

The Biology, Ecology, and Evolution of Chewing Lice

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BIOLOGY

Introduction

Chewing lice are small, dorsoventrally compressed insects and are parasites of virtually all birds (Fig. 1) and some mammals (Fig. 2). Many chewing lice are host specific, being found on only a single species of host. All chewing lice are permanent ectoparasites and complete their entire life cycle on the body of the host, where they feed mainly on feathers, dead skin, blood, or secretions. Chewing lice on mammals apparently do not ingest hair, rather they feed on skin and skin products (Wahrenhouse 1953). Some species of lice feed on the eggs and molting stages of mites and other lice, including members of their own species (Nelson and Murray 1971). Lice also ingest microbes, such as bacteria and fungi, which are of unknown nutritive value.

Chewing lice have a hemimetabolous life cycle that includes a large egg, three nymphal stages, and the adult (Marshall 1981a). Louse populations are normally controlled by host grooming and other factors. When not kept in check, however, dramatic increases in louse populations can severely degrade host condition, reproductive success, and survival (Durdan 2001, Clayton and Adams In press). Chewing lice are relatively easy to detect through careful visual examination, and their population sizes can be measured accurately both on live and dead hosts (Clayton and Walther 1997, Clayton and Drown 2001). Lice are usually identified on the basis of sclerotized features visible in cleared, slide-mounted specimens (Kettle 1974, also see Checklist Introduction).

Chewing lice are named for their mandibulate, chewing mouthparts. Chewing lice ("Mallophaga") do not form a monophyletic group but are paraphyletic with respect to sucking lice in the insect order Phthiraptera (Fig. 3). Modern classifications divide Phthiraptera into four suborders, three of which make up the chewing lice:

Suborders & Families	Genera	Species
Amblycera		
Menoponidae ^a	68	1,039
Boopitidae ^m	8	55
Laemobothridae ^a	1	20
Ricinidae ^a	3	109
Gyropidae ^m	9	92
Trimenoponidae ^m	6	18
Ischnocera		
Philopteridae ^{a,z}	138	2,698
Trichodectidae ^m	19	361
Rhynchophthirina		
Haematomyzidae ^m	1	3
Anoplura (16 families) ^m	49	532

Table 1. Higher level classification of lice (Insecta: Phthiraptera). Data for chewing lice (Amblycera, Ischnocera, and Rhynchophthirina) are from checklist data (see Checklist Introduction). Data for sucking lice (Anoplura) are from Durdan and Musser (1994a). ^aFound on birds; ^mFound on mammals; ^zOne genus (*Therodax*) occurs on birds (cassowaries); ^oOne genus (*Trichophilopterus*) occurs on mammals (lemurs) and sometimes is placed in the separate family Trichophilopteridae.

Amblycera, Ischnocera, and Rhynchophthirina. 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 (Table 1). Amblycera are generally more mobile than Ischnocera. For example, Amblycera will abandon a dead or distressed host in search of a new one. Most Ischnocera are so specialized for life on hair or feathers that they do not venture away from the host. Avian chewing lice are often called "feather lice," a phrase that is perhaps best applied to ischnoceran lice on birds, since they are true feather specialists.

2 The Chewing Lice

Members of the fourth suborder, Anoplura, parasitize mammals and are called sucking lice because they have piercing-sucking mouthparts. Sucking lice are easy to distinguish from chewing lice because they have heads that are narrower than their prothorax. With the exception of Rhynchophthirina, the sister group to Anoplura (Fig.

3), chewing lice have large, heavily sclerotized heads that are as wide as the prothorax, if not wider (Figs. 1-2). Durdan and Musser (1994a) provide a comprehensive checklist of the 532 valid species of Anoplura described through January 1993. Durdan and Musser (1994b)

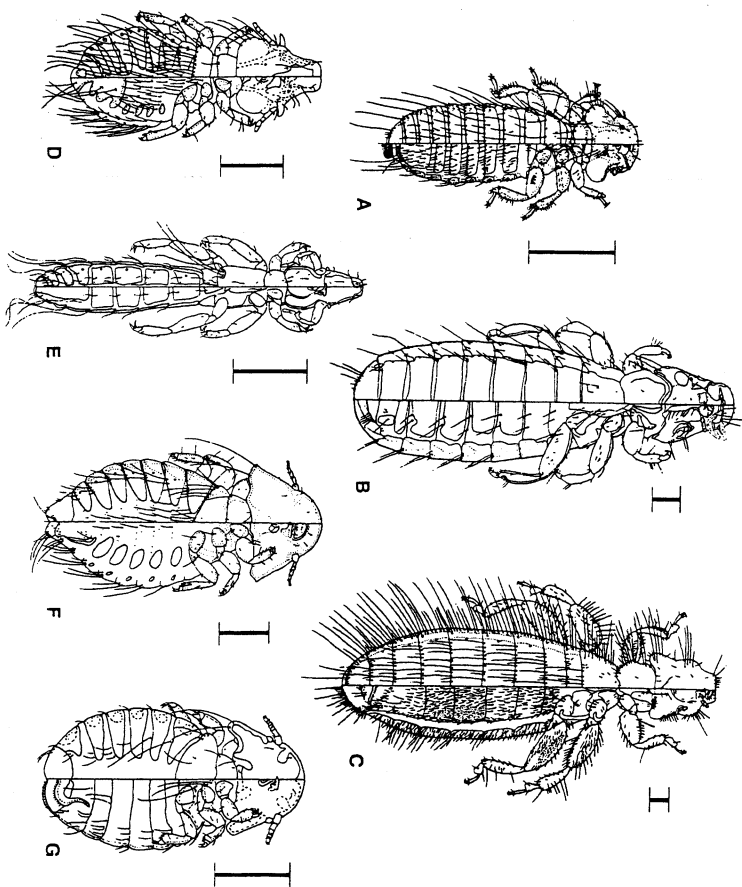


Figure 1. Representatives of the four families of avian chewing lice (see Table 1). Dorsal morphology to left of midline, ventral morphology to right. Scale bars = 0.5 mm. (A) *Calpocephalum holzschuhi* (Amblycera: Menoponidae), F, ex Barred Forest-falcon (*Micrastur ruficollis*); (B) *Ricinus* sp. (Amblycera: Ricinidae), F, ex Passeriformes sp.; (C) *Laemobolton maximum* (Amblycera: Laemobothridae), F, ex hawk (*Buteo* sp.); (D) *Philopterus* sp. (Ischnocera: Philopteridae), M, ex Passeriformes sp.; (E) *Columba columba* (Ischnocera: Philopteridae), M, ex Rock Dove = feral pigeon (*Columba livia*); (F) *Goniodes australis* (Ischnocera: Philopteridae (Goniotidae of some authors; see text)), F, ex Mallard Fowl (*Lepus ocellatus*); (G) *Hepalapsogaster* sp. (Ischnocera: Philopteridae (Hepalapsogasteridae of some authors; see text)), F, ex Tiarniiformes sp. (A) after Clayton and Price (1989); (B) after Ledger (1980); (C) after Nelson and Price (1965); (D) after Price and Helleenthal (1998); (E) original drawing by Richard Adams; (F) after Emerson and Price (1986); (G) original drawing by Richard Adams.

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provide a host list, and Durden (2001, 2002) succinctly reviews the biology of Anoplura.

Morphology, Physiology, and Behavior

Adult chewing lice vary in length from 0.8 mm to 11 mm. In most species the females are larger than the males, often by 20%. The body is dorsoventrally flattened with a horizontally positioned head. This shape is an adaptation for lying flat against feathers or hair,

which increases the tenacity of the louse in the face of host movement and grooming. Chewing lice vary in color from nearly white, through shades of yellow and brown, to black. Some taxa match the color of their host, suggesting that lice may use cryptic coloration to avoid detection by the host (Rohdendorf and Clay 1952). This interesting hypothesis has yet to be tested.

The three suborders of chewing lice are easily identified. Amblycera have maxillary palps, a primitive condition shared with their psocopteran ancestors.

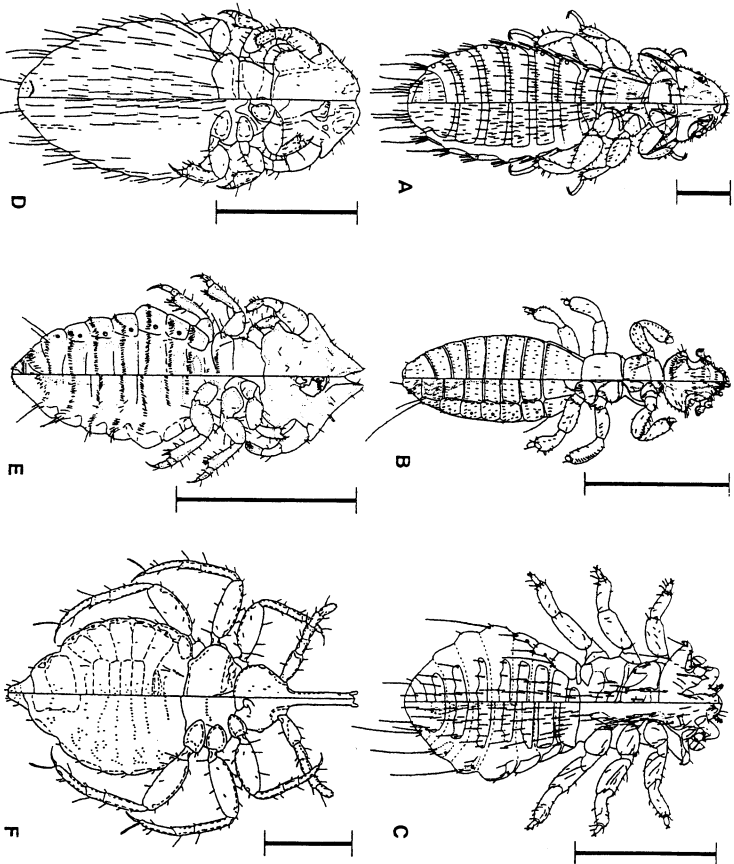


Figure 2. Representatives of the five families of mammalian chewing lice (see Table 1). Dorsal morphology to left of midline, ventral morphology to right. All drawings are of male lice. Scale bars = 0.5 mm. (A) *Heterodoxus spingeri* (Amblycera: Boopiiidae) ex Domestic Dog (*Canis familiaris*). (B) *Citricola weizsaeckeri* (Amblycera: Gyropidae) ex Central American Spiny Rat (*Proechinops semispinosus*). (C) *Harrisonia uncinata* (Amblycera: Trimenoponidae) ex Central American Spiny Rat (*P. semispinosus*). (D) *Neotrichodectes minutus* (Ischnocera: Trichodectidae) ex Long-tailed Weasel (*Mustela fennina novaboracensis*). (E) *Cebidicola extrarius* (Ischnocera: Trichodectidae) ex Red Howler Monkey (*Alouatta seniculus*). (F) *Haematomyzus elephantis* (Rhynchophthirina: Haematomyzidae) ex African and Indian elephants (*Loxodonta and Elephas*). [A-E after Emerson and Price (1975); F after Durden (2001)].

Ischnocera and Rhynchophthirina, which are more derived clades, lack maxillary palps. Members of the Amblycera have four segmented antennae, with a pedunculate third segment. The antennae are concealed in lateral grooves, making them difficult to see. Ischnocera and Rhynchophthirina have fully exposed, filiform antennae with 3 to 5 segments. Some male Ischnocera have large, dimorphic antennae (Figs. 1E, 2D, E) that are used to clasp the female during copulation, which can last for hours or even days (Rózsa Pers. comm)! Amblycera have opposable mouthparts that move in a vertical plane, perpendicular to the ventral surface of the head. Some Amblycera, such as ricinid bird lice (Fig. 1B), have chewing mouthparts that are essentially modified to suck blood (Clay 1949a, Nelson 1972). In contrast to Amblycera, the mouthparts of Ischnocera move in a horizontal plane parallel to the head. Rhynchophthirina, which are parasites of elephants, warthogs, and bush pigs, have chewing mouthparts borne on the end of a long proboscis, giving them a weevil-like appearance (Fig. 2F).

Ischnocera have only two apparent thoracic segments because the mesothorax and metathorax are fused to form

a prothorax (see Checklist Introduction, Fig. 2). In contrast, Amblycera have a distinct suture that divides the mesothorax and metathorax. The abdomens of chewing lice have 11 segments, but only 8 to 10 of these are visible because of fusion or reduction. The abdominal segments have dorsal, ventral, and lateral plates to help maintain structural integrity. The thorax has a single pair of respiratory spiracles and the abdomen has up to six pairs of spiracles, all linked to an elaborately networked tracheal system (Fig. 4A). The thorax supports three pairs of well-developed legs with two tarsal claws per leg in the case of bird lice, but only one claw per leg in the case of most mammal lice. This reduction in the number of claws in mammal chewing lice is paralleled both in the sucking lice and in hippoboscids flies that parasitize mammals (Kettle 1977). The reduction in claw number presumably relates to the simpler structure of hair compared to feathers.

Chewing lice are morphologically and behaviorally adapted for particular microhabitats on the host. As such, they can be assigned to informal categories on the basis of overall morphology and how they avoid host grooming. For example, one scheme for bird lice includes the following categories: 1) agile Amblycera that run quickly

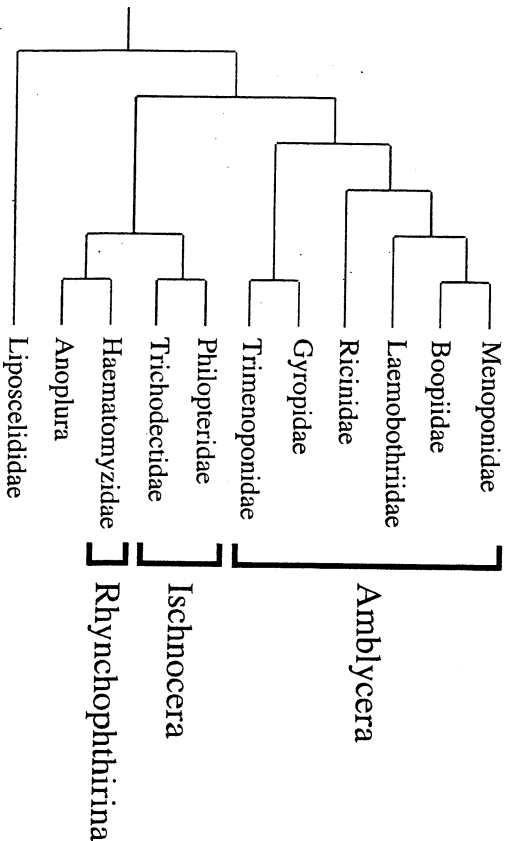


Figure 3. Composite phylogeny of the suborders of Phthiraptera, resolved to family level in chewing lice only. Phylogenetic relationships among the suborders are based on morphological (Lyal 1985a) and molecular (Johnson and Whiting 2002, Barker et al. In press) characters. Phylogenetic relationships within Amblycera are based on morphological characters (Marshall In press). See text for more discussion.

across the skin or feathers (Fig. 1A); 2) very large Amblycera that slip sideways between the feathers (Fig. 1B, C); 3) slugish, triangular-headed Ischnocera that avoid preening by dwelling mainly on the head and neck (Fig. 1D); 4) elongate Ischnocera that hide between the bars of wing and tail feathers (Fig. 1E); 5) slugish Ischnocera that burrow into the downy regions of the abdominal feathers (Figs. 1F, G). These categories have no formal taxonomic significance, and not all bird lice can be placed neatly into one of the categories. However, the scheme does illustrate some of the major adaptive zones occupied by most bird lice.

Chewing lice feed by shearing or scraping feathers or skin with their mandibles. Particles of food are pushed into the preoral cavity by the labrum. The maxillae and labium are much reduced in size and play only a minor role in feeding. Like Psocoptera, many Ischnocera and some Amblycera have lingual sclerites that are posted vertically between the labrum and labium. These sclerites are part of an efficient water-vapor uptake system that extracts water directly from the air (Rudolph 1983), enabling lice to feed solely on feathers and dry flakes of dead skin and other debris.

Lice have sense organs in their mouths, as well as on their antennae. The antennal sense organs of Ischnocera are more specialized than those of Amblycera (Clay 1970). A few species of chewing lice have small eyes, which are probably little more than light sensors. Lice are repelled by light, while being attracted to the warmth and odor of the host. Most lice have sensory hairs, or setae, distributed over the body. The number, length, and distribution of setae are important taxonomic characters. Backward pointing setae apparently also protect lice from being dislodged by host grooming. Additional features of external morphology, especially those that are important taxonomic characters, are illustrated in Figure 2 of the Checklist Introduction.

The internal morphology of chewing lice is dominated by the alimentary canal, which includes the esophagus, crop, midgut, smaller hindgut, four Malpighian tubules, and rectum. The crop differs considerably among the suborders of chewing lice, reflecting differences in diet. In Amblycera, many of which feed on skin products and blood, the crop is merely an enlargement of the esophagus (Fig. 4A). In Ischnocera, most of which feed on feathers, the crop is a diverticulum off the esophagus that runs nearly the entire length of the abdomen (Fig. 4B). In Rhynchoiphthirina, which are thought to feed mainly on blood, the crop is underdeveloped. Pieces of ingested feathers and other

material are often plainly visible in the crops of chewing lice. When a louse feeds, its crop pulsates, breaking up food particles by rubbing them against comb-like teeth in the crop walls. In an interesting parallel to their avian hosts, some lice have grit in their crops, which helps pulverize food during digestion. Although mechanical action initiates digestion, lice rely on powerful enzymes in the gut to complete the digestive process.

Endosymbiotic bacteria may also play a role in the nutritional physiology of chewing lice. Rickettsia-like bacteria are present in many avian Ischnocera, but absent from Trichodectidae and most Amblycera (Ries 1931, Reed and Hafner 2002). The bacteria are present in Rhynchoiphthirina and probably all Anoplura. They reside in specialized cells called bacteriocytes, or mycetocytes, which are sometimes concentrated in structures called mycetomes (see figures in Eichler et al. 1972). The bacteria undergo transovarial transmission by migrating from the bacteriocytes into developing eggs in the female louse. The importance of these bacteria is suggested by early ablation experiments in which human lice (Anoplura) deprived of bacteria did not feed properly, survive, or reproduce (reviewed in Buxton 1947). It is also worth noting that, with the exception of blood feeders, bacteria are mainly present in lice with diets that are particularly difficult to digest, such as feathers. Blagoveschensky (1959) suggested that the bacteria provide vitamins or other necessary supplements. More work is needed on this interesting topic.

The reproductive tract of chewing lice is large and taxonomically informative, particularly in the case of the external male genitalia. The genitalia are structurally complex and large (Fig. 4C), encompassing up to half the length of the male abdomen. A typical configuration includes a flattened or rod-like basal apodeme, which supports an endophallus and associated sclerotized structures, all of which get everted during copulation. The apparatus is often bordered by a pair of sickle-shaped parameres that help locate the female genital opening and protect the delicate endophallus during copulation (Lyal 1987). Male Amblycera have three pairs of testes, whereas male Ischnocera and Rhynchoiphthirina have only two pairs. The testes are connected to the vas deferens. These, in turn, coalesce to form the seminal vesicle, which stores sperm.

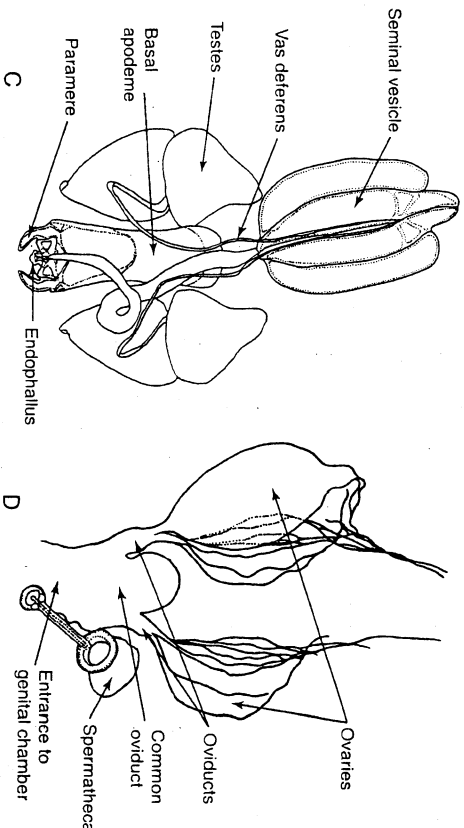
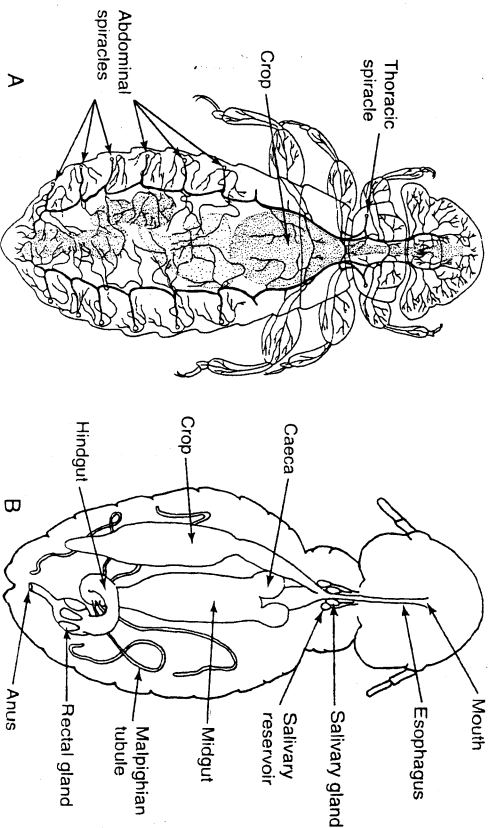


Figure 4. Internal features of chewing lice. (A) Tracheal system (bold) and alimentary canal (stippled) of *Myrszidea cucullaris* (Amblycera: Menoponidae) ex European Starling (*Sturnus vulgaris*). (B) Alimentary canal of *Borivola bovis* (Ischnocera: Trichodectidae) ex Domestic Cow (*Bos taurus*). (C) Male reproductive tract of *Craspedorhynchus spathulatus* (Ischnocera: Philopteridae) ex Black Kite (*Milvus m. migrans*). (D) Female reproductive tract of *Philopterus ocellatus* (Ischnocera: Philopteridae) ex Carrion Crow (*Corvus corone shampii*) [A adapted from Harrison (1915b); B adapted from Marshall (1981a); C and D adapted from Smith (2001)].

The female reproductive tract contains several ovaries (Fig. 4D) with eggs in various stages of development. The ovaries are connected by oviducts to a common oviduct, or uterus, that leads to the genital chamber. In many taxa, a spermatheca is connected to the genital chamber by a thin duct. Male lice deposit a spermatophore in the spermatheca during insemination. The spermatophore may be in continuous use until it is replaced at a future insemination (Khalifa 1949). Female lice have no ovipositor, but they do have finger-like gonopods that help position the eggs during laying. Most species of lice attach their eggs individually or in clumps to basal regions of the hair or feathers with a glandular cement. Many species deposit their eggs in regions that are relatively protected from host grooming, such as the scruff of the neck (Rust 1974), or between the bars of feathers (Nelson and Murray 1971).

The eggs, also known as nits, are whitish in color. They require 4 to 10 days of incubation, depending on the species. Eggs are often easier to detect than hatched lice because they glisten in reflected light, particularly before they hatch. Some species produce eggs that are heavily sculptured or equipped with projections that facilitate attachment and/or gas exchange (Balter 1968, Foster 1969a, Marshall 1981a, Cohen et al. 1991). The distal end of the egg has a cap known as the operculum. When a nymph is ready to hatch, it sucks air in through its mouth. This air passes down the alimentary canal and accumulates behind the nymph, below the operculum. When sufficient air has accumulated, the resulting pressure pops the operculum open. Hatching is further aided by a plate-like structure, the hatching organ, situated at the upper end of the pre-nymphal skin. Hatched eggs remain attached to the hair or feathers and are grayish and flattened in appearance.

Each nymphal stage requires 3 to 12 days for completion and is successively larger (Marshall 1981a). Nymphs lack reproductive organs and they have less sclerotization and fewer setae than adults. Some chewing lice have nymphs that look much like miniature adults. However, other species have early nymphal stages that differ considerably in appearance from the adults. These differences can be taxonomically useful, which is why it is desirable to preserve specimens of all life history stages, not just adults. Adult lice live about a month, with females producing an average of 1 egg per day, for a total of 12 to 20 eggs. Lice have chromosomes that are quite small with no localized centromere (holokinetic). The chromosomes are few in number, ranging from $n = 2$ to $n = 12$. Conspecific males and females have the same number of chromosomes, but identifiable sex

chromosomes are missing. The mechanism of sex determination in lice is unknown (Kettle 1977, Tombești and Papesschi 1993, Tombești et al. 1999). Males have achiasmatic meiosis, and spermatogenesis follows a particular course with mitotic divisions following meiosis, rather than preceding it, as in most insects. These factors markedly constrain genetic variability, which may be related to the predictable environment in which lice live.

Although most groups of ectoparasites tend to have even sex ratios (Marshall 1981a), lice sometimes have skewed ratios, usually with a female bias (Clayton et al. 1992). In an analysis of published data, Marshall (1981b) reported 31 of 50 species (62%) with significantly female biased sex ratios (none showed a male bias). In some ischnoceran lice, males are rare, or absent altogether, indicating parthenogenetic reproduction (Marshall 1981a, b, Westrom et al. 1976). The causes and consequences of biased sex ratios in chewing lice deserve further study.

ECOLOGY

Population Dynamics and Community Ecology

Chewing louse populations are profoundly affected by variation in temperature and humidity near the host skin. A good deal of work has been done on this topic, particularly for the lice of domesticated mammals; see reviews by Marshall (1981a) and Price and Graham (1997). Chewing lice are so attuned to conditions on the body of the host that few species can survive for more than a few days off the host. Indeed, most taxa are difficult to culture *in vitro*, even when provided with ample food in incubators with carefully regulated temperature and humidity. Marshall (1981a) reviews the literature concerning attempts to culture lice *in vitro*. Humidity near the skin is a function of ambient humidity, at least in the case of birds (Moyer et al. 2002). Birds in humid regions of the world have more lice than birds in arid regions, even when lice on birds of the same species are compared across broad geographic distributions (Moyer et al. 2002, Moyer et al. 2003).

Like many macroparasites, chewing lice have aggregated populations that often conform to a negative binomial distribution (Eveleigh and Threlfall 1976, Fowler and Williams 1985, Clayton and Tompkins 1995, Lee and Clayton 1995, Rózsa et al. 1996, Clayton et al. 1999). In other words, most individual hosts have few lice, whereas a few individual hosts have many lice. Lee and Clayton (1995) discuss factors underlying such distributions, and Rózsa et al. (1996) show that

aggregation is reduced in lice on colonial species, presumably because of an increase in opportunities for horizontal transmission.

Successful transmission is one of the greatest challenges faced by any parasite. The close physical association of lice with their hosts means that the greatest opportunity for transmission is during periods of direct contact between hosts. The rate of transmission of chewing lice has been measured directly between copulating birds (Hilgert 1996), and between parent birds and their offspring (Clayton and Tompkins 1994). Lee and Clayton (1995) showed that transmission from adult to nesting swifts (*Apus apus*) involved significantly more immature than adult lice. This fact, in conjunction with the fact that populations of lice on juvenile hosts tend to undergo a period of rapid expansion, explains why juvenile hosts often have more immature than adult lice (Eveleigh and Threlfall 1976). However, the reverse may be true for populations of lice on adult hosts. For example, Clayton et al. (1992) recorded significantly more adult than immature lice on adults of many species of Amazonian birds.

Some species of chewing lice may have life cycles that are synchronized with those of the host (Marshall 1981a). Foster (1969b) reported data showing an increase in populations of blood feeding lice concurrent with the bird breeding season. She went on to suggest that breeding in the lice may have been triggered by host reproductive hormones, as in the case of rabbit fleas (Rothschild and Ford 1964). The synchronization hypothesis requires direct testing because increases in lice could be due to host life history tradeoffs, such as an inability to devote sufficient time to preening during the breeding season. Marshall (1981a) reviews the population ecology of lice, including a variety of factors thought to influence population dynamics and age structure.

Although direct contact between host individuals facilitates transmission of lice, it is probably not the only route of transmission. Ischnoceran lice are capable of leaving the host by "hitchhiking" on hippoboscoid flies, a phenomenon known as phoresis (Keirans 1975). Corbet (1956) found lice attached to 43.5% of 156 hippoboscoid flies that he removed from European Starlings (*Sturnus vulgaris*). Although phoresis has been recorded for a few ischnoceran genera, it is unclear how common the phenomenon is among ischnocera. Phoresis is quite rare among Amblycera, apparently because attaching to flies is difficult with vertically oriented mouthparts (Keirans 1975). Since hippoboscids are not as host specific as lice,

phoresis may be a route by which some species of lice can wind up on the "wrong" species of host. Clay (1949b) and Timm (1983) suggested three additional routes by which bird lice could move between host species: 1) dispersal of lice (or eggs) on detached feathers, 2) shared dust baths, and 3) shared nest holes. The fact that birds steal nest material from other species of birds suggests yet another possible dispersal route (Fey et al. 1997). Clayton (1990a) showed that sharing of lice by unrelated species of owls is restricted to cases involving sympatric species of hosts with overlapping microhabitat.

Opportunities for dispersal notwithstanding, many chewing lice are quite host specific. Clayton et al. (1992) used carefully standardized collecting methods to compare the louse communities on 127 species of birds in 26 families, all from one region of Amazonian Peru. Of the lice that could be identified to species, nearly all were confined to one species of host. This is not to say, however, that all chewing lice are host specific. Some species occur on more than one genus, family, or even order of host. For example, Price (1975) recorded *Menacanthus eurysternus* from 118 bird species belonging to 70 genera and 20 families. In short, specificity should never be assumed. Chewing louse systematists has suffered greatly at the hands of taxonomists who have tended to describe new species on the basis of host associations, rather than on the basis of the lice themselves. This circular practice is in large part responsible for the regrettably high number of synonymies in chewing louse taxonomy.

Chewing louse communities vary considerably in their species richness, ranging from one species per host, as in the case of ostrich lice, to more than 20 species, as in the case of tinamous, which are terrestrial, Neotropical birds. Over 20 species of lice are known from the single species *Crypturellus soui*, and up to 9 species have been collected from a single individual of this species (Ward 1957). Why such variation exists is not well understood. In the case of tinamous, which are one of the oldest lineages of birds (Sibley and Ahlquist 1990), the explanation may be that there has been more time for speciation and colonization events to take place. An historical approach that incorporates phylogenies for both tinamous and lice would be useful here.

A recent phylogenetically independent comparative analysis of the louse communities on more than 50 species of neotropical birds revealed no features of host morphology or ecology that correlate significantly with louse species richness (Clayton and Walther 2001). However, richness itself was a significant predictor of the

