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Phthiraptera infestation of five shorebird species.—Chewing lice (Insecta: Phthiraptera) are a potentially important influence on the ecology and behavior of birds. Lice reduce host survival by increasing energetic costs (Booth et al. 1993) and by transmitting endoparasites and pathogens (Clayton 1990). Lice also influence reproductive success of birds by rendering individuals less attractive as mates (Clayton 1990) and by reducing fecundity (DeVaney 1976). Despite their importance, knowledge of variation in louse infestation is generally lacking. In fact, few studies have produced systematic surveys of lice across closely related bird taxa (but see Clayton et al. 1992). Accordingly, we sampled chewing lice from five shorebird species (Black Turnstone [*Arenaria melanocephala*], Western Sandpiper [*Calidris mauri*], Least Sandpiper [*C. minutilla*], Dunlin [*C. alpina*], and Long-billed Dowitcher [*Limnodromus scolopaceus*]) to assess interspecific and intraspecific variation in ectoparasite infestation.

Study area and methods.—We mist-netted shorebirds from 12 Sept.–24 Oct. 1992 within the Mad River estuary, about 8 km northwest of Arcata, California (40°56′N, 124°07′W). For a description of the study site see Colwell and Landrum (1993). To standardize our sampling of lice, one of us (JEH) conducted constant effort (5 min) searches of an area of the head (including the forehead, crown, and hindhead) bounded by imaginary lines running through anterior and posterior corners of the eyes (crown count; equivalent to the crown region of Eveleigh and Threlfall 1976). Using forceps, we removed lice and preserved them in 70% ethyl alcohol.

The use of area and time-constrained searches to produce indices of ectoparasite occurrence provides a feasible alternative to more intense or complicated methods (Marshall 1981). We used this type of sampling because it reduced handling time and did not require use of insecticides or necessitate that hosts be killed. We sampled the head region because it was readily accessible for sampling. In addition, a reduced ability of birds to preen the crown may result in a relatively higher density of lice (Stock and Hunt 1989), which would result in a larger proportion of the total parasite load being sampled than would be at another location on the host. However, this method may result in biased data (species lists and abundance for hosts) for chewing lice for several reasons. Louse species tend to concentrate on different body regions of the host (Marshall 1981). Consequently, some louse species may be overlooked, and the total number of lice on a bird may not be correlated with abundance in the head region (Eveleigh and Threlfall 1976, Choe and Kim 1988). In addition, on 10 of the birds we examined, we observed lice but failed to collect any during the 5-min sampling period. This suggests that our method may not be useful for sampling some of the more mobile species or age classes of lice. We also observed lice on other body parts or on our hands during processing of two of nine birds with crown counts of 0. Thus, a crown count of 0 does not necessarily indicate a complete absence of lice, only that the number of lice on that host was relatively low. Taken together, these observations suggest that our estimates of prevalence and abundance are conservative, and our results should be interpreted cautiously and with reference to the head region only. Despite these limitations, our standardized methodology produced data useful for direct comparisons between shorebirds.

For each shorebird species, we estimated louse prevalence as the percent of birds infested with at least one louse (Clayton et al. 1992); we indexed relative abundance as the average ($\pm$ SE) number of lice per individual (head). We examined interspecific differences in abundance using a Kruskal-Wallis test (Zar 1974). To evaluate the null hypothesis of random distribution of lice among individuals of a given species (*Calidris* species only), we compared observed patterns against a Poisson distribution using Chi-square goodness-of-fit tests (Ludwig and Reynolds 1988). Finally, we compared louse community composition between bird species using Renkonen's percent similarity index, a measure less sensitive to sample size variation and low species diversity than other similarity indices (Wolda 1981).

Results and discussion.—Eighty-six percent of the 65 shorebirds we examined had lice. Calidridine sandpipers exhibited the highest parasite prevalence (85–92% of individuals infested), and Long-billed Dowitcher and Black Turnstone had lower values (75 and 66%, respectively; Table 1). The relatively high prevalence values we observed for scolopacids, compared with some other bird species (e.g., Clayton et al. 1992), was not surprising because shorebirds are highly social and lice are transmitted between hosts via direct body contact (Marshall 1981).

Louse abundance (Table 1) did not differ significantly among shorebird species (Kruskal-Wallis test: $H = 4.6$, df = 5, $P = 0.33$). Although louse abundance may be influenced by molting (Marshall 1981), we observed no interspecific difference in louse numbers despite marked interspecific variation in molt patterns between shorebird species.

Composition of louse communities differed between shorebird species (Table 1). Of seven louse species collected, four occurred exclusively on one shorebird species. All louse species collected had previously been recorded from these birds (R. Price, pers. comm.). Congeneric shorebirds shared more louse species (50%, 24%, and 0% similarities between *Calidris* species) compared with shorebirds from different genera (no shared taxa). These data corroborate Fahrenholz's rule, which states that classification of permanent parasites (those completing their entire life cycle on a host) corresponds to the taxonomic relationships of hosts (Marshall 1981). In other words, as host organisms and their parasites coevolve, parasite communities track the cladogenic development of host groups. Relationships between host and parasite phylogenies are well documented, especially in the highly host-specific chewing lice and their bird hosts (Rothschild and Clay 1957, Marshall 1981). Clay (1962) noted that species within the subfamilies (Vanellinae and Charadriinae) of Charadriidae exhibited greater similarities in chewing lice (*Actornithophilus*) compared with species from different subfamilies. Interspecific (host) differences in louse communities have been studied in other charadriiforms as well. Choe and Kim (1987) found that louse communities of congeneric seabirds (Black-legged Kittiwake [*Rissa tridactyla*] and Red-legged Kittiwake [*R. brevirostris*]; Common Murre [*Uria aalge*] and Thick-billed Murre [*U. lomvia*]) were quite similar, whereas host species from different genera shared no chewing lice species.

Lice were nonrandomly distributed (clumped) among Least Sandpipers ($\chi^2 = 20.2$, df = 9, $P < 0.05$) and Western Sandpipers ($\chi^2 = 16.7$, df = 5, $P < 0.05$), but not Dunlins ($\chi^2 = 1.1$, df = 2, $P > 0.05$). With the exception of studies describing louse infestation of eggs (e.g., Rankin 1982), it appears that no report of systematic measurement of shorebird (Charadrii) chewing lice has been published; most available information is anecdotal. For example, Marshall (1981) reported that 3427 lice were removed from eight Eurasian Oystercatchers (*Haematopus ostralegus*), and Meinertzhagen and Clay (1948) found 3–11 lice on each of seven primaries of a Eurasian Curlew (*Numenius arquata*). Taylor (1981) suggested that the adventitious molt he observed in a Red Knot (*Calidris canutus*) was the result of feather damage caused by lice. Rothschild and Clay (1957) reported that Eurasian Curlews typically have 50–200 lice, although a few had none, and one individual had 1803. Host health and preening ability (Rothschild and Clay 1957, Clayton 1990), along with the same factors which affect louse prevalence and abundance, may also be important in determining individual parasite loads.

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TABLE 1

LICE INFESTATION OF FIVE SHOREBIRD SPECIES

Louse taxon	Black Turnstone (N = 3)	Western Sandpiper (N = 20)	Least Sandpiper (N = 25)	Dunlin (N = 13)	Long-billed Dowitcher (N = 4)
Family Philopteridae					
Quadraceps strepsilaris (Denny)	10[a]	0	0	0	0
Saemundssonia tringae (O. Fabricius)	0	34	0	7	0
Carduiceps zonarius (Nitzsch)	0	37	96	0	0
Carduiceps meinertzhageni Timmermann	0	0	0	21	0
Carduiceps cingulatus (Denny)	0	0	0	0	5
Family Menoponidae					
Actornithophilus umbrinus (Burmeister)	0	4	1	0	0
Austromenopon alpinum Timmermann	0	0	0	1	0
Prevalence	66%	85%	92%	85%	75%
Louse abundance (±SE)	3.3 ± 2.0	3.8 ± 0.7	3.9 ± 0.6	2.2 ± 0.4	1.3 ± 0.6

[a] Numbers indicate total number of lice collected from each shorebird species.

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Double brooding in Red-cockaded Woodpeckers.—In 1991, seven groups of the cooperatively breeding Red-cockaded Woodpecker (*Picoides borealis*) produced second broods after successfully fledging young from first broods. These seven groups were in three different populations, five in the sandhills of North Carolina, one in the sandhills of South Carolina, and one in coastal North Carolina. No previous observation of double brooding