nature of the mandibles of some species, it would be no surprise to find they are predators. Larvae of some species of fleas have gone beyond a strictly free-living existence and have made the transition to life on the bodies of their hosts. Larvae of *Euhoplopsyllus glacialis* (Taschenberg) inhabit the fur of their Arctic hare hosts. Larvae of *Glaciopsyllus antarcticus* Smit & Dunnet live in the down feathers of fulmar chicks in Antarctica. In both cases, larvae gain protection from an inhospitable environment by becoming more closely associated with the bodies of their hosts. However, these larvae display no specific morphological adaptation to ectoparasitic existence. Quite the opposite is found in larvae of *Uropsylla tasmanica* Rothschild which has gone one further step in its host-parasite association. Eggs are attached to the hair of dasyurid marsupials in Australia, and upon hatching, first instar larvae make their way down the length of the hair follicle to the skin. Subsequent instars, of which there may be three, are mesoparasites, that is they live beneath the surface of the skin. Second to final instar larvae are highly modified, with a reduction in the head capsule and setae, with the body covered by numerous, stout spines (Fig. 15). So unusual are these parasitic larvae that one specimen was found in a museum collection where it had been identified as a fly larva, which it very closely resembles. *Uropsylla tasmanica* is unusual in another way. Pearse (1981) observed mature larvae to enter a state of dormancy to survive extreme conditions encountered during the Australian spring and summer. Adults were present on their hosts only during the fall and winter. The pupal stage is perhaps the least known stage of development in fleas. As they prepare for pupation, mature larvae are quite fat in appearance, filled with reserves to support development to the adult stage. The larvae may use silk to spin a fine-meshed cocoon in which they pupate.
Surrounding debris and extraneous materials are often incorporated in the cocoon, most likely by the sticky nature of the silk rather than by active construction by the larva. Pupal development is seldom prolonged, but adults frequently emerge from the pupa and remain dormant in the cocoon. Adults of *Ceratophyllus* spp. which infest cliff swallows, *Hirundo pyrrhonota* Vieillot, in North America are present in cocoons in the nest after chicks fledge, and remain dormant until the birds return the next spring, eight or nine months later (Loye and Hopla 1983). The adults can be stimulated to emerge if temperatures rise to within their normal activity range and there is vibration in the nest which might signal return of the host.

Males of many species require blood before they become sexually mature, but some, such as the *Ceratophyllus* infesting cliff swallows, are capable of mating at the time of emergence and females are receptive to males, though they require blood before they can lay eggs.

Seasonal patterns in flea life cycles have gained considerable attention, and are of importance, especially related to epidemiology of flea-borne pathogens. These annual cycles have been variously summarized by Darskaya (1970), Bibikova and Zhovtyi (1980), and Krasnov (2008). Fleas on commensal rodents, *Xenopsylla cheopis* (Rothschild), for example, belong to a group of tropical and subtropical species that may reproduce all year round when conditions are favourable. The cat flea, *Ctenocephalides felis*, is typically a flea of warmer climates, but has adapted to the environment of its host which is a common pet of humans worldwide. Even in harsh temperate climates, the cat flea finds a way to continue reproducing through the long, cold winter, alongside cats, dogs and people in their homes. Some fleas may be present all year round, but reproduce primarily in the warmer months, or when their host is present. *Parapsyllus longicornis* (Enderlein) parasitizes white-flippered penguins on the Banks Peninsula of the South Island of New Zealand. It reaches its greatest abundance in the nests during the breeding of its host, when all four stages of development are present. When the chicks leave the nest and go to sea, eventually only adult fleas are present in the nest, and will actively feed when adult birds make intermittent visits to the nests during winter, but they will not reproduce until temperatures are more favorable and when the source of blood is more continuous (Galloway and Challies 1992). *Ceratophyllus celsus* Jordan and *Ceratophyllus scopulorum* Holland infest cliff swallows in North America. Unlike the bird fleas infesting penguins, where birds occasionally visit nests throughout the year, swallows undertake long-distance migration after the chicks fledge in late summer. These birds will not return to the same nests until the following spring, perhaps eight months later. Adult fleas remain in their cocoons through the winter, exposed to extreme temperatures perhaps below -40°C, to survive and become active when their hosts return to nest. Some fleas are present on their hosts and appear to reproduce only in the summer. *Corrodopsylla curvata curvata* (Rothschild) infests shrews in Canada, and adults are present and reproducing throughout the warmest months of the year. Curiously, shrews, along with mustelids, are hosts to a species representative of another life cycle type, *Nearctopsylla hygini* (Rothschild), in the fall and winter months, replacing *Corrodopsylla* with virtually no overlap in occurrence of adults on shrews. Adults of some fleas are present on their hosts for only a short time each year, despite their hosts being present and active all year long. *Peromyscopsylla catatina* (Jordan) infests a variety of small mammals such as deer mice, *Peromyscus maniculatus* (Wagner), and red-backed
voles, *Myodes gapperi* (Wilson & Reder), but adult fleas are present only during August to October.

Miriam Rothschild and Robert Ford (1966) revealed the remarkable life cycle of *Spilopsyllus cuniculi* (Dale) which infests the European rabbit, *Oryctolagus cuniculus* (Linnaeus). Adult fleas consume nothing but blood, and in this unusual case, the entire reproductive cycle of the flea is affected by circulating hormones, so that flea reproduction is closely synchronized with reproduction in the host. As female rabbits become reproductively active, fleas increase in numbers on female hosts. Somatotropin in the blood stimulates mating among the fleas, and corticosteroids initiate ovarian development. Ovaries in female fleas begin to develop, spermatozoa mature in males, and salivary glands and gut enlarge; feeding and defecation rates increase, to provide food for future larvae in the nest. Most fleas move onto the young rabbits shortly after birth, and estrogens, thyroxin and prolactin stimulate mating, egg maturation and oviposition. After about three weeks, fleas gradually return to the doe where luteinizing hormone and progestin cause ovarian regression in the fleas while the emerging generation of new fleas infests the young at the time they leave the nest. Although not so intensively studied, the rabbit flea, *Cediopsylla simplex* (Baker), may respond similarly in many ways to its rabbit hosts in North America (Rothschild and Ford 1972, 1973).

Patterns in seasonal dynamics in life cycles among fleas are diverse and complex (Krasnov 2008). It is often extremely difficult to study these life cycles in detail, in some cases, because hosts live in underground burrows, or the nests, where all stages of the fleas may be present and are extremely difficult to find. In some cases, investigations of life cycles might be hazardous. *Chaetopsylla tuberculaticeps* (Bezzi) infests the grizzly bear, *Ursus arctos* Linnaeus and clearly one would be an intrepid soul to venture into a host’s den to obtain samples. In addition, it can be extremely difficult to rear fleas successfully in the laboratory, where it might be easier to carry out detailed observations on reproductive activity and abundance if field conditions could be adequately simulated. In fact, the details of the life cycle of most species of fleas are completely unknown, but offer many challenges for future research.

**Medical and Veterinary Importance**

**Lice**

Humans share three ecologically distinct sucking lice: the head louse, *Pediculus humanus capitis* de Geer, the body louse, *Pediculus humanus humanus* Linnaeus, and the crab louse, *Pthirus pubis* (Linnaeus). Head lice typically infest the finer hair of the head, where eggs are laid on the hair follicles, close to the scalp. These “nits” are often the first stage detected by public health personnel in routine screening for infestations in school children. School children are often at greatest risk of infestation because of close contact with classmates or the result of sharing personal items such as combs and brushes. Fortunately, this louse has not been shown to be a vector for important human pathogens, though a heavy infestation can be extremely irritating. Scratching from this irritation can result in secondary bacterial infections. Body lice on the other
hand are unique in the louse world in laying their eggs in the clothing of their hosts. Body lice do best among the homeless and under conditions of social upheaval, when war or displacement put people in a position where personal hygiene suffers, where a clean change of clothes is a luxury, and where people are housed in close proximity to one another. Prolonged and heavy infestations result in a thickening of the skin, known as vagabond’s disease. Of greater concern are the pathogens transmitted by body lice. The causative agents of epidemic typhus (Rickettsia prowazeckii da Rocha-Lima), trench fever (Bartonella quintana (Schmincke)), and louse-borne relapsing fever (Borrelia recurrentis (Lebert)) are all transmitted by body lice. In each case, the pathogen has to gain secondary entry to the body. The agents of epidemic typhus and trench fever are passed in louse feces and are scratched through the skin or rarely inhaled to cause infection. The agent of louse-borne relapsing fever infuses the body of an infected louse, ultimately resulting in the death of the louse. In the meantime though, a person may be infected when the louse is crushed and its fluids scratched into the skin. The crab louse, or pubic louse, infests areas of the body where coarser hair grows, the pubic area, chest hair, armpits, moustache and beard, for example. Fortunately, crab lice cause only intense irritation from their bites and are not known to transmit pathogenic agents to humans.

Any time animals are maintained under conditions where they are in close proximity with one another for prolonged periods of time, probability and frequency of transmission of lice increase. Therefore, domestic animals are prone to heavy infestations of lice, and economic losses can be substantial. This is particularly the case when animals are under stress from other conditions as well, including poor nutrition, crowding, or severe cold in temperate latitudes. Animals may suffer reduced rate of weight gains, a drop in milk production, and the irritation from a louse infestation may cause the animals to bite, scratch and rub their bodies to the point of causing damage to the hair coat and skin. Large animals may even damage pens and fences by their frequent rubbing to relieve irritation. The quality and condition of the fleece can be seriously affected in sheep. Louse infestations in many commercial poultry flocks are largely a thing of the past, where birds all originate from hatcheries. However, where communal birds are the source for a flock, louse infestations can be prevalent, especially where birds are housed closely together in a sheltered roost overnight. Heavily infested birds can suffer reduced weight gain and egg production and losses and damage to feathers. Companion animals such as dogs and cats and pets, such as guinea pigs, rabbits and caged birds may also be severely impacted by heavy louse infestations.

There has been very little work to assess the impact of louse infestations on wildlife. Chewing lice certainly affect their hosts by reducing feather mass, with the resulting impact on thermoregulation and requirement for compensatory food intake (Booth et al. 1993). Lice may also affect the appearance of a male host and affect its success at acquiring a mate. Some amblycearan lice serve as vectors for filarial nematodes in waterfowl (e.g., Pseudomenopon pilosum (Scopoli) for Pele citrus fulicaeatrae (Diesing) in coots (Bartlett and Anderson 1989); Trinoton anserinum (Fabricius) for Sarconema eurycerca (Wehr) in geese and swans (Seegar et al. 1976)). The remarkable relationship between Eulimidana spp. (Filarioidea) and various chewing lice vectors infesting shore birds will reveal how finely tuned interactions between host,
parasite and vector can be (Bartlett et al. 1989; Bartlett 1993). Numerous bacterial and viral pathogens have been detected (e.g., Linn et al. 2001; Reeves et al. 2005, 2006), especially in sucking lice, but the role of these lice in the epidemiology of these agents requires further study. For the most part, there is little evidence louse infestations at typical levels of intensity in wildlife cause serious impact. If the effectiveness of a host to groom is impaired, numbers of lice can reach extraordinary numbers. In the case of blood-feeding lice, if the host’s immune system is compromised by stress or other factors, numbers of lice can soar with deleterious effects on the host. There are cases where exotic lice have been accidentally introduced into wildlife populations and where the impact has been severe. An introduced species of chewing lice (Damalinia (Cervicola) sp., a presumed parthenogenetic species, and Bovicola tibialis (Piaget)) have caused massive hair loss in Columbian black-tailed deer in Oregon and Washington (Bildfell et al. 2004; Mertins et al. 2011).

Fleas

Perhaps more than any other arthropod-borne pathogen, Yersinia pestis (Lehmann & Neumann), a bacterium transmitted through flea bites, has changed the course of human history through several great pandemics resulting in the death of many millions of people. Mention of bubonic plague, the Black Death, elicits a strong response in public health officials even today. In the case of urban plague, which at least includes the Oriental rat flea (Xenopsylla cheopis) and domestic rats, fleas which feed on infected rats acquire the bacteria from their host’s blood and the bacteria replicate in the midgut lumen. A mass of bacteria associated with the proventricular spines causes a complete blockage of the gut, preventing further ingestion of blood. However, the starving flea continues to attempt feeding by regurgitating gut contents to clear the blockage. In so doing, bacteria from the mass are passed back through the mouthparts into the bloodstream of the host. Plague bacteria can be transmitted by many species of fleas in which the bacterial mass in the midgut causes a blockage. The sylvatic form of the disease is maintained in many endemic foci by rodent fleas and their hosts, and may pose a threat in recovery programmes for endangered mammals (e.g., black-footed ferret (Miller and Reading 2012)). The number of cases of human plague today is approximately 2,000 annually worldwide, but it is still a disease of concern wherever it occurs.

Fleas are important vectors of many additional potentially pathogenic agents to humans. The rickettsia that causes murine typhus (Rickettsia typhi (Wolbach & Todd)) is almost worldwide, transmitted by a variety of fleas which commonly infest peridomestic rodents and associated animals (Azad et al. 1997). This agent is transmitted when the feces of infected fleas or infected fleas themselves are crushed and scratched into a bite wound, emphasizing again the importance of the allergic response and subsequent itching caused by the host response to blood-sucking insects. Fleas are rarely vectors of other bacterial agents such as Francisella tularensis (McCoy & Chapin) (causative agent of tularemia), Coxiella burnettii (Derrick) (causative agent of Q fever) and the newly emerging Rickettsia felis Bouyet et al. (Azad et al. 1997; Pérez-Osorio et al. 2008; Reif and Macaluso 2009). The agent of cat scratch disease, Bartonella henselae Regnery et al.,
and other *Bartonella* spp. are also important bacterial agents transmitted by fleas, the former responsible for many thousands of human cases each year.

Fleas are vectors for important protozoan parasites. As many as ten species of *Trypanosoma*, all parasites of rodents, are transmitted by fleas worldwide. Although most of these are poorly known, *T. lewisi* (Kent) has been extensively studied as a model for human trypanosomiasis. The infective stage of the protozoan is passed in flea feces and scratched through the skin or ingested by the rodent host to become infected. There are no doubt many other flea-borne trypanosomes that await discovery.

Fleas have not been widely identified as vectors of viral pathogens, though the myxoma virus which infects rabbits is one important example. This virus can be mechanically transmitted through the bite of infected fleas, notably the European rabbit flea, *S. cuniculi*, and causes high mortality in susceptible populations of rabbits. This flea-virus combination was used widely in the war against rabbits in Europe and Australia.

Fleas are the intermediate hosts for a number of parasites of domestic animals and wildlife. *Acanthocheilonema reconditum* (Grassi) is an onchocercid nematode found beneath the skin of infected dogs. Cat fleas acquire microfilariae with a blood meal, and the juvenile nematodes reach the infective stage in the body of the flea, where presumably they remain until the flea is eaten by a host dog (Napoli *et al.* 2014). Cat fleas among others are also intermediate hosts for a number of tapeworms. *Dipylidium caninum* (Linnaeus) is a parasite of dogs; *Hymenolepis nana* (Siebold), *H. diminuta* (Rudolphi) and *H. citelli* (McLeod) are all parasites of rodents. Flea larvae become infected when they consume tapeworm eggs and which hatch and develop to the cysticercoid stage in the adult flea. The final hosts are infected when fleas bearing mature cysticercoids are consumed.

Interactions of fleas with the dermecos of their hosts can cause severe reactions. Humans and various animals develop severe sensitivities and potentially dermatitis, after repeated, prolonged exposure to flea bites. For this reason, flea control in the domestic setting is a major commercial endeavor in many parts of the world. Irritation from flea bites in serious infestations of hen fleas (*Ceratophyllum gallinaceae* (Schrank) and *C. niger* C. Fox) in poultry operations and *Orchopeas caedens* (Jordan) in mink farms can affect animal performance and condition. Stick-tight fleas (e.g., *Echidnophaga gallinacea*) on poultry and alakurts on ungulates in Asia can have major impact on animal health and wellbeing. Perhaps one of the most unusual problems caused by fleas is tungiasis. Female tungid fleas (e.g., *Tunga penetrans* Linnaeus) penetrate the skin, often on the bottoms of the feet, under toe nails or between the toes of domestic and wild animals as well as humans, where they undergo the rare process of neosomy; the adult flea actually generates new body tissue to increase in size from a body length of about one millimeter to more than a centimeter. In its neosomic state, the female literally becomes an egg-laying machine, shedding eggs into the environment where the larvae may develop quite independent of the host home or nest. Injury caused by females beneath the skin is extremely painful and can be debilitating.

**Community Diversity of Lice and Fleas**
The diversity of these important groups of ectoparasites is limited by the diversity of the birds and mammals available as hosts. However, not all potential species of ectoparasites may be present in an ecosystem, for a variety of reasons. Not all species of ectoparasites are present in the entire range of their hosts, perhaps because environmental conditions in parts of the range are unsuitable. Some ectoparasites infest only one species of host (monoxenous), a range of closely related hosts (oligoxenous), or they may infest a wide variety of unrelated hosts (polyxenous). The degree of dependency on one or more species of hosts may affect the geographic range of the ectoparasites and be reflected in local communities and ecosystems. Some hosts, especially birds, may have tremendous capacity for dispersal, or may undertake seasonal migration over thousands of kilometers. In this way, their presence in an ecosystem may vary seasonally as they bear with them the permanent ectoparasites that live on their bodies. For fleas, immature stages or dormant adults may be present in the nests of their hosts, but not easily detected and their presence underestimated. Local disturbance by humans may alter habitat so that some species of ectoparasites may be extirpated, or factors which affect abundance and occurrence of host species may impact the prevalence of their ectoparasites.

Determination of community diversity of lice and fleas is essential to understand ecological structure and interactions, yet offers a number of challenges to the ectoparasitologist. The hosts must be examined directly to determine whether or not particular species of lice and fleas are present. It is also desirable to learn something about the ecological relationships of the ectoparasites, so some quantitative data in infestation parameters are typically collected. These parameters have been described by Bush et al. (1997). Those most often reported are prevalence (proportion of the host population infested), mean intensity (the mean number of parasites per infested host) and mean abundance (the mean number of parasites per individual host).

To undertake a study to investigate diversity of ectoparasites, it is important to obtain necessary permission and permits. These include permission from authorities who may regulate access to land included in the community analysis. Permits are required from government regulatory agencies to capture, handle or have in a person’s possession, the host animals and/or their nests. It may be necessary to meet appropriate animal care regulations when handling any live animals. All personnel must be sufficiently trained and experienced in handling animals and collecting ectoparasites.

Marshall (1981) included a chapter on field and laboratory methods for collecting ectoparasites. Hosts may be collected and examined alive. Birds may be captured in mist nets, box traps, baited cages, lures and cannon traps. Small mammals are usually collected in variously designed, appropriately baited traps. It may be necessary to use special techniques and personnel for larger mammals. These animals may be examined alive by visual inspection, bearing in mind many ectoparasites have evolved specific behavior to escape host grooming and may be rather difficult to collect. Large animals, such as cattle, may be difficult to examine unless restrained, and even then offer interesting challenges. Live animals are often anesthetized, placed in fumigation chambers or treated with fast-acting insecticides, after which the hosts may be examined more closely and ectoparasites may be ruffled from the feathers or hair. These techniques can provide
information on the composition of the ectoparasite fauna and relative measures for infestation parameters.

More precise data on infestation parameters may be collected if dead hosts are examined. Hosts may be collected in snap traps, shot or salvaged from wildlife rehabilitation facilities. It is not always possible, practical or desirable to kill animals to study ectoparasites. Therefore the latter option offers considerable potential for detailed quantitative study. When a dead host is examined, the body can be closely examined directly for a longer period of time, with superior results. Orifices such as the ear canals and nasal passages can be more deeply explored. The body may also be washed in detergent (Henry and McKeever 1971; Mironov and Galloway 2002) or the skin can be removed and dissolved in a combination of enzymes and potassium hydroxide solution (Hilton 1970). The collections can be passed through a fine mesh screen to retain even the smallest of ectoparasites, which can be sorted by hand under the stereomicroscope.

Examining birds and mammals may not always provide information about the entire ectoparasite community, especially for fleas where the larvae and pupae may be restricted to the nest, or for some species where even adults are found almost exclusively in the nest. There may be special challenges in finding the hosts’ nests (especially for fossorial mammals), but from the nests, adult and larval fleas can be extracted using Berlese-style funnels or by hand sorting.

Studies in which birds and mammals are sampled are often under constraints to minimize the number of animals collected. Parasite populations are notoriously aggregated (Shaw and Dobson 1995), an important consideration in determining sample sizes in diversity and ecological studies (Rékási et al. 1997). Consideration should also be given to time of the year, because hosts as well as parasites may vary in their status in the community. Parasites may differ in their initiation of new infestations and certain ages of hosts may be less heavily infested (Thompson et al. 1998; Galloway 2012).

Regardless of the method of collection, it is always prudent to remember that wild hosts may carry agents of potentially serious human diseases (e.g., hantavirus and rabies) and the ectoparasites of interest may carry their own risks to human infection (e.g., epidemic typhus and plague). It is important to follow recommended protocols in any investigation of ectoparasite ecology.

Conservation of Lice and Fleas

In a discussion about conservation of biodiversity, lice and fleas rarely spring to mind. They are more likely considered to be detrimental parasites, perhaps even a threat to conservation efforts by their very presence or by the disease agents they may transmit. Despite the evolutionary importance of parasites (Price 1980), we still know very little about their biodiversity and especially about their ecological interactions with their hosts. As populations of so many species of birds and mammals decline worldwide, often in response to habitat fragmentation, deterioration and destruction at the hands of humans, lice and fleas, especially monoxenous and oligoxenous species face extirpation or even extinction (Rózsa 1992; Galloway and Lamb 2015b).
Coextinctions of ectoparasites will no doubt increase as the numbers of their hosts suffer declining populations and extinctions (Koh et al. 2004), but what does this mean for community function? Ectoparasites may influence host fitness and genetic diversity (Rózsa 1992) and ectoparasites have the capacity to affect sexual selection (Kose et al. 1999). Whiteman and Parker (2005) stressed new applications of molecular techniques using ectoparasites and their roles in genetic processes and phylogenetic relationships and in management of endangered species where horizontally transmitted pathogens were involved. Pérez et al. (2013) emphasized the importance of a more objective approach to conservation strategies by abandoning overemphasis placed on charismatic fauna and setting priorities in ecological management of wider biodiversity issues.

Despite the diversity in the known louse and flea fauna (Durden and Musser 1994; Price et al. 2003; Lewis 2000), there is a tremendous amount of work remaining before the world fauna is known. Valim and Weckstein (2013), for the genus Myrsidea (Phthiraptera: Menoponidae) in Brazil alone, estimated that the number of species would increase from the 90 species, to more than 900 if all potential hosts could be examined. Similarly, many flea species, especially those with greater host specificity and narrow geographic distributions (Krasnov et al. 2005) remain to be discovered.

ACKNOWLEDGEMENTS

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REFERENCES


Table 1. Suborders and families of lice (Phthiraptera) with approximate numbers of known genera and species in each family, as of 2014. Families are listed in alphabetical order, rather than in phylogenetic sequence. Classification is based on Price et al. (2003) for the chewing lice (Amblycera, Ischnocera, Rhynchophthirina) and Durden and Musser (1994) for the sucking lice (Anoplura). Some genera (e.g., Brueelia, Philopterus) are in a state of nomenclatural flux, so a conservative estimate has been adopted for the table below.

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Table 2. Families and subfamilies of fleas (Siphonaptera) with approximate numbers of known genera and species in each, as of 2014. Families are listed in alphabetical order, rather than in phylogenetic sequence. Classification is based on a combination of Lewis (2000), Whiting et al. (2008) and Hastriter (2012).
| Family                  | Subfamily    | Neopsyllinae | Rhadinopsyllinae | Stenoponiinae | Hystrichopsyllidae | Ischnopsyllidae | Ischnopsyllinae | Thaumapsyllinae | Leptopsyllidae | Amphipsyllinae | Leptopsyllinae | Lycopsyllidae | Bradiopsyllinae | Choristopsyllinae | Lycopsyllinae | Uropsyllinae | Macropsyllidae | Malacopsyllidae | Pulicidae | Pygiopsyllidae | Rhopalopsyllidae | Parapsyllinae | Rhopalopsyllinae | Stephanocircidae | Craneopsyllinae | Stephanocircinae | Stivaliidae | Farhangiinae | Stivaliinae | Tungidae | Vermipsyllidae | Xiphiopsyllidae | Total |
|------------------------|--------------|--------------|------------------|---------------|-------------------|-----------------|----------------|----------------|---------------|----------------|----------------|--------------|----------------|-------------------|----------------|-------------|---------------|----------------|-----------|-----------|--------------|-----------|-------------|--------------|--------|
|                        |              | 11           | 7                | 1             | 4                 | 20              | 19             | 1              | 28            | 22             | 6              | 6             | 1               | 1                 | 3              | 1           | 1             | 2              | 22        | 10         | 10           | 6         | 10          | 24          | 245     | 2183        |
Figure 1. Eggs of *Pectinopygus farallonii* (Kellogg) laid between the barbs of a primary feather of a double-crested cormorant.

Figure 2. Hog louse (*Haematopinus suis* (Linnaeus)) egg, with fine sculpture over the surface of the egg and a distinct operculum to allow escape of the hatching nymph.
Figure 3. Modified claw of a hog louse, *Haematopinus suis*, for grasping onto coarse body hairs of its host.

Figure 4. Head of a chewing louse, *Rotundiceps* sp. Note well developed chewing mandibles.
Figure 5. Combs of setae on the ventral surfaces of the hind femora and abdominal sterna in a chewing louse, *Colpocephalum* sp.

Figure 6. Head of a chewing louse, *Trichodectes euarctidos* Hopkins, from a black bear. Note the antennae modified for grasping a female during copulation.
Figure 7. Chewing lice, *Piagetiella peralis*, inside the pouch of an American white pelican.

Figure 8. Head of a crown-of-thorns flea, *Stephanocircus dasyuri* Skuse. Note modified ctenidial spines.
Figure 9. Head and thorax of a male nest flea, *Anomiopsyllus*. Note absence of distinct ctenidia and spines. Also note extended position of the antenna, which is used to hold a female in place during copulation.

Figure 10. The male genitalia of fleas are enormously complicated, as in this example, *Opisodasys pseudarctomys* (Baker), a parasite of flying squirrels in North America.
Figure 11. Female fleas in the genus *Hystrichopsylla* have two sperm storage organs, spermathecae, as opposed to only one, as seen in most species.

![Image of a flea](image1.png)

200 µm

Figure 12. The long, serrated mouthparts of the stick-tight flea, *Echidnophaga gallinacea*, allow it to attach more or less permanently to its host.

![Image of a stick-tight flea](image2.png)

200 µm
**Figure 13.** Neosomic female chigoe flea, *Tunga penetrans*, embedded in the bottom of a human toe. (Photo by W. E. Ralley)

**Figure 14.** Paired anal struts on the end of abdominal segment 10 in the larval flea, *Notiopsylla enciari* Smit. The struts are used in locomotion in the legless flea larva.
**Figure 15.** The larva of the flea, *Uropsylla tasmanica*, lives as a subdermal parasite on its dasyurid hosts in Australia. The head is reduced to a tiny disc surrounded by large thoracic spines.