

GROUP-LIVING AND INFESTATION BY ECTOPARASITES IN PASSERINES¹

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Abstract. Using data from an 11-year field study, I determined whether group-living passerine species showed greater infestation by contact-transmitted ectoparasites (feather mites) than sympatric, solitary species. Differences in infestation by mobile hippoboscids flies between group-living and solitary passerine species were also examined. Among the 45 species included in the analysis, feather mite prevalence was significantly greater on group-living species than on solitary ones. Two other factors investigated, bird size and migratory habit, had no effect on infestation levels. Similar results were obtained when the analysis was performed on all species outside the most species-rich family (Fringillidae), or only within the family Fringillidae itself. An analysis at the family level also suggested greater feather mite infestations in families made up only of group-living species as opposed to families including only solitary species; however, the difference was not significant. No differences were observed in hippoboscid fly abundance between group-living and solitary passerines, in all analyses at either the species or family level. These results suggest that individuals of group-living species incur a greater risk of acquiring contact-transmitted ectoparasites than individuals of solitary species, a cost which may not be negligible.

Key words: Group-living; ectoparasites; feather mites; hippoboscid flies; passerines.

INTRODUCTION

In animals in general, an increased transmission of ectoparasites is usually considered to be a universal cost of group-living (Alexander 1974). Social animals have a greater chance of acquiring and accumulating contact-transmitted ectoparasites, because of the greater proximity and number of physical contacts among group members than among solitary individuals. In birds, a few studies have already demonstrated this cost of group-living in nesting colonies of swallows (Hirundinidae). For instance, positive relationships have been observed in Bank Swallows (*Riparia riparia*) between colony size and both the mean number of fleas per nest and the percent of flea-infested nests per colony (Hoogland and Sherman 1976). Similar relationships are reported for Cliff Swallows (*Hirundo pyrrhonota*) between colony size and levels of nest infestation by fleas and swallow bugs (Brown and Brown 1986).

However, no one has yet looked at this cost of group-living at the interspecific level, to determine whether individuals of social species in-

cur a greater risk of acquiring contact-transmitted ectoparasites (e.g., fleas, ticks, or mites) than individuals of solitary species. By aggregating, individuals of group-living species come into contact with more infested conspecifics (or heterospecifics) than individuals of solitary species, thus increasing their probability of acquiring parasites themselves. However, there should be no differences between group-living and solitary species in infestation by more mobile ectoparasites, such as blood-sucking flies. These flies are not transmitted through contact between different hosts, but can fly from one host to another over distances comparable to those separating solitary birds. Thus, I do not expect group-living species to incur a greater risk of parasitism by these flies than solitary species. There is even evidence from studies on mammals parasitized by blood-sucking flies, that forming a group may reduce the risk of individual animals of being attacked (Freeland 1977, Duncan and Vigne 1979, Rutberg 1987, and Rubenstein and Hohmann 1989).

Here, I test these ideas using published data from an 11-year field study on the occurrence of feather mites (Acarina: Proctophylloidae) and hippoboscid flies (Diptera: Hippoboscidae) among birds of Ventura County, California

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(McClure 1984, 1989, unpubl. data). More specifically, I test the following predictions: 1. group-living species show greater infestation by contact-transmitted feather mites than solitary species; and 2. there is no difference between group-living and solitary species in infestation by hippoboscids, as these ectoparasites can fly and do not depend on contact or proximity among hosts for transmission (Price 1980, Balashov 1984).

METHODS

From 1977 to 1988, McClure (1984, 1989) sampled a total of 47,326 birds, belonging to 90 different species. The birds were trapped or netted weekly during the study at two sites a few km apart. Individual birds were examined for the presence of easily-seen, adult feather mites on their remiges. The measure of infestation by feather mites I used was prevalence (% infested individuals; from McClure 1989, unpubl. data). Until 1982, birds were also bagged immediately following capture; after a few minutes, hippoboscids were collected from the bags or directly from the birds. Since McClure's data on fly infestation were pooled for all the birds of a given species, a different measure of infestation level, i.e., relative abundance (total number of flies divided by total number of birds examined; from McClure 1984), had to be used for this parasite. For all statistical analyses, feather mite prevalence data were normalized with arcsine transformations, while fly abundance data were normalized with logarithmic transformations.

I limited the analysis to passerine birds (order Passeriformes) only, since they were by far the most abundant and diverse group. The analysis was carried out at both the species and family levels, to determine whether phylogeny influenced the observed infestation patterns. A relationship found across a higher taxonomic level that is repeated at the species level is unlikely to be due to phylogenetic effects (Pagel and Harvey 1988). Furthermore, I excluded from the data set all species for which less than 10 individuals had been examined, as estimates of their levels of infestation were considered unreliable. A total of 45 species (listed in Table 1 along with their characteristics), for which 43,539 individuals have been examined, were included in the analysis of feather mite prevalence. Since not all species were examined for flies, only 40 species (22,470 individuals examined) were included in

the analysis of relative abundance of hippoboscids flies.

Information on the social behavior of each species was obtained from the literature (Jewett et al. 1953, Lack 1968, Harrison 1984, Orians 1985, James and Neal 1986, Ehrlich et al. 1988). The different authors complemented each other without contradictions. A species was considered as group-living if it aggregated during either or both the breeding season (e.g., colonial or communal nesting) and the rest of the year (e.g., flocking, communal roosting). Individuals of such species come into contact with several other birds during at least part of the year, while solitary species, which either remain territorial or simply do not aggregate, interact only with very few other birds, such as mates. Since McClure (1984, 1989) sampled birds every week throughout the year, individuals of any given species were examined both during and outside the breeding season. This includes migratory species, which were sampled immediately following their arrival and just prior to their departure from the site. Thus the mite prevalence and fly abundance data I used were probably not biased by a species' current social behavior at the time of sampling, but represented average, or typical, values. Of the bird species included in the analysis, 25 were classified as group-living and 20 as solitary (for flies, these numbers were 23 and 17, respectively; see Table 1). All the group-living species aggregate outside the breeding season, while only four are social breeders.

In addition, I determined whether two other variables, which can influence ectoparasite populations, had any effect on the levels of infestation in the different species. The first variable was bird size, since the number of attachment sites for mites on feathers and for flies on the body probably increases with size of the host. Sizes, i.e., length from the tip of the bill to the end of the tail, were obtained from Pough (1957). The second variable investigated was migratory habit, i.e., whether the species is a permanent resident of the study area or is only present for a few months before migrating elsewhere. It has been suggested that host migration may reduce feather mite populations (see McClure 1989), thus possibly influencing the prevalence of mite infestations on a given bird species. McClure (1989) lists species which are permanent residents in Ventura County and those that are migrants. Of the species included in the present analysis, 24

TABLE 1. List of passerine species used in the present study. For each species, the following data are provided: prevalence of feather mite infestations (number of infested birds/number of birds examined; from McClure 1989, unpubl. data), relative abundance of hippoboscids flies (number of flies seen/number of birds examined; from McClure 1984), social behavior during the breeding, B, and non-breeding, NB, seasons (+ denotes group-living), residency status (+ denotes permanent, year-round resident), and size (length from the tip of the bill to the end of the tail).

Family Species	Mite prevalence	Fly abundance	Social			Size (cm)
			B	NB	Resident	
Tyrannidae						
Western flycatcher, <i>Empidonax difficilis</i>	1/39	0/23	-	-	-	14.6
Black phoebe, <i>Sayornis nigricans</i>	0/34	-	-	-	+	16.5
Ash-throated flycatcher, <i>Myarchus cinerascens</i>	3/14	-	-	-	-	21.0
Corvidae						
Scrub jay, <i>Aphelocoma coerulescens</i>	52/311	30/159	-	+	+	29.2
Paridae						
Plain titmouse, <i>Parus inornatus</i>	6/22	2/20	-	+	+	14.0
Common bush-tit, <i>Psaltriparus minimus</i>	0/232	1/70	-	+	+	11.4
Troglodytidae						
Cactus wren, <i>Campylorhynchus brunneicapillus</i>	0/16	0/10	-	-	-	20.3
Bewick's wren, <i>Thryomanes bewickii</i>	0/131	1/69	-	-	+	13.3
House wren, <i>Troglodytes aedon</i>	1/51	0/15	-	-	+	12.1
Sylviidae						
Ruby-crowned kinglet, <i>Regulus calendula</i>	0/161	22/99	-	-	-	10.8
Turdidae						
Swainson's thrush, <i>Catharus ustulatus</i>	1/14	-	-	-	-	17.8
Hermit thrush, <i>Catharus guttatus</i>	48/360	4/256	-	-	-	17.8
American robin, <i>Turdus migratorius</i>	6/19	-	-	+	-	25.4
Chamaeidae						
Wrentit, <i>Chamaea fasciata</i>	5/181	1/126	-	-	+	16.5
Mimidae						
Mockingbird, <i>Mimus polyglottos</i>	20/180	0/76	-	-	+	26.7
California thrasher, <i>Toxostoma redivivum</i>	4/75	0/45	-	-	+	30.5
Bombycillidae						
Cedar waxwing, <i>Bombycilla cedrorum</i>	35/56	-	-	+	-	18.4
Ptilonotidae						
Phainopepla, <i>Phainopepla nitens</i>	0/18	0/15	-	+	-	19.1
Laniidae						
Loggerhead shrike, <i>Lanius ludovicianus</i>	5/18	1/10	-	-	+	22.9
Sturnidae						
European starling, <i>Sturnus vulgaris</i>	16/108	1/59	-	+	+	21.6
Parulidae						
Orange-crowned warbler, <i>Vermivora celata</i>	2/31	0/17	-	-	+	12.7
Yellow-rumped warbler, <i>Dendroica coronata</i>	31/607	0/279	-	-	-	14.0
Yellowthroat, <i>Geothlypis trichas</i>	0/78	0/15	-	-	+	13.3
Wilson's warbler, <i>Wilsonia pusilla</i>	0/33	0/18	-	-	-	12.7
Fringillidae						
Black-headed grosbeak, <i>Pheucticus melanocephalus</i>	2/36	0/11	-	-	-	18.4
Lazuli bunting, <i>Passerina amoena</i>	4/48	1/40	-	+	-	13.3

TABLE 1. Continued.

Family Species	Mite prevalence	Fly abundance	Social			Size (cm)
			B	NB	Resident	
Rufous-sided towhee, <i>Pipilo erythro-</i> <i>phthalmus</i>	126/507	10/308	-	+	+	20.3
Brown towhee, <i>Pipilo fuscus</i>	296/986	9/437	-	+	+	21.6
Rufous-crowned sparrow, <i>Aimophila</i> <i>ruficeps</i>	5/106	1/65	+	+	+	11.4
Chipping sparrow, <i>Spizella passerina</i>	6/16	0/16	-	+	-	13.3
Lark sparrow, <i>Chondestes grammacus</i>	68/154	8/125	-	+	-	15.9
Savannah sparrow, <i>Passerculus</i> <i>sandwichensis</i>	13/31	0/15	-	+	+	14.6
Fox sparrow, <i>Passerella iliaca</i>	6/16	1/18	-	+	-	18.4
Song sparrow, <i>Melospiza melodia</i>	22/261	9/85	-	-	+	15.9
Lincoln's sparrow, <i>Melospiza lincolnii</i>	3/67	0/26	-	-	+	14.6
Golden-crowned sparrow, <i>Zonotrichia</i> <i>atricapilla</i>	132/491	4/210	-	+	-	16.5
White-crowned sparrow, <i>Zonotrichia</i> <i>leucophrys</i>	3,668/9,066	110/5,045	-	+	-	17.8
Dark-eyed junco, <i>Junco hyemalis</i>	146/707	4/248	-	+	-	15.9
House finch, <i>Carpodacus mexicanus</i>	13,655/20,600	173/9,973	-	+	+	14.0
Lesser goldfinch, <i>Carduelis psaltria</i>	16/153	1/136	-	+	+	10.2
Icteridae						
Brewer's blackbird, <i>Euphagus</i> <i>cyanocephalus</i>	64/1,461	27/666	+	+	+	24.1
Redwing blackbird, <i>Agelaius phoeniceus</i>	5/48	0/49	+	+	-	24.1
Brown-headed cowbird, <i>Molothrus ater</i>	12/223	12/45	-	+	+	20.3
Northern oriole, <i>Icterus galbula</i>	7/84	0/67	-	+	-	19.1
Ploceidae						
House sparrow, <i>Passer domesticus</i>	393/5,739	372/3,504	+	+	+	16.1

were permanent residents and 21 were migrants (for flies, the numbers were 23 and 17, respectively).

RESULTS

I found no correlation between size of the bird species and either feather mite prevalence (product-moment correlation coefficient; $r = 0.184$, $n = 45$, NS) or fly abundance ($r = 0.139$, $n = 40$, NS) among the whole set of passerine species studied. The data were then divided into two subsets based on the social behavior of the bird species. The mean size of group-living species (17.8 ± 4.8 cm) did not differ (two-tailed t -test; $t = 0.476$, $df = 43$, NS) from that of solitary species (17.1 ± 5.1 cm), and there were no significant correlations, in either subset, between size and either mite prevalence or fly abundance. Size was thus excluded from further analyses.

I used two-way analyses of variance to test for effects of social behavior, migratory habits, and of the interaction between these two factors on ectoparasitism in passerines. Social behavior had

a significant effect on the prevalence of mite infestations ($F = 16.554$, $df = 1, 41$; $P < 0.001$); group-living species had a greater mean mite prevalence than solitary ones (Fig. 1). Migratory habits ($F = 0.527$, $df = 1, 41$; NS) and the interaction between social behavior and migratory habits ($F = 0.651$, $df = 1, 41$; NS) had no effect on mite prevalence. Since a prevalence of zero might indicate lack of exposure to feather mites and not lower susceptibility, I repeated this analysis after removing the eight species with a zero prevalence. The analysis gave the exact same results, again showing greater mite prevalence in group-living species ($25.3 \pm 18.0\%$) than in solitary ones ($8.8 \pm 7.5\%$).

The mean relative abundance of flies on group-living species was slightly greater than that on solitary species (Fig. 1). However, this difference is not significant, as I found no effect of social behavior on the abundance of hippoboscids flies ($F = 0.501$, $df = 1, 36$; NS). In addition, I observed no effect of migratory habits ($F = 0.675$, $df = 1, 36$; NS) and of the interaction between

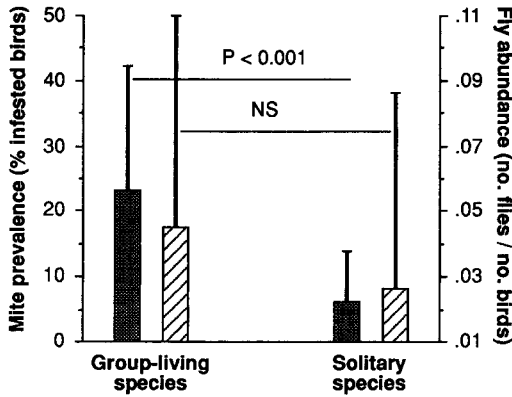


FIGURE 1. Prevalence of feather mites (grey bars) and relative abundance of hippoboscoid flies (striped bars) on group-living and solitary species of passerines. Shown are means (± 1 standard deviation) of untransformed data. Details about the statistical comparisons are provided in the text.

social behavior and migratory habits ($F = 1.722$, $df = 1, 36$; NS) on fly abundance. Here again, when the analysis was repeated after removal of species with a fly abundance of zero, similar results were obtained (0.057 ± 0.070 for group-living species, 0.078 ± 0.084 for solitary ones, not significantly different).

I also compared infestation levels between group-living and solitary species within the family Fringillidae only, the best represented family which included 13 group-living species and three solitary ones. Feather mite prevalence was significantly greater in group-living ($30.3 \pm 17.1\%$) than in solitary ($6.2 \pm 2.0\%$) species (one-tailed t -test; $t = 2.638$, $df = 14$, $P < 0.01$). No significant difference was observed in the abundance of flies between these two groups (two-tailed t -test; $t = 0.635$, $df = 14$, NS). These comparisons were also made between group-living and solitary species belonging to all families but Fringillidae, thus excluding the only species-rich family which might have influenced the results of the earlier analyses. Again, group-living birds showed a greater mite prevalence ($15.7 \pm 17.8\%$) than solitary ones ($6.2 \pm 8.1\%$), and the difference was significant (one-tailed t -test; $t = 2.018$, $df = 27$, $P < 0.05$), while I observed no differences in fly abundance (two-tailed t -test; $t = 1.543$, $df = 22$, NS).

The analysis at the family level included only families (14 out of 16) that were made up entirely of either group-living or solitary species. The spe-

cies-rich Fringillidae, which might have influenced the general patterns at the species level, were thus excluded. Mean infestation levels were computed for each family by averaging the species values. No significant difference was found in feather mite prevalence between group-living families and solitary ones (one-tailed t -test; $t = 1.245$, $df = 12$, NS), although group-living families had an average prevalence more than twice that of solitary families ($17.4 \pm 20.7\%$ vs. $7.2 \pm 9.6\%$). Finally, I found no difference (two-tailed t -test; $t = 0.658$, $df = 11$, NS) in fly abundance between group-living families and solitary ones.

DISCUSSION

The above results support the predictions tested in the present study, that group-living passerine species, as opposed to solitary ones, show higher infestation by contact-transmitted ectoparasites (feather mites), but not by flying or mobile ectoparasites (hippoboscoid flies). Since the results of the analysis on mite prevalence performed at the family level were not quite significant, it is possible that infestation levels are also influenced by a species' phylogenetic history and its coevolution with parasites. However, the parasites studied here are not very host-specific, and the role of social behavior appears undeniable. Other variables are probably important also; although host size and migratory habits showed no effects in this study, McClure (1984, 1989) reports that mite and fly infestations were affected by seasons.

It is interesting to look at feather mite prevalence in the other groups of birds examined by McClure (1989). He reports no infested individuals in two groups of mostly solitary birds, the Falconiformes (three species, $n = 10$ individuals sampled) and the Apodiformes (five species, $n = 164$). However, in woodpeckers (order Piciformes), another group of solitary birds, no infested birds were found in four species ($n = 26$), while the other two species captured had an average mite prevalence of 30.4% ($n = 68$). In addition, no infested birds were found among Columbiformes (five species, $n = 3,342$), a group of birds known to feed in flocks. A look at fly abundance in other groups of birds shows that no flies were observed on Falconiformes, Apodiformes, and Piciformes, while some were found on Columbiformes (McClure 1984). Obviously, comparisons among higher taxa are complicated by phylogenetic history and difficult to make with confidence; however, it is possible that the pat-

terns observed among passerines are different in other groups of birds.

The present study demonstrates that, among the birds investigated by McClure (1984, 1989) in California, individuals of group-living passerine species had a much greater probability of harboring feather mites, than individuals of solitary passerine species. This result is independent of bird size or whether birds are permanent residents of the study area or seasonal visitors only. The effects of feather mites, and of other contact-transmitted ectoparasites, on a bird's fitness range from small blood losses to transmission of viral diseases and death (Herman 1955). Infestations by these ectoparasites can also lead to decreased reproductive success without resulting in the death of the host, as some female birds recognize and avoid infested males (Borgia and Collis 1989). Thus, both within (e.g., Hoogland and Sherman 1976, Brown and Brown 1986) and among passerine species, higher levels of infestation by contact-transmitted ectoparasites appear to be a common and important cost of living in groups.

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