J. Parasitol., 90(5), 2004, pp. 939–947

EFFECTS OF HOST SOCIALITY ON ECTOPARASITE POPULATION BIOLOGY

Noah Kerness Whiteman and Patricia G. Parker

Department of Biology and International Center for Tropical Ecology, 223 Research Building, 8001 Natural Bridge Road, University of Missouri–St. Louis, St. Louis, Missouri 63121. *e-mail: nkwf38@studentmail.umsl.edu*

ABSTRACT: Theory predicts a positive relationship between parasite infection intensity and host density. However, this generalization is complicated in natural systems by differences in life history among parasite taxa, e.g., transmissibility. Accordingly, predictions relating host density to parasite load should be specific to each parasite taxon. To illustrate this, we studied parasites that differed greatly in life history in the context of the Galapagos hawk's (*Buteo galapagoensis*) variably cooperative mating system. Two louse (Phthiraptera) species were collected: *Colpocephalum turbinatum* (Amblycera), with 53 host species, and *Degeeriella regalis* (Ischnocera), with 10 host species, although *B. galapagoensis* was the only known Galapagos host. Sixty territorial adult male hawks from 26 groups of 1–6 males were quantitatively sampled for lice. Average abundance and intensity of *C. turbinatum* but not *D. regalis* were significantly larger in large groups of hawks than small groups. Males from the same polyandrous group harbored significantly correlated abundances of *C. turbinatum* but not *D. regalis*. Prevalence, average abundance, and intensity of *C. turbinatum* were significantly higher than *D. regalis*. These are the first results to demonstrate significant differences in a suite of population responses between these louse suborders in the context of host sociality.

There are several presumed benefits and costs to group living (Alexander, 1974). The benefits, which may include direct and inclusive fitness returns and enhanced access to resources, have been the focus of intense investigation (e.g., Stacey and Koenig, 1990; Queller and Strassmann, 2002). However, the costs, such as increased risk and intensity of parasite infection, are less well studied (Anderson and May, 1978; May and Anderson, 1978; Dobson, 1990; Poiani, 1992; Brown et al., 1995; Krasnov et al., 2002). Although theoretical models predict a positive relationship between parasite infection intensity and host density, this generalization is complicated in natural systems by basic life-history differences among parasite taxa, e.g., transmissibility. Accordingly, predictions relating host density to parasite abundance should be specific to each parasite taxon.

Investigations into the parasite–host sociality nexus have focused on colonially breeding host species (C. R. Brown and M. B. Brown, 1986; Rózsa et al., 1996; Avilés and Tufiño, 1998; Hoi et al., 1998) or those that form nonbreeding aggregations (Moore et al., 1988; Blanco et al., 1997). However, little attention has been given to cooperative breeders, despite abundant data on other aspects of their biology (Brown, 1987; Stacey and Koenig, 1990; Ligon, 1999; Bennett and Owens, 2002). Well-documented intraspecific variation in sociality (de Vries, 1975; Bollmer et al., 2003), a characteristic of some cooperative breeders, is a key advantage when relating host density to parasite abundance (Rózsa et al., 1996).

Populations of parasites that are at least partially horizontally transmitted (mediated through contact other than parent–offspring contact) should be affected by changes in the size of their host's reproductive coalitions because parasite infrapopulation size is partially controlled by transmission rate (Anderson and May, 1978; May and Anderson, 1978; Dobson, 1990). Conversely, species that are more dependent on the vertical transmission (parent–offspring) route should be less responsive to such changes in host group size. We tested these predictions within the context of the Galapagos hawk's (Aves: Falconiformes: *Buteo galapagoensis*) (Gould) variably cooperative mating system.

Galapagos hawks establish social groups that vary in size from monogamous pairs to cooperatively polyandrous groups (de Vries, 1973, 1975; Faaborg et al., 1980, 1995; Faaborg, 1986; Bollmer, 2000; Donaghy Cannon, 2001; Bollmer et al., 2003). Polyandrous groups comprise 1 female and 2–8 males. Each social unit (monogamous or polyandrous) occupies an all-purpose territory, which is defended year-round (de Vries, 1975; Faaborg et al., 1980, 1995). Adults within groups are not offspring that have delayed their dispersal and are not close relatives (de Vries, 1973, 1975; Faaborg et al., 1995). Hawks rarely leave the territorial boundary, which, along with group composition, is generally stable over time (de Vries, 1975; Faaborg, 1986; Faaborg and Bednarz, 1990; Donaghy Cannon, 2001). For example, of 62 male birds marked on Isla Santiago in 1999, 95% were present on the same territory 1 yr later (Donaghy Cannon, 2001). This relative stability increases the likelihood that parasite populations will track the host's social system (Moore et al., 1988; Rózsa et al., 1996). In 1999–2000 on Isla Santiago, territory sizes were statistically independent of the number of males within a territory (Donaghy Cannon, 2001). If this pattern is general, group size and host density should increase concomitantly, and parasites, if horizontally transmitted, should also respond positively to this increase in host density. Within territorial groups, opportunities for parasite transfer occur with regularity. Each male repeatedly copulates with the female (5–10 copulations per day), male–male copulations occur within polyandrous groups (N. K. Whiteman, pers. obs.), group members use communal roosts, and all birds within the breeding group brood the young (de Vries, 1975; Faaborg et al., 1995; Donaghy Cannon, 2001).

Lice (Insecta: Phthiraptera) comprise the largest number of ectoparasitic insect species (Marshall, 1981) and along with their hosts have emerged as model systems in which a variety of ecological and evolutionary theories have been tested (Borgia, 1986; C. R. Brown and M. B. Brown, 1986; Hafner and Nadler, 1988; Borgia and Collis, 1989, 1990; Clayton and Tompkins, 1994; Rózsa et al., 1996; Rékási et al., 1997; Hoi et al., 1998; Clayton et al., 1999; Poiani et al., 2000; Page, 2003).

The 2 most species-rich lineages within the chewing–biting lice (the paraphyletic Mallophaga) are the Amblycera and Ischnocera, which are each monophyletic (Marshall, 1981; Cruickshank et al., 2001; Johnson and Whiting, 2002). Amblycerans feed on epidermal tissues and blood, and are generally less host specific, less restricted to a particular region of the host's body, and more vagile than feather-feeding ischnoceran

---

Received 30 December 2003; revised 2 February 2004; accepted 3 February 2004.

lice (Ash, 1960; Askew, 1971; Marshall, 1981). Horizontal transmission may be a more important dispersal route in amblyceran lice than ischnoceran lice (DeVaney et al., 1980; Marshall, 1981; Clayton and Tompkins, 1994; cf. Hillgarth, 1996). Such general parasite life-history differences may interact with host social behavior to generate predictable differences in parasite population parameters. For example, an amblyceran was less aggregated among hosts within a population of social crows (Corvidae), relative to its distribution within a population of an asocial species, where they were more aggregated within a few members of the population (Rózsa et al., 1996). This is in contrast to the distributions of the ischnocerans, which were similarly aggregated between the 2 host populations (Rózsa et al., 1996). Several studies have shown that when these suborders co-occur on hosts, amblycerans were more abundant than ischnocerans (Nelson and Murray, 1971; Eveleigh and Threlfall, 1976), which among many other factors may indicate that parasite population growth is constrained by rate of transmission among hosts (Arneberg et al., 1998).

Two louse species, the amblyceran *Colpocephalum turbinatum* Denny (Menoponidae) and the ischnoceran *Degeeriella r. regalis* (Giebel) (Philopteridae), were previously collected from *B. galapagoensis* (de Vries, 1975). The 2 species are at opposite ends of the host-range spectrum. *Degeeriella r. regalis* (referred to hereafter as *D. regalis* sensu Price et al. [2003]) occurs on 10 hosts worldwide, only 2 of which are found in the New World, *B. galapagoensis* and *Buteo swainsoni* (Clay, 1958; Price et al., 2003). This is in contrast to the hosts of *C. turbinatum* (although considered to be a single species by Price and Beer [1963] and Price et al. [2003], it was given sensu lato status by the former), which include 53 species according to Price et al. (2003). In the Galapagos, these species have only been reported from *B. galapagoensis*. However, Price et al. (2003) reported *C. turbinatum* from the barn owl (*Tyto alba*), a subspecies of which (*T. alba punctatissima*) occurs on Santiago (but not Marchena). Whether it occurs on *Tyto* in Galapagos is not known. Given that barn owls are nocturnal (and hawks diurnal), roost during the day in lava tubes out of reach of hawks (Kricher, 2002), and are not preyed on by *B. galapagoensis*, we consider the direct interaction between hawks and owls unlikely. Therefore, we assumed that any effect on *C. turbinatum*'s population size or distribution on the hawks from parasite transfer is negligible.

We assumed that host range correlated positively with parasite dispersal abilities, consistent with reports of other authors (e.g., Johnson, Williams et al., 2002; Clayton and Johnson, 2003). Thus, we formed a series of predictions of louse population responses to host social behavior. Prevalence was defined as the number of infected hosts/total number of hosts sampled, mean abundance was the average number of parasites on hosts, including uninfected hosts, and mean and median intensity were the average and typical number of parasites on infected hosts, respectively (Margolis et al., 1982; Bush et al., 1997).

First, given that parasite load should increase with host density, the importance of dispersal ability in determining transmission rates among hosts (Anderson and May, 1978; May and Anderson, 1978; Dobson, 1990), and other basic life-history differences, prevalence, mean abundance, and mean and median intensities of amblyceran (*C. turbinatum*) lice (more mobile) but not ischnoceran (*D. regalis*) lice (less mobile) are positively related to size of social groups (number of males/group) of the Galapagos hawk.

Second, given that almost all parasites display a lumped distribution among hosts (a negative binomial distribution) and differences in parasite dispersal abilities, infrapopulations (1 infrapopulation = the number of parasite individuals occurring on 1 host individual) of amblyceran (*C. turbinatum*) but not ischnoceran (*D. regalis*) lice are less aggregated among males from large groups than those from small groups, sensu Rózsa et al. (1996).

Third, given that in other bird species intersex pair members have significantly correlated louse infrapopulation sizes (Potti and Merino, 1995; Hoi et al., 1998), abundances of amblyceran (*C. turbinatum*) but not ischnoceran (*D. regalis*) lice are more similar among polyandrous territorial group mates than among polyandrous territorial males randomly paired with males from other groups after controlling for the effects of group size.

Finally, given higher inferred dispersal rates, the importance of transmission in constraining parasite population growth (Arneberg et al., 1998), and other basic life-history differences, prevalence, abundance, and intensity of amblyceran (*C. turbinatum*) lice are always greater than those of ischnoceran (*D. regalis*) lice, regardless of host group size.

MATERIALS AND METHODS

Study site

The Galapagos Archipelago is located on the equator, ~1,000 km west of mainland Ecuador, South America. *Buteo galapagoensis* is endemic to 9 main islands within the archipelago (de Vries, 1973, 1975). It is listed in the IUCN Red List of Threatened Species (IUCN, 2002) and has been anthropogenically extirpated from at least 5 islands within the archipelago (de Vries, 1973, 1975). Data are presented from 2 island populations in the archipelago, Santiago and Marchena. Isla Santiago, located in the center of the archipelago, is 585 km^2 in area and rises to a height of 907 m (Kricher, 2002). Hawks were sampled from 2 locations on Santiago: James (Espumilla) Bay, along the western coastline (~0°20′S, 90°82′W), and Sullivan Bay, along the eastern shore (~0°30′S, 90°58′W). The locations of most hawk territories studied on Santiago were determined previously (DeLay, 1992; Donaghy Cannon, 2001). Isla Marchena, located in the northern part of the archipelago, is 130 km^2 in area and rises to a height of 343 m (Kricher, 2002). The study site was located along and inland from a beach situated on the south-southwestern coastline (~0°18′N, 90°32′W).

Host capture

Territorial Galapagos hawks were characterized by at least 2 of the following criteria. First, all group members defended territories against foreign hawks. Second, territorial birds gave a distinct warning call when humans or foreign hawks crossed the territorial bounds (de Vries, 1973). Third, if nesting, group members actively defended the nest when approached by us. Fourth, both sexes were seen in aerial display (soaring–circling–spiral flight, de Vries, 1973). Group sizes were recorded for each territory.

Territorial adult male hawks from Marchena were captured during a 12-day period from 4–15 June 2001. Hawks on Santiago were captured during a 45-day period from 14 May to 29 June 2002. Females were not included in this study because of the requirements of an ongoing and unrelated experiment. Individuals were live-captured by pole noosing or Bal-chatri traps (Santiago only) baited with live rats introduced to the island previously (Berger and Mueller, 1959). To calm each bird after capture, a loose cloth hood was placed over the head and neck region during handling until release (to avoid contamination, the hood was thoroughly cleaned between handlings and visually inspected). Unless banded previously all birds were marked with aluminum alphanumeric colored or numeric aluminum bands.

Collection and quantification of louse load

To quantify ectoparasite loads, birds were sampled by dust ruffling (Walther and Clayton, 1997) with pyrethroid insecticide (derivatives of the chrysanthemum flower and nontoxic to birds; Zema® Z3 Flea and Tick Powder for Dogs, St. John Laboratories, Harbor City, California) composed of 0.10% pyrethrins and 1% of the synergist piperonyl butoxide. Although other methods, e.g., body washing, may remove more parasites (but require dead birds), the number of lice removed after a 60-sec dust-ruffling bout adequately predicted total louse abundance of feral rock doves (*Columba livia*; Clayton and Drown, 2001).

In this study, a small amount (~2 g) of insecticide was applied to each bird's plumage (all feather tracts except the head). This was followed by 5–8 timed bouts (30 sec each) of feather ruffling to dislodge the parasites. Ruffling was stopped when the last bout yielded <5% of the total number of lice collected during all previous bouts combined. Our louse removal efficiencies were congruent with other studies attempting to quantify such loads (Clayton et al., 1992). Each bird was held over a clean plastic tray during ruffling to collect dislodged ectoparasites, which were stored in 95% ethanol.

Statistical analyses

Because of the aggregated nature of their distributions, many authors have used nonparametric statistics when comparing parasite populations. However, Rózsa et al. (2000) cautioned that using such statistics yields misleading results. Thus, to the extent possible, we used distribution-free statistical tests designed specifically for such data sets (Rózsa et al., 2000; Reiczigel and Rózsa, 2001). All our analyses included both adult and nymphal lice.

To test if the frequency distributions of lice among hosts could be described by the negative binomial distribution (an expectation of parasite distributions; Crofton, 1971), expected negative binomial distributions were calculated using the program Ecological Methodology (Krebs, 1989). Frequency classes were pooled to increase the expected number of hosts to ≥3. The observed frequency distributions were then tested to determine if they differed from the expected distributions using chi-square tests.

Prevalence, mean and median intensity, and mean abundances (sensu Margolis et al., 1982) were calculated using the program Quantitative Parasitology 2.0 (Rózsa et al., 2000; Reiczigel and Rózsa, 2001). Fisher's exact tests were used to compare parasite prevalences between host populations. Distribution-free 2-sample bootstrap *t*-tests were used to compare mean intensities and abundances (each with 2,000 replicates). Mood's median tests were used to compare median (typical) intensities. Because standard deviations are uninformative in aggregated distributions (Rózsa et al., 2000), in this study we report bootstrap confidence intervals for mean abundance and intensity. We also calculated the moment *k,* which is inversely related to the degree of aggregation of parasite abundances among members of the host population (Crofton, 1971), and the index of discrepancy *D,* which is directly related to the degree of aggregation of parasite abundances among members of the host population (Poulin, 1993). The index of discrepancy is the degree to which the observed distribution of parasites among the host population differs from a hypothetical one in which each host harbors the same number of parasites (Poulin, 1993). We used 2-sample Kolmogorov–Smirnov tests to compare distributions within large groups of hawks with those within small groups for each parasite species.

We tested if louse infrapopulation abundances were more similar among polyandrous group mates than among pairs of birds drawn from different groups. Louse infrapopulation sizes from dyads of males from the same or different polyandrous groups were tested for similarity using Pearson's correlation in SPSS (1 analysis for each louse species). In this analysis the effect of group size was controlled as a partial correlation. However, these data represented a fraction of the total available because we used only 2 males from each polyandrous group rather than using each available male. Thus, Mantel tests (Mantel, 1967) were used with PC-ORD to test if louse infrapopulation abundances were more similar among polyandrous group mates than non–group mates. In the Mantel analysis, louse abundance data from dyads of 53 polyandrous males of 60 total males were used (7 males were not used because 6 were from monogamous pairs or in the case of 1 male, the other polyandrous group members were not captured). Thus, 1 matrix comprised the differences in louse abundances between 2 birds (the difference was calculated by first adding 1 to each count to eliminate 0 values and then using the formula [larger abundance − smaller abundance]/smaller abundance) for all possible dyad combinations. A second matrix was constructed in which the same dyads were given a 0 (indicating that the paired males were from the same group) or a 1 (indicating that the paired males were from different groups). A Monte Carlo randomization approach was then used to test if the matrices were independent.

RESULTS

On Marchena, a total of 14 territorial adult male Galapagos hawks from 6 territories were sampled for ectoparasites. On Santiago, a total of 46 territorial adult male Galapagos hawks from 20 territories were sampled for ectoparasites. Thus, in total, 60 males from 26 territorial groups were sampled. The number of territorial adult male hawks per group ranged from 1 to 6 individuals; thus, males from both monogamous pairs and polyandrous groups were sampled (mean number of males/group for both islands combined = 2.85 ± 1.49 SD). We were unable to sample 14 of the males present in 9 of the territorial groups.

A total of 1,510 lice were collected from the 60 male hawks. Of these, 1,229 were *C. turbinatum* and 281 were *D. regalis.*

TABLE I. Comparisons of *Colpocephalum turbinatum* and *Degeeriella regalis* (Insecta: Phthiraptera) loads between Marchena and Santiago island populations of *Buteo galapagoensis* (Aves: Falconiformes).

Metric	Parasite	1–3 males, Marchena (n = 9)	1–3 males, Santiago (n = 25)	*P*	*t*	4–6 males, Marchena (n = 5)	4–6 males, Santiago (n = 21)	*P*	*t*
Prevalence*	*C. turbinatum*	88.9%	92.0%	1.000	—	100%	95.2%	1.000	—
	D. regalis	77.8%	68.0%	0.692	—	100%	66.7%	0.278	—
Mean abundance†	*C. turbinatum*	13.889	10.560	0.6460	0.475	47.000	28.810	0.3665	1.158
	D. regalis	4.111	2.160	0.4275	0.889	10.600	3.619	0.2550	1.378
Mean intensity†	*C. turbinatum*	15.625	11.478	0.5940	0.545	47.000	30.250	0.3870	1.068
	D. regalis	5.286	3.176	0.4665	0.780	10.600	5.429	0.3570	1.015
Median intensity‡	*C. turbinatum*	7.5	7.0	1.000	—	43.0	30.5	0.623	—
	D. regalis	2.0	1.0	0.659	—	6.0	5.0	1.000	—

* Prevalences were compared with Fisher's exact tests.

† Abundances and intensities were each compared with 2-sample bootstrap *t*-tests.

‡ Medians were compared with Mood's test of comparing medians. All *P* values are 2 sided.

In addition, 8 *Columbicola macrourae* (Wilson) (Philopteridae) lice were collected from 4 hosts and were not considered in our analyses (they were presumed stragglers from *Zenaida galapagoensis* hosts, which are preyed on by *B. galapagoensis*; de Vries, 1973; Donaghy Cannon, 2001). Most *D. regalis* specimens were collected from wing and tail feathers, whereas specimens of *C. turbinatum* were collected from throughout the body. Individuals of *C. turbinatum* were seen actively crawling on the skin and feathers of the host and would often crawl on our hands; *D. regalis* individuals were never seen actively crawling on the host or on our hands.

To facilitate analyses, parasite counts from hosts were grouped into small groups (those from groups of 1–3 males) and large groups (those from groups of 4–6 males). Each measure of parasite load, including prevalence, mean abundance, mean intensity, and median intensity, did not differ significantly between Marchena and Santiago for either parasite species within either large or small group (Table I). Thus, to increase sample sizes, data from Marchena and Santiago were combined. With the exception of *D. regalis* within small groups, frequency distributions of either species within each class did not differ from an expected negative binomial distribution (small groups—*C. turbinatum*: $\chi^2 = 8.3664$, $P = 0.593$; *D. regalis*: $\chi^2 = 11.5824$, $P = 0.021$; large groups—*C. turbinatum*: $\chi^2 = 4.089$, $P = 0.665$; *D. regalis*: $\chi^2 = 6.2367$, $P = 0.397$).

Prediction 1

Given that parasite load should increase with host density, the importance of dispersal ability in determining transmission rates among hosts (Anderson and May, 1978; May and Anderson, 1978; Dobson, 1990), and other basic life-history differences, prevalence, mean abundance, and mean and median intensities of amblyceran (*C. turnbinatum*) (more mobile) but not ischnoceran (*D. regalis*) (less mobile) lice are positively related to size of social groups (number of males/group) of the Galapagos hawk.

Mean intensity, abundance, and median intensity of *C. turbinatum* were significantly higher among hosts from larger social groups than smaller social groups (Fig. 1A; Table II). The same measures were not statistically different for *D. regalis* between small or large groups (Fig. 1B; Table II). Infected males from large groups had an average of 2.68 times as many *C. turbinatum* individuals as males from smaller groups (Fig. 1A). Likewise, the typical (median) level of infestation within infected males from large groups was 4.57 times greater than that of males from small groups (Fig. 1A). There was no overlap in the 95% confidence limits of mean *C. turbinatum* abundance between small and large groups, whereas these limits overlapped by 56.83% between average abundances of *D. regalis* from small and large groups (Table II). Prevalence of *C. turbinatum* or *D. regalis* did not differ statistically between small and large groups.

Prediction 2

Given the lumped distribution of parasites among hosts (a negative binomial distribution) and differences in parasite dispersal abilities, infrapopulations of amblyceran (*C. turbinatum*) but not ischnoceran (*D. regalis*) lice are less aggregated among males from large groups than those from small groups, sensu Rózsa et al. (1996).

We compared the distributions within a louse species between small and large groups. These distributions differed significantly between the groups for *C. turbinatum* (Fig. 2A) but not for *D. regalis* (Fig. 2B). The *C. turbinatum* population was less aggregated among hosts from larger social groups than those from smaller social groups, as is indicated by differences in their respective *k* and *D* values (Table II). The magnitude of *k* within large groups was more than 2.5 times higher than its magnitude within small groups. The same is not true for *D. regalis*, where the magnitude of *k* differed by 0.02 between the louse populations from small and large groups (Table II).

Prediction 3

Given that in other bird species intersex pair members have significantly correlated louse infrapopulation sizes (the number of lice on an individual host; Potti and Merino, 1995; Hoi et al., 1998), abundances of amblyceran (*C. turbinatum*) but not ischnoceran (*D. regalis*) lice are more similar among polyandrous territorial group mates than among territorial males randomly paired with males from other groups after controlling for the effects of group size.

Correlational analyses using only 2 males/group resulted in

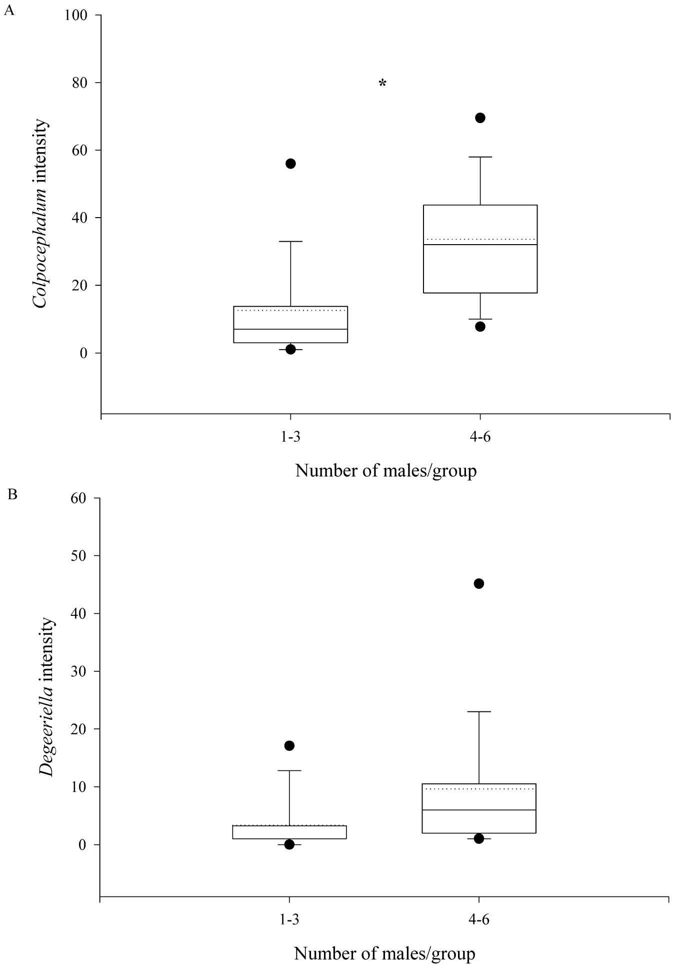

FIGURE 1. **A.** Box and whisker plots of median (solid line within box) and mean (dotted line within box) intensities (uninfected hosts are not considered by these measurements) of *Colpocephalum turbinatum* among territorial adult male Galapagos hawks (*Buteo galapagoensis*) from small (1–3 males/group; n = 31) and large (4–6 males/group; n = 25) breeding groups. Hosts from small groups yielded significantly lower mean ($t = -4.002$, 2-sided $P = 0.0005$) and median ($P = 0.000$) intensities of *C. turbinatum* than those from large groups at the 95% level. Dots above and below whiskers are 5th and 95th percentiles. **B.** Box and whisker plots of median (solid line within box) and mean (dotted line within box) intensities (uninfected hosts are not considered by these measurements) of *Degeeriella regalis* among territorial adult male Galapagos hawks (*B. galapagoensis*) from small (1–3 males/group; n = 25) and large (4–6 males/group; n = 19) breeding groups. Hosts from small groups yielded mean ($t = -1.541$, 2-sided $P = 0.1275$) and median ($P = 0.066$) intensities of *D. regalis* intensities that, at the 95% level, were equal to those from large groups. Dots above and below whiskers are 5th and 95th percentiles.

a significantly positive relationship between the pairwise abundances of *C. turbinatum* (Fig. 3; Pearson's $r = 0.771$, $P = 0.000$ [1 sided], n = 19; after controlling for group size, Pearson's $r = 0.663$, $P = 0.001$ [1 sided]) but not *D. regalis* (Pearson's $r = -0.23$, $P = 0.462$ [1 sided] n = 19; after controlling for group size, Pearson's $r = 0.0087$, $P = 0.486$ [1 sided]). In the expanded Mantel analysis, dyads of males from the same polyandrous group were more similar in *C. turbinatum* infection abundance than dyads from different groups (1,000 randomized runs, standardized Mantel $r = 0.0592$, observed $Z = 17{,}382$, average $Z = 16{,}997$, $P = 0.011$). The same relationship was true for abundances of *D. regalis* (1,000 randomized runs, standardized Mantel $r = 0.0551$, observed $Z = 8{,}064$, average $Z = 7{,}927$, $P = 0.023$).

Prediction 4

Given higher overall dispersal rates, the importance of transmission in constraining parasite population growth (Arneberg et al., 1998), and other basic life-history differences, prevalence, abundance, and intensity of amblyceran (*C. turbinatum*) lice are always greater than those of ischnoceran (*D. regalis*) lice, regardless of host group size.

Within the small groups, mean abundance (Table II), intensity (*C. turbinatum* = $12.55^{(7.10\text{–}18.61)}$, *D. regalis* = $3.92^{(1.96\text{–}6.00)}$, $P = 0.0465$, $t = 2.690$), and median intensity (*C. turbinatum* = 7, *D. regalis* = 1, $P = 0.007$) were significantly higher in *C. turbinatum* than in *D. r. regalis*. The same pattern was observed within large groups for mean abundance (Table II), intensity (*C. turbinatum* = $33.60^{(25.64\text{–}41.48)}$, *D. regalis* = $6.79^{(4.00\text{–}9.79)}$, $P = 0.0000$, $t = 5.872$), and median intensity (*C. turbinatum* = 32, *D. regalis* = 6, $P = 0.000$). Prevalence of *C. turbinatum* was higher than *D. regalis* within both small and large groups but only significantly so in large groups (Table II).

DISCUSSION

"One of the most intimate of biological relationships is that which exits between a parasite and its host. This closeness is strikingly illustrated by the Mallophaga or avian biting lice . . . ." (Foster, 1969)

Regardless of the metric used, birds from larger groups harbored significantly larger numbers of lice (both species combined) than birds from smaller groups (Table II). This result is largely consonant with epidemiological theory (Anderson and May, 1978; May and Anderson, 1978; Dobson, 1990; Arneberg et al., 1998) and corroborates findings of similar studies that have examined parasite population sizes in relation to host density and group size (e.g., Hoogland, 1979; C. R. Brown and M. B. Brown, 1986; Moore et al., 1988; Côté and Poulin, 1995; Arneberg et al., 1998; Avilés and Tufiño, 1998; Hoi et al., 1998; Krasnov et al., 2002; cf. Rózsa, 1997). However, the situation in this study was more complex than this generalization. When the 2 louse suborders are considered separately, our study is the first, to our knowledge, to document significant differences in abundance and intensity between these louse clades in the context of host sociality. Thus, differences in parasite natural history should be considered when such comparisons are made because disparate responses by each species to host sociality may yield misleading results and incorrect interpretations thereof.

Galapagos hawks within small groups harbored similarly aggregated (where most hosts harbored few parasites and few hosts harbored many parasites) distributions of both louse species. As host group size increased, however, the more mobile amblyceran (*C. turbinatum*) was less aggregated among hosts than the less mobile ischnoceran (*D. regalis*). Rózsa et al. (1996) found similar patterns between colonial and territorial crow (*Corvus* spp.) host species. The amblycerans (*Myrsidea* spp.) were less aggregated within the population of the colonial host species relative to those found within that of the territorial

TABLE II. Prevalences, mean infection abundances, and degree of aggregation (k and D) of the lice *Colpocephalum turbinatum* and *Degeeriella regalis* (Insecta: Phthiraptera) within and between small and large groups of *Buteo galapagoensis* (Aves: Falconiformes) from Galapagos, Ecuador.*

	Prevalence			Mean abundance†				k		D	
	1–3 males	4–6 males	P‡	1–3 males	4–6 males	t‡	P‡	1–3 males	4–6 males	1–3 males	4–6 males
Both species	91.2%	96.2%	0.626	15.71 (9.58–22.81)	38.76 (28.76–48.60)	−3.682	0.0000	0.78	1.91	0.571	0.350
C. turbinatum	91.2%	96.2%	0.626	11.44 (5.94–16.53)	32.31 (24.15–40.15)	−4.036	0.0000	0.71	1.95	0.597	0.344
D. regalis	73.5%	73.1%	1.000	2.88 (1.29–4.44)	4.96 (2.65–7.31)	−1.374	0.1760	0.59	0.61	0.667	0.595
t§	—	—	—	2.908	6.061						
P§	0.109	0.050		0.0400	0.0000						

* n = 34. Hosts from groups with 1–3 males/group, and n = 26 hosts from groups with 4–6 males/group. Fisher's exact tests were used to compare prevalences; 2-sample bootstrap *t*-tests were used to compare mean abundances; all *P* values are 2 sided.

† Values in parentheses indicate 95% bootstrap confidence limits around the mean abundance (2,000 replications).

‡ Values represent comparisons within a taxonomic class (both species, *C. turbinatum* only, and *D. regalis* only).

§ Values represent separate comparisons between *C. turbinatum* and *D. regalis* within small and large host groups.

host, whereas the ischnocerans (*Philopterus* spp.) were similarly aggregated in a negative binomial fashion between the 2 host populations. Thus, in both cases only the populations of amblyceran lice responded positively to an increase in degree of host sociality. Similarly, a more general comparative study of louse distributions in the context of sociality (where both louse suborders were pooled) found that lice were less aggregated among social hosts than asocial hosts (Rékási et al., 1997). However, these studies were interspecific in nature, and our results, although similar, are novel because we compared intraspecific variance in host sociality.

Our bivariate correlational analysis revealed significant similarities in abundances of *C. turbinatum* but not *D. regalis* between individuals of the same sex within a reproductive coalition. To our knowledge, this is the first report demonstrating such differences between these louse lineages. In a separate analysis that used data from more individuals within polyandrous groups, the differences between individuals in their louse abundances were significantly smaller in magnitude among polyandrous group members than nongroup members for both louse species, although a much stronger relationship was found for *C. turbinatum* than *D. regalis*.

The most parsimonious explanation for these results is that repeated horizontal transfer of lice occurs between individual group members during sexual contact, provisioning of the young at the nest, or roosting communally, similar to that argued by others for findings within intersex breeding pairs (Potti and Merino, 1995; Blanco et al., 1997; Darolova et al., 2001). Other general avenues for louse transmission include loose feathers, shared dust baths, and phoresis by way of hippoboscid flies, which are present on Galapagos hawks (de Vries, 1973, 1975; Keirans, 1975; Clayton et al., 2003). Transmission through phoresy by hippoboscid flies as a source of dispersal between hosts may not likely explain the patterns observed in this study, given that ischnocerans, not amblycerans, are most commonly observed attached thereto (Keirans, 1975). Specifically, morphological constraints prevent most amblycerans, e.g., *C. turbinatum*, from effectively dispersing by way of hippoboscids. If phoresy was a driving force in the dispersal of *D. regalis*, patterns in abundance between host classes should have been similar to those of *C. turbinatum*, which they were not.

We expected and found that differences in both host and parasite biology reflected differences in parasite infection abundance, intensity, and their distribution among hosts. This prediction was formulated in part because Amblycera species are generally ''more mobile than Ischnocera'' (Clayton and Tompkins, 1995). In particular, *C. turbinatum* individuals run rapidly on the host's body surface (Nelson and Murray, 1971), and amblycerans in general are readily horizontally transmitted to humans who have handled their hosts (Ash, 1960; Eveleigh and Threlfall, 1976; N. K. Whiteman, pers. obs.); *C. turbinatum* has an unusually large host range (Price and Beer, 1963; Askew, 1971; Marshall, 1981; Price et al., 2003) relative to the host-restricted ischnoceran *D. regalis* (Clay, 1958; Price et al., 2003).

Within the ecologically simplified setting of the Galapagos Islands, where no other known host is present, *C. turbinatum* was both more widespread among Galapagos hawk hosts and more abundant than *D. regalis*, regardless of the degree of host sociality. Similar logic derived from observations on basic differences in parasite life histories, e.g., inferred dispersal abilities, has been used to formulate hypotheses and to interpret results regarding studies of micro- and macroevolutionary processes and patterns within the Phthiraptera (Johnson, Adams et al., 2002; Johnson, Williams et al., 2002; Clayton and Johnson, 2003).

Although parasite populations with negligible effects on host fitness will increase in size with increasing host density per group size (Arneberg et al., 1998), it is worthwhile to consider the implications if the parasites actually had an impact on host fecundity or mortality. First, host infestation by lice may lead to decreased fitness (Derylo, 1974; DeVaney, 1976), feeding efficiency (DeVaney, 1976), survivorship (Brown et al., 1995; Clayton et al., 1999), thermoregulatory abilities (Booth et al., 1993), male courtship displays (Clayton, 1990), and male mating success (Borgia and Collis, 1989) and increased mortality (Ash, 1960; Eveleigh and Threlfall, 1976; Marshall, 1981). Second, parasite transmission modes and virulence are linked (Clayton and Tompkins, 1994, 1995; Ewald, 1994, 1995). Horizontal transmission allows parasites to evolve increased virulence relative to those vertically transmitted because the fitness of horizontally transmitted parasites is not tied to the hosts, unlike that of vertically transmitted parasites (Clayton and Tompkins, 1994, 1995; Ewald, 1994, 1995). Thus, the formation of larger groups of Galapagos hawks, which have higher overall loads of *C. turbinatum*, may be disfavored if such par-

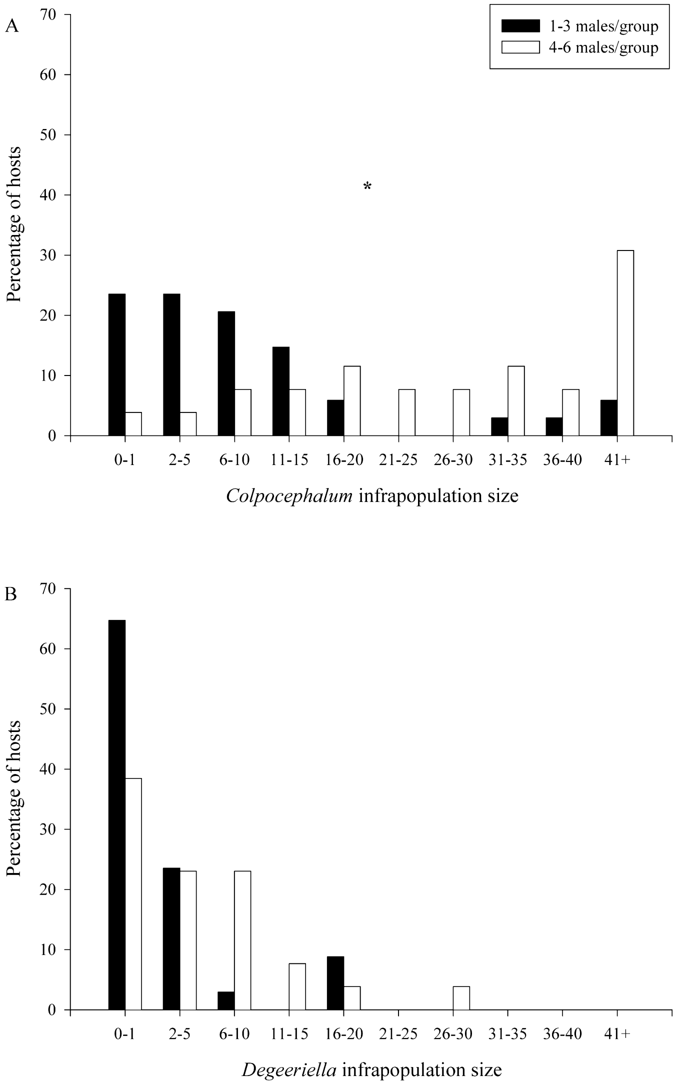

FIGURE 2. **A.** Frequency distributions of *Colpocephalum turbinatum* among territorial male Galapagos hawks (*Buteo galapagoensis*) from small (1–3 males/group; n = 34) and large (4–6 males/group; n = 26) breeding groups. To test if the 2 distributions differed, frequency classes were pooled such that each class contained ≥3% of the total. The 2 distributions were significantly different from each other (most extreme absolute differences = 0.670, Kolmogorov–Smirnov $Z = 2.571$, $P = 0.000$). **B.** Frequency distributions of *Degeeriella regalis* among territorial male Galapagos hawks (*B. galapagoensis*) from small (1–3 males/group; n = 34) and large (4–6 males/group; n = 26) breeding groups. The 2 distributions were not significantly different from each other (most extreme absolute differences = 0.267, Kolmogorov–Smirnov $Z = 1.025$, $P = 0.244$).

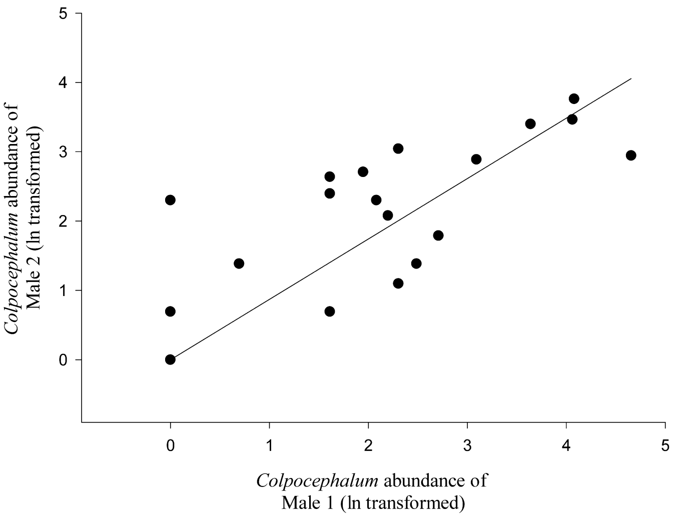

FIGURE 3. Scatterplot of correlation between *Colpocephalum turbinatum* abundances (ln transformed) from 19 dyads of male Galapagos hawks (*Buteo galapagoensis*). Dyads represent louse abundances of 2 males from the same polyandrous group. In cases where the number of males sampled per group is >2, dyads are composed of 2 randomly chosen males from the same polyandrous group. Groups were sampled only once. Pearson's $r = 0.711$, $P = 0.000$ (1 tailed); after controlling for the effect of group size, Pearson's $r = 0.66$, $P = 0.001$ (1 tailed).

asites are at least partially horizontally transmitted and negatively affect host fitness. The relatively low level of aggregation (and high k value of 1.95) of *C. turbinatum* within hosts from large groups may correlate with high virulence. Hudson and Dobson (1995) observed that k values for macroparasites typically ranged from 0.1 to 1.0 and values above this were correlated with parasite populations that regulated host populations. The hypothesized mechanism lies in the observation that aggregation of parasites within a small proportion of the host population stabilizes host–parasite interactions and departure from this distribution destabilizes them (Anderson and May, 1978; May and Anderson, 1978; Hudson and Dobson, 1995). These factors may explain why polyandrous groups of 2–3 males are the most typical size within the populations of Galapagos hawks considered in this study and why larger groups are more rare (Donaghy Cannon, 2001).

The breadth of influence imposed by pathogens on the evolution of breeding systems extends beyond the classical parasite-mediated sexual selection paradigm of Hamilton and Zuk (1982), particularly if pathogens are capable of horizontal transmission (Antonovics et al., 2002). Thus, more general ecological phenomena, e.g., classic density dependence of parasite population size on host density, may continue to influence the evolution of the host's reproductive tactics (e.g., C. R. Brown and M. B. Brown, 1996, 2000). This study shows that emergent phenomena, such as host–parasite interactions, only make sense in the context of the basic life-history characteristics of each participant.

ACKNOWLEDGMENTS

This research was funded by grants from the Field Research for Conservation Program of the Saint Louis Zoo and the International Center for Tropical Ecology and funds from the E. Desmond Lee and Family Fund's Collaborative Vision in Zoological Studies from the University of Missouri–St. Louis and the Saint Louis Zoo. We gratefully acknowledge the logistical support and research permits provided by the Servicio Parqué Nacional de Galápagos and the Estación Científica Charles Darwin, Isla Santa Cruz, Galápagos, Ecuador, with special thanks to Poly Robayo, Howard Snell, Hernan Vargas, and David Wiedenfeld. Jennifer Bollmer, Pedro Castillo, Gustavo Jiménez, Pilar Jiménez, Adriana Mesa, and Ken Levenstein were steadfast field companions during fieldwork. Tame provided discounted round-trip air travel within Ecuador. We thank Ivan Jiménez and Jennifer Bollmer, who aided in the development of ideas and results presented in this study. Gerald Borgia, 2 anonymous reviewers, and the Parker Lab Group at the University of Missouri–St. Louis provided helpful reviews of previous versions of the manuscript.

LITERATURE CITED

Alexander, R. D. 1974. The evolution of social behavior. Annual Review of Ecology and Systematics **5:** 325–383.

Anderson, R. M., and R. M. May. 1978. Regulation and stability of host-parasite population interactions. I. Regulatory processes. Journal of Animal Ecology **47:** 219–247.

Antonovics, J., M. Hood, and J. Partain. 2002. The ecology and genetics of a host shift: *Microbotryum* as a model system. American Naturalist **160:** S40–S53.

Arneberg, P. A., A. Skorping, B. Grenfell, and A. F. Read. 1998. Host densities as determinants of abundance in parasite communities. Proceedings of the Royal Society of London Series B **265:** 1283–1289.

Ash, J. S. 1960. A study of the Mallophaga of birds with particular reference to their ecology. Ibis **102:** 93–110.

Askew, R. R. 1971. Parasitic insects. Heinemann Educational, London, U.K., 316 p.

Avilés, L., and P. Tufiño. 1998. Colony size and individual fitness in the social spider *Anelsoimus eximius*. American Naturalist **3:** 403–418.

Bennett, P. M., and P. F. Owens. 2002. Oxford series in ecology and evolution: Evolutionary ecology of birds: Life histories, mating systems and extinction. Oxford University Press, Oxford, U.K., 278 p.

Berger, D. D., and H. C. Mueller. 1959. The bal-chatri: A trap for birds of prey. Bird-Banding **30:** 18–26.

Blanco, G., J. L. Tell, and J. Potti. 1997. Feather mites on group-living red-billed choughs: A non-parasitic interaction? Journal of Avian Biology **28:** 197–206.

Bollmer, J. L. 2000. Genetic and morphologic differentiation among island populations of Galapagos hawks (*Buteo galapagoensis*). M.S. Thesis. Ohio State University, Columbus, Ohio, 84 p.

———, T. Sanchez, M. S. Donaghy Cannon, D. Sanchez, B. Cannon, J. C. Bednarz, T. de Vries, S. Struve, and P. G. Parker. 2003. Variation in morphology and mating system among island populations of Galápagos hawks. The Condor **105:** 428–438.

Booth, D. T., D. H. Clayton, and B. A. Block. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. Proceedings of the Royal Society of London Series B **253:** 125–129.

Borgia, G. 1986. Satin bowerbird parasites: A test of the bright male hypothesis. Behavioral Ecology and Sociobiology **19:** 355–358.

———, and K. Collis. 1989. Female choice for parasite-free male stain bowerbirds and the evolution of bright male plumage. Behavioral Ecology and Sociobiology **25:** 445–454.

———, and ———. 1990. Parasites and bright male plumage in the satin bowerbirds (*Ptilonorhynchus violaceus*). American Zoologist **30:** 279–285.

Brown, C. R., and M. B. Brown. 1986. Ectoparasites as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). Ecology **67:** 1206–1218.

———, and ———. 1996. Coloniality in the cliff swallow: The effects of group size on social behavior. University of Chicago Press, Chicago, Illinois, 566 p.

———, and ———. 2000. Heritable basis for choice of group size in a colonial bird. Proceedings of the National Academy of Sciences of the United States of America **97:** 14825–14830.

———, ———, and B. Rannala. 1995. Ectoparasites reduce long-term survival of their avian host. Proceedings of the Royal Society of London Series B **262:** 313–319.

Brown, J. L. 1987. Helping and communal breeding in birds: Ecology and evolution. Princeton University Press, Princeton, New Jersey, 354 p.

Bush, A. O., K. D. Lafferty, J. M. Lotz, and A. W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology **83:** 575–583.

Clay, T. 1958. Revisions of Mallophaga genera. *Degeeriella* from the Falconiformes. Bulletin of the British Museum of Natural History Entomology **7:** 121–207.

Clayton, D. H. 1990. Mate choice in experimentally parasitized rock doves: Lousy males lose. American Zoologist **30:** 251–262.

———, S. Al-Tamini, and K. P. Johnson. 2003. The ecological basis of coevolutionary history. *In* Tangled trees: Phylogeny, cospeciation, and evolution, R. D. M. Page (ed.). University of Chicago Press, Chicago, Illinois, p. 310–341.

———, and D. M. Drown. 2001. Critical evaluation of five methods for quantifying chewing lice (Insecta: Phthiraptera). Journal of Parasitology **87:** 1291–1300.

———, R. D. Gregory, and R. D. Price. 1992. Comparative ecology of Neotropical bird lice (Insecta: Phthiraptera). Journal of Animal Ecology **61:** 781–795.

———, and K. P. Johnson. 2003. Linking coevolutionary history to ecological process: Doves and lice. Evolution **57:** 2335–2341.

———, P. L. M. Lee, D. M. Tompkins, and E. D. Brodie III. 1999. Reciprocal natural selection on host-parasite phenotypes. American Naturalist **154:** 261–270.

———, and D. M. Tompkins. 1994. Ectoparasite virulence is linked to mode of transmission. Proceedings of the Royal Society of London Series B **256:** 211–217.

———, and ———. 1995. Comparative effects of mites and lice on the reproductive success of rock doves (*Columba livia*). Parasitology **110:** 195–206.

Côté, I. M., and R. Poulin. 1995. Parasitism and group size in social animals: A meta-analysis. Behavioral Ecology **6:** 159–165.

Crofton, H. D. 1971. A quantitative approach to parasitism. Parasitology **62:** 179–193.

Cruickshank, R. H., K. P. Johnson, V. S. Smith, R. J. Adams, D. H. Clayton, and R. D. Page. 2001. Phylogenetic analysis of partial sequences of elongation factor 1α identifies major groups of lice (Insecta: Phthiraptera). Molecular Phylogenetics and Evolution **19:** 202–215.

Darolova, A., H. Herber, J. Kristoflik, and C. Hoi. 2001. Horizontal and vertical ectoparasite transmission of three species of Malophaga [sic], and individual variation in European bee-eaters (*Merops apiaster*). Journal of Parasitology **87:** 256–262.

DeLay, L. S. 1992. Paternal care in the cooperatively polyandrous Galapagos hawk (*Buteo galapagoensis*). M.S. Thesis. University of Missouri, Columbia, Missouri, 51 p.

Derylo, A. 1974. Studies on the economic harmfulness of the Mallophaga II. Influence of lice infestation on egg laying and hatching of hens. Medycyna Weterynaryjna **30:** 406–410.

DeVaney, J. A. 1976. Effects of the chicken body louse, *Menacanthus stramineus*, on caged layers. Poultry Science **55:** 430–435.

———, J. H. Quisenberry, I. B. H. Dorn, and J. W. Bradley. 1980. Dispersal of the northern fowl mite, *Ornithonyssus sylvariaum* (Canestrini and Fanzago), and the chicken body louse, *Mencanthus stramineus* (Nitzsch), among some thirty strains of egg-type hens in a caged laying louse. Poultry Science **59:** 1745–1749.

de Vries, T. 1973. The Galapagos hawk: An ecogeographical study with special reference to its systematic position. Ph.D. Dissertation. Vrije Universiteit te Amsterdam, Amsterdam, The Netherlands, 108 p.

———. 1975. The breeding biology of the Galapagos hawk, *Buteo galapagoensis*. Le Gerfaut **65:** 29–57.

Dobson, A. P. 1990. Models for multi-species parasite-host communities. *In* Parasite communities: Patterns and processes, G. W. Esch, A. O. Bush, and J. M. Aho (eds.). Chapman and Hall, London, U.K., p. 261–288.

Donaghy Cannon, M. 2001. Breeding ecology of cooperatively polyandrous Galapagos hawks (*Buteo galapagoensis*) on Santiago Island, Galapagos. M.S. Thesis. Arkansas State University, Jonesboro, Arkansas, 119 p.

Eveleigh, E. S., and W. Threlfall. 1976. Population dynamics of lice (Mallophaga) on auks (Alcidae) from Newfoundland. Canadian Journal of Zoology **54:** 1694–1711.

Ewald, P. W. 1994. Evolution of infectious disease. Oxford University Press, Oxford, U.K., 298 p.

———. 1995. Evolution of virulence: A unifying link between parasitology and ecology. Journal of Parasitology **81:** 659–669.

Faaborg, J. 1986. Reproductive success and survivorship of the Galapagos hawk (*Buteo galapagoensis*): Potential costs and benefits of cooperative polyandry. Ibis **128:** 337–347.

———, and J. C. Bednarz. 1990. Galapagos and Harris' hawks: Divergent causes of sociality in two raptors. *In* Cooperative breeding in birds: Long term studies of ecology and behavior, P. B. Stacey and W. D. Koenig (eds.). Cambridge University Press, Cambridge, U.K., p. 359–383.

———, T. de Vries, C. B. Patterson, and C. R. Griffin. 1980. Preliminary observations on the occurrence and evolution of polyandry in the Galapagos hawk (*Buteo galapagoensis*). Auk **97:** 581–590.

———, P. G. Parker, L. DeLay, T. de Vries, J. C. Bednarz, S. Maria Paz, J. Naranjo, and T. Waite. 1995. Confirmation of cooperative polyandry in the Galapagos hawk (*Buteo galapagoensis*). Behavioral Ecology and Sociobiology **36:** 83–90.

Foster, M. S. 1969. Synchronized life cycles in the orange-crowned warbler and its mallophagan parasites. Ecology **50:** 315–323.

Hafner, M. S., and S. A. Nadler. 1988. Phylogenetic trees support the coevolution of parasites and their hosts. Nature **332:** 258–259.

Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: A role for parasites? Science **218:** 384–387.

Hillgarth, N. 1996. Ectoparasite transfer during mating in the ring-necked pheasant *Phasianus colchicus*. Journal of Avian Biology **27:** 260–262.

Hoi, H., A. Darolova, C. König, and J. Kristofik. 1998. The relation between colony size, breeding density and ectoparasite loads of adult European bee-eaters (*Merops apiaster*). Ecoscience **5:** 156–163.

Hoogland, J. L. 1979. Aggression, ectoparasitism, and other possible costs of prairie dog (Sciuridae, *Cynomys* spp.) coloniality. Behaviour **1–2:** 1–35.

Hudson, P. J., and A. P. Dobson. 1995. Macroparasites: Observed patterns in naturally fluctuating animal populations. *In* Ecology of infectious diseases in natural populations, B. T. Grenfell and A. P. Dobson (eds.). Publications of the Newton Institute, Cambridge University Press, Cambridge, U.K., p. 144–176.

IUCN. 2002. 2002 IUCN red list of threatened species. Available at: http://www.redlist.org

Johnson, K. P., R. J. Adams, and D. H. Clayton. 2002. The phylogeny of the louse genus *Brueelia* does not reflect host phylogeny. Biological Journal of the Linnean Society London **77:** 233–247.

———, and M. F. Whiting. 2002. Multiple genes and the monophyly of Ischnocera (Insecta: Phthiraptera). Molecular Phylogenetics and Evolution **22:** 101–110.

———, B. L. Williams, D. M. Drown, R. J. Adams, and D. H. Clayton. 2002. The population genetics of host specificity: Genetic differentiation in dove lice (Insecta: Phthiraptera). Molecular Ecology **11:** 25–38.

Keirans, J. E. 1975. A review of the phoretic relationship between Mallophaga (Phthiraptera: Insecta) and Hippoboscidae (Diptera: Insecta). Journal of Medical Entomology **12:** 71–76.

Krasnov, B., I. Khokhlova, and G. Shenbrot. 2002. The effect of host density on ectoparasite distribution: An example of a rodent parasitized by fleas. Ecology **83:** 164–175.

Krebs, C. J. 1989. Ecological methodology. Addison-Welsey, Boston, Massachusetts, 654 p.

Kricher, J. 2002. Galápagos. Smithsonian Institution Press, Washington, D.C., 221 p.

Ligon, J. D. 1999. The evolution of avian breeding systems. Oxford University Press, Oxford, U.K., 504 p.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Research **27:** 209–220.

Margolis, L., G. W. Esch, J. C. Holmes, A. M. Kuris, and G. A. Schad. 1982. The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). Journal of Parasitology **68:** 131–133.

Marshall, A. G. 1981. The ecology of ectoparasitic insects. Academic Press, London, U.K., 459 p.

May, R. M., and R. M. Anderson. 1978. Regulation and stability of host-parasite population interactions. II. Destabilizing processes. Journal of Animal Ecology **47:** 249–267.

Moore, J., D. Simberloff, and M. Feehling. 1988. Relationships between bobwhite quail social-group size and intestinal helminth parasitism. American Naturalist **131:** 22–32.

Nelson, B. C., and M. D. Murray. 1971. The distribution of Mallophaga on the domestic pigeon (*Columba livia*). International Journal for Parasitology **1:** 21–29.

Page, R. D. M. 2003. Tangled trees: Phylogeny, cospeciation and coevolution. The University of Chicago Press, Chicago, Illinois, 350 p.

Poiani, A. 1992. Ectoparasitism as a possible cost of social life: A comparative analysis using Australian passerines (Passeriformes). Oecologia **92:** 429–441.

———, A. R. Goldsmith, and M. R. Evans. 2000. Ectoparasites of house sparrows (*Passer domesticus*): An experimental test of the immunocompetence handicap hypothesis and a new model. Behavioral Ecology and Sociobiology **47:** 230–242.

Potti, J., and S. Merino. 1995. Louse loads of pied flycatchers: Effects of host's sex, age, condition and relatedness. Journal of Avian Biology **26:** 203–208.

Poulin, R. 1993. The disparity between observed and uniform distributions: A new look at parasite aggregation. International Journal for Parasitology **23:** 937–944.

Price, R. D., and J. R. Beer. 1963. Species of *Colpocephalum* (Mallophaga: Menoponidae) parasitic upon the Falconiformes. Canadian Entomology **95:** 731–763.

———, R. A. Hellenthal, and R. L. Palma. 2003. World checklist of chewing lice with host associations and keys to families and genera. *In* The chewing lice: World checklist and biological overview, R. D. Price, R. A. Hellenthal, R. L. Palma, K. P. Johnson, and D. H. Clayton, (eds.). Illinois Natural History Survey Special Publication 24, Champaign, Illinois, p. 1–448.

Queller, D. C., and J. E. Strassmann. 2002. The many selves of social insects. Science **296:** 311–313.

Reiczigel, J., and L. Rózsa. 2001. Quantitative parasitology 2.0. Budapest, Hungary. [Distributed by the authors.]

Rékási, J., L. Rózsa, and B. J. Kiss. 1997. Patterns in the distribution of avian lice (Phthiraptera: Amblycera, Ischnocera). Journal of Avian Biology **28:** 150–156.

Rózsa, L. 1997. Patterns in the abundance of avian lice (Phthiraptera: Amblycera, Ischnocera). Journal of Avian Biology **28:** 249–254.

———, J. Reiczigel, and G. Majoros. 2000. Quantifying parasites in samples of hosts. Journal of Parasitology **86:** 228–232.

———, J. Rékási, and J. Reiczigel. 1996. Relationship of host coloniality to the population ecology of avian lice (Insecta: Phthiraptera). Journal of Animal Ecology **65:** 242–248.

Stacey, P. B., and W. D. Koenig. 1990. Cooperative breeding in birds: Long-term studies of ecology and behavior. Cambridge University Press, Cambridge, U.K., 615 p.

Walther, B. A., and D. H. Clayton. 1997. Dust-ruffling: A simple method for quantifying ectoparasite loads of live birds. Journal of Field Ornithology **68:** 509–518.