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Population Dynamics of
Chewing Lice (Phthiraptera)
Infesting Birds (Aves)

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Abstract

In the past 25 years, studies on interactions between chewing lice and their bird hosts have increased notably. This body of work reveals that sampling of live avian hosts, collection of the lice, and the aggregated distributions of louse infestations pose challenges for assessing louse populations. The number of lice on a bird varies among host taxa, often with host size and social system. Host preening behavior limits louse abundance, depending on bill shape. The small communities of lice (typically one–four species) that live on individual birds show species-specific patterns of abundance, with consistently common and rare species, and lower year-to-year population variability than other groups of insects. Most species of lice appear to breed continuously on their hosts, with seasonal patterns of abundance sometimes related to host reproduction and molting. Competition may have led to spatial partitioning of the host by louse species, but seldom contributes to current patterns of abundance.

INTRODUCTION

Lice (Phthiraptera) are permanent ectoparasites of birds (the chewing lice *Amblycera* and *Ischnocera*) and mammals (the chewing lice *Ischnocera* and the sucking lice *Anoplura*). All developmental stages, including eggs, are found on the body of the host. People may be familiar with the head, body, and pubic lice that infest humans, or perhaps lice on their domestic animals (81), but few entomologists have examined the diverse louse fauna that occurs on birds. Yet this large group of ectoparasites consists of more than 5,300 described species (46) and perhaps as many more that have yet to be described.

The chewing lice that infest birds make up a diverse fauna found worldwide. Taxonomic status of many of these lice was long confused and scattered throughout the literature. The world checklist of chewing lice published in 2003 by Price et al. (93) consolidated information and stimulated interest among researchers who previously struggled to understand their regional fauna. The result has been a cascade of taxonomic research using traditional and molecular techniques to describe phylogenetic relationships among lice and coevolutionary relationships of these lice with their hosts. As parasites in general and lice specifically have begun to be analyzed through this evolutionary perspective (22, 25, 73, 91), field and laboratory investigations on the relationships between lice and their hosts have shifted to favor quantitative ecological analyses. Clayton & Walther (29) contributed to this expansion of research on lice with a thorough treatment of sampling methods for ectoparasites of birds. Rózsa et al. (101) then reinforced unification of the terminology proposed by Bush et al. (11) and provided a user-friendly analytical approach to quantification of commonly applied measures of parasite infestations. These three publications (29, 93, 101) stimulated the growth of ecological and evolutionary research on this group that occurred from the beginning of this century. In this review, we consider studies described in 424 research articles from 1945 to January 2020, 75% of which were published since 2000. A complete list of references is provided in **Supplemental Appendix 1**.

Chewing lice infesting birds live on the skin and among the feathers, largely free of invertebrate predators but at risk from grooming activities by their hosts (12, 22). They are sheltered from, but still affected by, external abiotic conditions experienced by the host. Consequently, their population dynamics are subject to internal and external factors that we are only beginning to understand. Chewing lice live most of their lives invisible to investigators wishing to explore these relationships. In 1981, Marshall (76) summarized much of what was known at the time about the population dynamics of chewing lice on birds, citing only 12 quantitative studies on seasonal changes in populations. He did not cite every paper on population dynamics of lice, but few of those that he did not cite contributed substantially to the field at the time.

This situation changed enormously as the number of people studying and reporting on lice around the world increased; to date, at least one study has been conducted on each continent. For this review, we select 276 studies conducted in 62 countries in which authors investigate measures of infestation of chewing lice on birds. Our objective is to examine how chewing louse populations change over time and space. We first examine how sampling hosts, and their lice, contributes to understanding louse populations, as well as some limitations of the current methods. We describe patterns of abundance for lice on some of the better-studied hosts. We then summarize how interactions with the host, and interactions within louse communities, affect louse populations. Next, we examine how host ecology influences louse populations, the seasonal patterns of abundance of lice on birds, and the stability of louse populations. We end with some thoughts on conservation of lice and recommendations for future work.

SAMPLING HOSTS AND THEIR CHEWING LICE

The natural sampling unit for chewing lice is the host bird. Throughout the history of this research, sampling of hosts has been an opportunistic process (shooting, trapping, or mist-netting wild birds or collecting sick and injured birds) that is not strictly based on any randomized selection from a defined population. The exceptions to this are studies of domesticated and semidomesticated birds such as chickens, *Gallus gallus domesticus* (e.g., 113), and feral rock pigeons, *Columba livia* (e.g., 2). In many countries, obtaining wild host specimens is now regulated by strict animal care guidelines for collecting and handling live birds. Killing birds for research purposes is resisted by researchers and regulatory agencies. However, an increase in environmental awareness has resulted in the general public collecting injured or disabled birds and surrendering them to wildlife officers or rehabilitation facilities. Many such birds are too seriously injured to rehabilitate; they are euthanized and often made available to researchers. Most of these specimens are collected in urban or suburban habitats, not throughout the range of the host, and in temperate regions may consist primarily of individuals on migration north or south. Juvenile or sickly birds may also be disproportionately represented. The birds may be handled in a way that leads to an increase or decrease in louse abundance. Nevertheless, these birds represent a large source of common hosts, and also of some species that are rare or rarely encountered. Some of the concerns in using these hosts can be overcome by weighing specimens to determine their condition, by assessing their age, and by assessing the handling time for injured birds. It is not known whether any of these methods provide samples that are truly random with respect to the abundance of lice on hosts, and rarely is it practical, or even possible, to find out.

After obtaining a host specimen, counting the lice on a host is the next step. In response to preening behavior by the host, lice have evolved avoidance mechanisms to escape preening (22, 82), which can also frustrate the attempts of researchers to count and collect them. Many methods have been developed to determine louse abundance, depending on whether living or dead hosts are being examined, whether examination occurs in the field or the laboratory, and how much time is available to examine each host (29). Live hosts offer the greater challenge because the time available for examination and the potential methods of handling are limited. Visual inspection is the simplest and most frequently used technique (used in 47% of reviewed studies where the collection method is specified; see **Supplemental Appendix 2**). Unfortunately, visually assessing numbers of live lice is fraught with difficulty when there are very many or very few lice, when species move quickly among the feathers, when lice are the same color as plumage, or when small early-instar nymphs are present. It is also important to recognize that different species of lice may occupy different regions of a host (18, 19, 38, 82), and in some cases, nymphs may occupy different regions of the body than adults (53). Fumigation or applications of insecticide, followed by ruffling the feathers and visual examination (84, 120), are also widely used (42% of reviewed studies). In some cases, this method has been used with success to examine large numbers of hosts (20). Occasionally, holes in wing and tail feathers are used as a surrogate for some species of lice (77), but further investigation is required to determine the validity of this approach (115).

Processing dead birds offers greater freedom in time and methodology. Birds can be carefully examined visually; lice can be vacuumed from a carcass (108, 111); skin and feathers can be chemically dissolved (19); or birds can be washed mechanically (23) or manually (49, 50) in soapy water, lice being collected over a fine mesh screen. Relative efficiency of collection methods has been compared for several host species (23, 40). Washing assures the highest recovery, 90% or more of nymphs and adults, but because this method can only be applied to dead birds, it has been used in only approximately 10% of studies reviewed. The only method available to quantify louse eggs is a painstaking visual examination of individual feathers.

Supplemental Material >

The relative efficiencies of the methods depend on the species and size of the host, the nature of the plumage, and the species of louse being assessed. For feral pigeons, washing removes approximately twice as many lice as dry ruffling (23). For bald eagles (*Haliaeetus leucocephalus*), however, washing removes 10 times as many *Colpocephalum* spp. and three times as many *Degeeriella discocephalus* as does dry ruffling and increases the nymph-to-female ratio approximately 1.5 times (70). Hopkins (57) emphasizes the importance of obtaining an unbiased estimate of nymphs. Researchers should also be aware that certain species occupy cryptic or unusual sites on the host, such as inside feather shafts (94), inside the plume of an emerging feather (80), or in the gular pouch (92).

Once identified and counted, louse populations are best quantified based on parameters commonly used by parasitologists: prevalence, intensity, abundance, sex ratio, nymph-to-female (or adult) ratio, and measures of their variability (11, 101). Prevalence is the proportion (percentage) of hosts with any lice. Intensity is the number of lice on a bird with lice, which quantifies the size of the infrapopulation; the arithmetic average of intensities for a sample of infrapopulations is mean intensity. Note that prevalence times mean intensity equals mean abundance. Separating mean abundance into these two parameters has both conceptual and statistical advantages (88, 101). Sex ratio can be important to population growth when infrapopulations are small, as they often are in chewing lice. Nymph-to-female ratios are thought to be high in growing infrapopulations and low when an infrapopulation is declining (76).

Although the number of studies is now far greater than was the case when Marshall (76) introduced us to the population processes of lice, questions about the validity and reliability of sampling of both hosts and lice remain an important impediment to understanding the population dynamics of chewing lice.

Supplemental Material > **ABUNDANCE OF CHEWING LICE ON THEIR AVIAN HOSTS**

How many lice can an observer expect to find on a sample of birds? In broad but short-term surveys of many bird species in Peru (24) and China (20, 54), host species had 0.4–1.9 species of lice and 0.5–4.2 louse individuals per bird specimen. In long-term studies in Canada with large numbers of specimens per host, 16 bird species hosted 1–4 species of lice (mean of 2.3), with a mean abundance of 93 lice per specimen, 67% having some lice, and a mean intensity of 188 lice per infested bird (47, 49, 50, 52). The range in mean abundance among these 16 hosts was wide, however, from 5–447. A variety of factors contribute to the 20-fold differences in numbers of lice among these multispecies studies. Perhaps most important are the methods for extracting lice, sources of hosts for examination, the sample size of hosts, and host species composition. A summary of observed louse abundances from additional studies of individual or small numbers of host species could be included in our review, but confounding differences in methods among these studies limit the value of such a broad comparison (**Supplemental Appendix 2**).

Studies of the dynamics of abundance often begin with an examination of the timing of developmental stages in a life history and changes over time in the age structure of a population (109). This approach is not much used for avian lice because of the difficulty of sampling eggs and of observing nymphal instars on the host, or even of collecting nymphs. For example, estimates of nymph-to-female (or adult) ratios are often low when visual inspection or fumigation are used to collect lice, compared to when more efficient washing techniques are used, suggesting that nymphal populations are underestimated when visual inspection or fumigation are used. Total counts of lice are often provided without breakdown into nymphs and adults. However, there are exceptions where the numerical distribution of nymphs in the various instars is provided (e.g., 41, 42, 61). Rearing lice on detached feathers can provide information on the durations of the

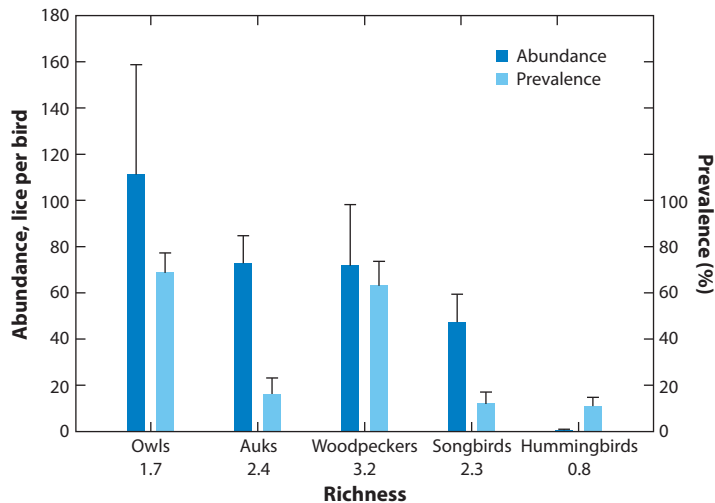


Figure 1

The mean abundance and prevalence (with standard errors) of avian lice on their host species: 8 species of owls (*Strigidae*, $n = 508$) (52), 6 species of auks (*Alcidae*, $n = 270$) (38), 5 species of woodpeckers (*Picidae*, $n = 614$) (50), 7 species of songbirds (*Passeriformes*, $n = 144$) (118), and 15 species of hummingbirds (*Trochilidae*, $n = 112$) (24). The mean species richness of lice associated with each host taxon is provided below the taxon name.

developmental stages (82). Typically, population data on avian lice consist of the number of individuals in the louse community, often, but not always, with a breakdown of the abundance (and sometimes prevalence and intensity) of species for a sample of hosts.

Setting aside sampling issues, the taxa of hosts included in a study affect the numbers of lice that birds typically support. Among five taxa where lice have been assessed on multiple species, owls have the highest louse abundance, over 100 per bird; songbirds have approximately half as many; and hummingbirds have less than one louse per bird, on average (**Figure 1**). Prevalence shows a different pattern, with owls and woodpeckers having prevalence greater than 60%, whereas less than 20% of auks and songbirds, and less than 5% of hummingbirds, are infested (**Figure 1**). These differences cannot simply be attributed to differences in sampling procedures among studies; the same louse extraction method and similar sample sizes were used in studies of owls and woodpeckers where different abundances were found, and the same was true for studies of auks, songbirds, and hummingbirds (**Figure 1**). Differences in louse abundance might be expected for hosts of different size (see below), or for populations from different habitats, for example, Peru or southern China versus north-temperate Canada, but comparison of related host species indicates that host abundance is likely affected by specific interactions between louse communities and their individual hosts, rather than simple habitat difference. For example, among three *Turdus* hosts, one migratory and breeding in north-temperate habitats (118) and the other two permanent residents in a tropical habitat (72), the north-temperate species and one of the tropical species had similar abundances of 15 or 16 lice per bird, whereas the other tropical species had 31 lice per bird. Within a family of hosts, the abundance of lice often varies 10-fold or more among host species (50, 52). Nevertheless, broad differences in louse abundance are evident for louse species that inhabit different higher taxa of hosts.

The lice found on individual birds represent a small community of species, where the complete habitat of the community is the body surface of an individual bird (117). The number of species

that form each community of chewing lice varies among host taxa (**Figure 1**) but is typically two–four. Owls typically host fewer species of lice (1–2) than do woodpeckers (2–4), and hummingbird species often host only one species, or none so far detected (24; but see also 97) (**Figure 1**). Numbers of species infesting a host can be much greater in some host orders, for example, eight species or more on Tinamiformes (117) and some Procellariiformes (93). In such cases, most genera on one host are represented by only one species (93). The different species of lice often occur on different parts of the host, i.e., head, body, and wing lice (18, 38, 83).

In communities of parasites, the densities of infrapopulations are thought to be characteristic of the individual species of louse (3, 64, 90). However, for species of lice living on the skin and feathers of the same endothermic birds and dependent on a similar resource, the dynamics of the populations of co-occurring species might be expected to be more similar than those of other parasites or nonparasitic species. Nevertheless, chewing lice, too, exhibit species-specific population dynamics (105). Some species on a host are consistently common from year to year, while some are rare; some have relatively stable populations, and some show high temporal variability in abundance (47, 48, 67, 69). The abundance of louse species does vary broadly among host taxa, but the dynamics of individual louse species depends on the interactions of individual species and their hosts.

INTERACTIONS BETWEEN HOST AND LOUSE POPULATIONS

Chewing lice have the potential to affect the health and fitness of their hosts by reducing feather mass (9), causing irritation and trauma (81), serving as intermediate hosts for parasitic infections (4, 5), and affecting social interactions (63). As a result, the host may exert selective pressure on louse populations and suppress their numbers.

Perhaps the most important factors in determining the number of lice on an individual bird are host defenses: behavioral defenses such as grooming, bathing, and sunning, and also immune responses. These defenses and their effects at suppressing louse numbers have been reviewed in detail elsewhere (12, 24, 26, 78). Of particular importance, however, is preening, which can dramatically suppress louse populations. For example, a minor manipulation of bird bills that prevents complete closure at the tip of the beak interferes with preening and causes large increases in louse populations (27). Preening is thought to be an important factor in maintaining avian lice at the relatively low densities often observed, and bird bill morphology that affects preening ability is hypothesized to be an important factor in determining differences in abundance of lice on different bird taxa (26, 30). An inability to preen effectively, as a result of ill health or damage to or malformation of beaks, is thought to be a cause of extreme abundances of lice on a small proportion of the host population. These extreme infrapopulations are partly responsible for the highly aggregated distributions of louse abundance (88) and contribute to the difficulty in precisely estimating mean intensity of lice (101).

Allopreening fulfils a range of social functions in birds, but its role in reducing ectoparasite populations is not well known. Radford & Du Plessis (95) found that prevalence of ectoparasites was highest in winter but was also higher in subordinate versus dominant green woodhoopoes in South Africa, associated with the presumed amount of allopreening. In an experimental study, Villa et al. (116) demonstrated a negative correlation between extent of allopreening and intensity of louse infestation on rock pigeons. Colonial birds or birds with a greater level of social interaction might be expected to show more allopreening and, therefore, lower louse abundance (e.g., 86, 102, 119). However, colonial birds do not necessarily have lower louse abundance than do less social species (99). Another possibility is that a colonial lifestyle facilitates louse dispersal and, therefore, a higher prevalence of lice.

Host body size affects ectoparasite populations in general, and avian lice in particular: Large hosts tend to be infested by large louse species (117), have more species, and have greater intensity of ectoparasites than do small ones (32, 99, 100). The relationship between species richness and body size was challenged, however, by Clayton et al. (24), referring to Poulin's (89) argument that early analyses did not sufficiently account for phylogenetic relationships among hosts. The relatively small range in number of species that co-occur on any species of bird makes testing the hypothesis difficult. Moreover, recent data provide no support for a relationship between louse species richness and host size. In studies of eight owl and five woodpecker species that vary in mass by more than an order of magnitude, the largest species in each host taxon harbored no more species of lice than did smaller ones (51, 68).

Studies across a range of host taxa do support the conclusion that louse abundance (24, 99) and its components, prevalence and mean intensity (20), often increase with host size. For five species of woodpeckers, host body size accounts for most of the variation in abundance among species, due to the effect of body size on mean intensity but not prevalence (51). Where large samples of birds are available, intensity also increases with the mass of individual birds, both for the community of all lice and for the infrapopulations of individual species (36, 51, 71). However, the relationship between host body mass and mean intensity in eight species of owls is weak, and no relationship was detected between intensity and body mass for individual birds (68). Similarly, no relationship was detected between intensity and body mass for individual feral pigeons (47).

Rózsa (99) offers three hypotheses to explain the relationship between ectoparasite abundance and avian host size. Larger hosts have greater surface area and resources to support a larger diversity and number of ectoparasites. This larger habitat may provide a greater opportunity to escape grooming activity by the host. Within one host species, body size may also be correlated with age; larger hosts may be older, and depending on the age at which infestation by ectoparasites occurs, there may be more time for ectoparasite populations to increase. Furthermore, large species tend to have longer lifespans (106) and, therefore, more time on average to acquire ectoparasites.

Host defenses against lice, particularly preening, and host body size are two host characteristics that are important determinants of louse populations for many taxa of birds. The extent to which host defenses and body size affect louse population requires further investigation, especially through controlled experimental studies.

INTERACTIONS AMONG INFRAPOPULATIONS OF CHEWING LICE

Partitioning of the host surface by louse species has been viewed as the outcome of competition over evolutionary time (14, 60). However, there is little direct evidence of current competition that might influence population processes of lice. One exception is a convincing study of a wing louse (*Columbicola columbae*) and a body louse (*Campanulotes compar*) that often co-occur on domestic pigeons, where they feed on the same types of feathers. In this case, the wing louse population is suppressed when body lice are present, but body louse populations are unaffected by the presence of wing lice; competition is detected only at high densities induced by limiting the preening ability of the host (14). In some cases, environmental conditions may affect competition among species of lice. For example, *Columbicola macrourae* outcompetes and displaces *Columbicola baculoides* on their shared host, the mourning dove, except under conditions of low relative humidity (74). The possibility of competition is also suggested by the observation that some louse species do not co-occur as often as expected by chance, which is the case for lice on sharp-tailed grouse (8), but unexpectedly high levels of co-occurrence of species is found in many other communities of lice (47, 50, 52, 117). Ward (117, p. 455) concludes that co-occurrence is facilitated by "a

conditioning of the environment” by one or more species, which allows “additional species to occur.” Furthermore, the abundances of many co-occurring louse species are positively correlated among individual hosts, counter to the expectation of competition, although occasional negative correlations are also observed (47, 50, 52). The importance of competition among species of lice in the community in determining population size remains to be determined.

Interactions between members of the louse community may take the form of intraguild predation. Predation of ectoparasites by other arthropods is known, but not for chewing lice (35). Cannibalism by chewing lice has been observed (76) and is further evidenced by partially predated corpses and body parts in digestive systems of lice (8, 82). Distinguishing cannibalism from predation or scavenging has not been attempted, and there is no evidence to date that intraguild predation or cannibalism among chewing louse species play an appreciable role in the population dynamics of lice.

HOST ECOLOGY AND LOUSE POPULATIONS

Lice can be abundant on birds that live in environments with extreme low temperatures, so such conditions do not limit louse populations (47, 52, 66, 68, 111). However, relative humidity in the host’s environment can influence louse abundance; lice on domestic pigeons are eliminated if birds are maintained at less than 25% relative humidity in the laboratory (79), the optimum relative humidity being 60–70% (79, 82). In nature, some species of lice are apparently excluded from hosts living in parts of their range where relative humidity is low (13). Ischnoceran lice, compared to species in other taxa of lice, are better able to extract water from air at low relative humidity via extrusion of lingual sclerites on the hypopharynx (104). Some louse species, however, thrive on hosts living in arid environments (16).

In a broad study of Neotropical bird lice, including host ecological parameters such as geographic range, population density, and microhabitat use, Clayton et al. (24) found no relationships between these host parameters and louse abundance. In a large study of lice on birds in China, louse prevalence is similar on birds from a wide range of climatic zones and birds differing in migratory status, but lice on insectivorous hosts are less prevalent than on birds from other feeding guilds (20). Also in China, high-altitude resident populations of birds have higher louse prevalence than do migrants passing through this alpine habitat (54). In contrast, Canadian populations of woodpeckers and owls show no consistent differences in louse abundance between migratory and nonmigratory species (50, 52). Prevalence of lice is higher on both migratory and nonmigratory hosts in larger forest fragments than in smaller ones (15).

SEASONAL VARIATION IN LOUSE ABUNDANCE

The habitat of avian lice, the skin and feathers of the host, is a relatively stable abiotic environment through the seasons compared to that of the host, particularly hosts that live at high latitudes or altitudes. Seasonal changes in louse populations might be expected to be more muted than those of other multivoltine insects that are more exposed to the weather (121). All lice that have been studied are present in all seasons, and where sample sizes are adequate, the presence of nymphs indicates that breeding is continuous. However, many bird species exhibit seasonal changes in their life histories and behavior associated with reproduction, molting, and migration, which may affect the seasonal biology of their ectoparasites (55). Foster (39) concluded that the life cycles of some blood-feeding chewing lice (*Ricinus picturatus*, *Menacanthus* sp.) and their host, the orange-crowned warbler (*Leiothlypis celata*), are synchronized, with the lice stimulated to oviposit by hormonal changes in the host’s blood associated with reproduction. The adaptive values of such

synchronization are thought to be increased opportunity for nymphs to disperse to juvenile hosts still in the nest; reduced loss of eggs or nymphs during the molt; reduced opportunity for louse dispersal in winter, when hosts are essentially solitary (39); and the opportunity to take advantage of the energetic requirements of breeding and molting, which limit hosts' immune responses and preening behavior (8, 55). One direct test of the coordination of louse reproduction by host physiology showed that lice infesting the Indian common mynah (*Acridotheres tristis*) produced more eggs when host ovary and testis weight increased prior to breeding (17, 110).

Most research has focused not on the seasonality of egg production, but rather on the abundance of lice in different months and the proportion of nymphs in the population as a measure of the rate of reproduction and population growth. In monthly comparisons of up to a year, louse abundance is often higher at the beginning of the breeding period than before or after (8, 17, 21, 38, 42, 43, 61). The pattern does not hold for all lice, however (37, 59, 75). Within louse communities, some species peak when the host breeds, but others do not (6, 49, 61, 112). Louse abundance also sometimes drops during the molt, which usually occurs after breeding (61, 84). In some cases, louse populations appear to respond more to seasonal changes in temperature and relative humidity than to host life cycle (1, 65).

In multiyear studies of abundance, sex ratios, and nymph-to-female ratios, with replicate samples of hosts through the seasons, reproduction by lice was usually continuous year-round, if the host spent the winter in situ, or occurred at the beginning and end of the breeding season, if the host migrated to a warmer wintering habitat (48, 49, 66; but see 8). In these studies, eight species of lice on five hosts showed no consistent association with periods of breeding or molting, although they had distinct seasonal patterns of abundance. Nymph-to-female ratios remained above one for seven species of lice throughout the nesting and molting periods, confirming that reproduction is neither enhanced nor interrupted during these periods. One exception is *Brueelia straminea* on downy woodpeckers, *Picoides pubescens*, which has low prevalence, mean intensity, and nymph-to-female ratios through the breeding period (66).

Clear seasonal patterns of abundance occur for many louse species. To clarify the causes of these patterns, careful attention must be paid to seasonal changes in population processes. The timing of egg production is difficult to estimate directly, but the presence of nymphs and the distribution of nymphal instars can clarify population changes associated with reproduction (42). Moreover, the relative abundance of nymphs and adults on hosts of different age, particularly in relation to the timing of dispersal from adults to chicks or juveniles, can be helpful. Chicks of some species are colonized early in their life (10, 38), while others are not colonized until the emergence of flight feathers (5); some are colonized by nymphs, while others are colonized by adults (10, 71). The timing of this colonization and the age distribution of the colonizers provide clues to the adaptive significance of seasonal population changes, but additional long-term studies to include greater diversity in host-parasite systems are needed.

STABILITY OF LOUSE POPULATIONS

Few studies of avian lice provide the repeated estimates of louse abundance from year to year that would allow the stability of louse populations to be assessed. Of 64 studies in which infestation parameters were examined in the context of seasonal or annual variation, 30 provided data for one year or less. Of the 34 studies that were longer than one year in duration, only nine were conducted for 10–22 years (45, 47–50, 58, 59, 66, 68). Annual variation in abundance of lice in two-year studies is usually lower than within-year variation (38, 41, 114). This relatively low variation between successive years suggests that annual variation may be low. For other hosts (Passeriformes), similarly low levels of annual variation in abundance have been observed in

three-year studies (16, 87). In a seven-year study of *Amyrsidea lagopi* on Icelandic rock ptarmigan (*Lagopus muta*), louse populations showed little annual variation in prevalence or population aggregation (111).

Studies of 12 species of avian lice on five diverse host species showed that the lice all had relatively stable populations over 14–22 years. For these lice, temporal population variability (PV) (56) is 0.51 ± 0.03 (standard error) on a scale of 0–1 (47, 49, 67, 69). In comparison, populations of other taxa of insects exhibit higher levels of temporal variability and, therefore, lower stability: The temporal variability of aphids (Hemiptera) is 0.70 ± 0.05 , $n = 5$; that of beetles (Coleoptera) is 0.64 ± 0.03 , $n = 14$; and that of flies (Diptera) is 0.57 ± 0.04 , $n = 4$ (69). Most of the temporal variation in louse abundance is due to annual variation in mean intensity rather than of prevalence, which has a low average PV of 0.28 (47, 48, 67, 69).

The relative stability of the abiotic environment for lice among the feathers of their homeothermic hosts relative to that of free-living insects may contribute to the stability of the louse populations, but the causes of year-to-year variation in louse population dynamics are little understood. Variation in relative humidity, particularly a low relative humidity, contributes little to variation in annual prevalence of lice over three years, although month-to-month variation in prevalence may be associated with changes in relative humidity (16). A louse infesting rock ptarmigan showed much higher population stability than its host, and its prevalence was not related to host abundance (111).

Two other components of population stability are persistence and the absence of long-term trends in abundance. Louse species studied over multiple years, even the less common ones, show high persistence, usually being detected on some host birds each year. Of the eight louse species studied over long periods (>20 years), five show no trends in abundance with time (48, 67, 69). *Menacanthus pici* on both northern flicker (*Colaptes auratus*) and yellow-bellied sapsucker (*Sphyrapicus varius*) do show increasing prevalence, resulting in 5–18-fold increases in abundance on the two hosts over approximately 20 years. The cause of the rise in abundance is unknown.

CONSERVATION

Recently, several researchers have pointed out that parasites have been neglected as threatened and endangered species despite their critical role in biodiversity and ecosystem function (91), emphasizing specific examples and risks of coextinction (e.g., 31, 33, 34, 62, 85, 103). Most studies on population dynamics of chewing lice on birds investigate common hosts, largely because they are available, and because large sample sizes are possible, but such studies seldom extend for longer than 10 years. As host populations decline to critical levels, their accessibility becomes limited by an inability to sample significant numbers and by ethical concerns. Yet important changes can be detected when host populations are still reasonably numerous, although in reported decline. Although chewing lice are not identified at the species level in their studies, Freed et al. (44, 45) observed multiple-fold increases in louse populations on threatened species of Hawaiian forest birds following introduction of exotic, invasive species of birds and emphasized the critical need for more long-term studies of the effects of exotic hosts on the populations of lice on native hosts. Galloway & Lamb (48) observed a steady decrease in prevalence of *Mulitcola macrocephalus* infesting common nighthawk (*Chordeiles minor*) in Manitoba, Canada, although intensity of infestation was unchanged; this decrease in prevalence was associated with a decline in the population of its host. While nearly 1,500 (about 14%) bird species are listed as threatened or endangered (7), populations of many species of birds in a variety of ecosystems, including previously abundant species, appear to be in decline (98). As the hosts decline, ultimately, so will the many species of chewing lice that depend on them.

CONCLUSIONS AND RECOMMENDATIONS

Research on chewing lice infesting birds has increased greatly since Marshall's (76) review of the ecology of ectoparasitic insects 40 years ago. Hundreds of papers have been published on infestation parameters that allow us to begin to explore relationships among chewing lice and their avian hosts. A typical bird hosts 1–4 louse species that usually occupy species-specific locations on the host, with the community of lice consisting of approximately 90 (5–450) individual lice, on average. The distribution of lice among individual birds is highly aggregated, with a small proportion of host individuals supporting very large infrapopulations, complicating estimates of mean intensity. The number of lice found on a host specimen is dependent on the sampling method, with methods used on living birds usually underestimating the number of species, their prevalence, and their intensity. The number of lice on a bird varies among host taxa, often with the size of the host and possibly with the social system of the host. Preening behavior of the host is an important factor in limiting louse abundance. Lice usually show strong, species-specific patterns of seasonal abundance but lower year-to-year PV than do other orders of insects.

FUTURE ISSUES

1. Details of collection methods should be carefully and thoroughly described. It follows that interpretations of results should consider possible ramifications of sampling efficiency given the variation in efficiency among methods. Consistency in reporting of infestation parameters is also important and should follow standardized terminology (11).
2. Given the aggregated distribution of chewing lice on birds (90, 96, 107), at least 30 infested host specimens are recommended per population or time period for estimates of mean intensity (101) before population size can be estimated with meaningful confidence intervals.
3. More long-term studies are needed to determine patterns of annual variation, the stability of populations, and population trends, especially where host populations may be in decline.
4. Two-thirds of studies are on just three orders of birds (Passeriformes, Columbiformes, and Galliformes). More research is needed on a greater diversity of species of hosts and their lice, and especially on a greater variety of larger species of birds.
5. Baseline and long-term studies of avian lice are urgently needed for future conservation efforts.
6. If the diversity of studies of hosts and lice is to increase, then more taxonomic expertise will be required. Accurate identification of the species involved in host–parasite interactions is critically important.

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