Relationship of host coloniality to the population ecology of avian lice (Insecta: Phthiraptera)

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Summary

1. We test the hypothesis that avian social system (territorial vs. colonial) has an impact on the ecological characteristics of avian lice. We compared the louse loads of two congeneric host species, the territorial hooded crow (*Corvus corone cornix* L.) and the colonial rook (*C. frugilegus* L.). Each species harboured the same five genera of lice; one species of louse was shared, while the other four species on each host were host-specific.

2. More rooks harboured *Myrsidea*, *Philopterus*, *Brueelia* and *Allocolpocephalum* spp. than crows.

3. Rooks harboured more species-rich louse loads than crows.

4. Louse loads were also more diverse on rooks than on crows.

5. The frequency distributions of lice on rooks were less aggregated than on crows.

6. Sex ratios of lice were less biased on rooks than on crows. Biased sex ratios were correlated with the subpopulation size of lice on individual hosts, making it necessary to control for subpopulation size in comparative analyses.

7. These findings may result from the increased frequency of horizontal transmissions via increased body-to-body contacts among colonial rooks, compared to territorial hooded crows.

Key-words: biased sex ratio, frequency distribution, horizontal transmission, local mate competition, *Phthiraptera*, species richness.

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Introduction

Colonial species of hosts should have more parasites than solitary species, assuming that proximity of host individuals increases the probability of parasite transmission. On the other hand, parasite diversity may decrease with group size if group living has a dilution effect (Møller, Dufva & Allander 1993). To test these opposing predictions, we examined the relationship between coloniality and the richness and abundance of ectoparasites on two congeneric species, the territorial hooded crow and the colonial rook. We also examined the relationship of host coloniality to additional features of parasite ecology, such as distribution among host individuals and sex ratios. The parasites we studied were nine species of chewing lice (Insecta: Phthiraptera). Avian chewing lice are good subjects for such a study as they are permanent ectoparasites that complete their entire life cycle on the body of the host. Hence, their transmission is dependent on direct contact among hosts.

Conspecific parasites living on the same individual host form a more or less isolated breeding community called a subpopulation or 'infrapopulation'. The collection of subpopulations among the members of a host population form a metapopulation or 'suprapopulation' (Margolis *et al.* 1982). The term 'louse load' refers to all lice found on one bird, including one or more subpopulations representing one or more species. The presumption that subpopulations act as more or less isolated subgroups within a metapopulation was verified by Lonc (1991) who detected morphological differences among subpopulations of avian lice, and by Nadler & Hafner (1989) and Nadler *et al.* (1990) who showed genetic differences among them.

Abundance of fleas, blow-flies and mites has been reported to correlate with host colony size in most cases (Brown & Brown 1986; Shields & Crook 1987; Duffy 1991; Chapman & George 1991; Loye & Carroll 1991), but not all cases (Rogers, Robertson & Stutchbury 1991). Increased proximity of hosts facil-

itates transmission of the free-living invasive forms of these nest-dwelling haematophagous arthropods. Lice have no free-ranging invasive forms; their normal route of transmission depends on direct contact between hosts. Whether host coloniality facilitates their transmission is not known.

Both intraspecific and interspecific comparisons of avian social systems (territorial vs. colonial) might be used for this purpose. An intraspecific comparison could be carried out by studying a bird species in which coloniality is facultative. However, such a comparison might have the disadvantage that bird individuals easily switch between different social systems (see, e.g. Sasvári & Hegyi 1994) and therefore lice cannot develop their adaptive features to a particular social system. A comparison within an avian genus involving both obligatory terrestrial and obligatory colonial species is a better choice.

The louse loads of the hooded crow, an obligatory territorial breeder, and those of the rook, an obligatory colonial breeder (Madge & Burn 1993) are analysed in the present study. The lice of these host species were suitable candidates for such a comparison for several reasons. Both host species harbour a relatively species-rich (five species) louse fauna. The lice represent five different genera, and all the five genera are represented on both bird species. The most abundant louse species of these hosts belong to some of those genera (*Myrsidea, Philopterus, Brueelia*) that were previously documented to include species with skewed sex ratios (Wheeler & Threlfall 1986; Clayton, Gregory & Price 1992). Thus, these hosts are a good choice for examining the relationship between coloniality and parasite sex ratio. Preening by the bill is the main defence against lice by birds (reviewed by Clayton 1991). The bill size of these species is roughly similar; 47–54 mm in the hooded crow and 52–62 mm in the rook (Keve 1958). This difference in bill morphology is far smaller than those documented to cause differences in the preening behaviour of birds (Clayton & Cotgreave 1994).

We tested the following predictions about the relative louse loads of rooks and crows.

1. More rooks harbour lice than crows.
2. Rooks harbour more species rich louse loads than crows.
3. Rooks harbour more diverse louse loads than crows.
4. The frequency distributions of parasites among hosts is aggregated (overdispersed): most hosts have few parasites whereas a few have many (Crofton 1971). The degree of aggregation is supposed to depend on many factors including parasite transmission rates (Anderson & May 1985). Therefore, the louse species on rooks are predicted to be less aggregated among individual hosts than those on the crow.

Skewed sex ratio is not an uncommon phenomenon in avian lice. Marshall (1981) listed several examples

in his review and suggested that these might have been caused either by sampling bias or by unequal longevity of the two sexes. Clayton *et al.* (1992) found about 10% of avian louse metapopulations to exhibit a skewed sex ratio and suggested that local mate competition (LMC) might have caused most of these biases. LMC arises when a population is divided into small subpopulations where inbreeding is pronounced (Hamilton 1967). Under such conditions, females can maximize their breeding success by reducing the proportion of sons to decrease sexual competition among their offspring. If LMC is responsible for the skewed sex ratios in avian lice, the following two predictions can be made.

5. The louse mating system in large subpopulations is closer to random than that in small ones where inbreeding is more pronounced. Therefore, the sex ratio in large subpopulations is predicted to be less skewed than that in small ones.
6. The louse mating system in less isolated subpopulations will be closer to random than that in more isolated subpopulations. If the lice of colonial hosts are more often transmitted than those of the territorial hosts, then louse sex ratio is predicted to be less skewed in the colonial birds than in the territorial ones.

Materials and methods

Most of the data analysed in the present study were collected as part of a long-term faunistic survey aimed at describing the louse fauna of Hungary and Romania (Rékási 1973, 1978 1984, 1986 1991, 1993; Rékási & Kiss 1977, 1980, 1984 and unpublished data). Hosts were those being banded at ornithological stations or which had been recently shot, hit by cars, poisoned, etc. Since the birds originated from many distant locations, the rooks probably represent many different colonies (except for 11 rooks shot at the same site for the purpose of the present study). The plumage was visually searched for lice, with special attention to sites known to be preferred by lice. Lice seen were collected with forceps. All lice were collected and identified by the second author. Nymphs which can be difficult to see were excluded from the present study.

The following parameters were calculated.

1. Prevalences (birds infested/birds examined) of congeneric louse species were compared by χ^2-test. The subpopulations sizes of congeneric louse species were compared by Mann–Whitney's test.
2. Species richness of louse loads. Conspecific birds were pooled together into louse species richness pools. The frequency distributions of hooded crows and rooks among these groups were compared by a χ^2-test.
3. The diversity of louse loads with two or more species. The Shannon–Wiener function (Krebs 1989) was used to quantify diversity.

4. Frequency distribution of *Myrsidea* lice on each host species was characterized by fitting a negative binomial distribution to the observed distribution according the maximum likelihood method of Bliss & Fisher (1953). The degree of aggregation was quantified as the exponent k of this distribution. The significance of the difference between the observed frequency distribution of *Myrsidea cornicis* on the hooded crows and that of *M. isostoma* on the rooks was determined by a χ^2 test. The distributions of *Philopterus* lice on the two host species were analysed in the same way. Frequency distributions of lice in the remaining three genera were not compared because of their small sample size (see below).

Since the expected frequencies were less than five for several classes (for more than half of the classes in some tables) the significance of differences was also tested by Monte Carlo methods (based on 2000 randomizations). Monte Carlo significance levels were in full accordance with the previous results.

Please note that the parameters 1, 2, 3 and 4 are not independent measures.

5 & 6. Sex ratios of *Myrsidea* and *Philopterus* were compared for the two host species after pooling conspecific subpopulations of equal size (the same number of adult lice), in order to correct for the large variance in sex ratios at low levels of infestation. Since louse subpopulation size might be correlated with sex ratio skewness, we performed a variance–covariance analysis with host species and parasite genus as factors and subpopulation size as a covariate. The covariate was processed prior to the factors. This allowed us to examine the effect of species with the effect of subpopulation size removed. Finally, the distribution of the residuals was examined.

Results

The same five genera were present on both host species (Table 1). Two congeneric pairs of species; *Myrsidea*

cornicis DeGeer, *Myrsidea isostoma* Nitzsch, *Philopterus ocellatus* Scopoli and *Philopterus atratus* Nitzsch were represented by sample sizes large enough for all comparisons. Species of the other genera: *Brueelia uncinosa* Burmeister, *Brueelia tasniamae* Ansari, *Menacanthus cornicis* Blagoveschchenskii, *Menacanthus laticeps* Blagoveschchenskii and *Allocolpocephalum fregili* (Ansari 1955) (syn.: *Colpocephalum subequale* Burmeister) were included only in the first and second comparisons, and later excluded because of small sample sizes.

1. Of the 89 hooded crows examined, 47 (53%) were infected by adult lice and the rest harboured no lice or only nymphs. Of the 37 rooks inspected, 34 (92%) were infested by adult lice. Significantly more rooks were infected by *Myrsidea*, *Philopterus*, *Brueelia* and *Allocolpocephalum* than hooded crows ($\chi = 18\cdot18$, d.f. = 1, $P < 0\cdot01$; $\chi^2 = 4\cdot78$, d.f. = 1, $P < 0\cdot03$; $\chi^2 = 32\cdot32$, d.f. = 1, $P < 0\cdot01$; $\chi^2 = 19\cdot25$, d.f. = 1, $P < 0\cdot01$, respectively). The prevalence of *Menacanthus* was similar on crows and rooks ($\chi^2 = 0\cdot00$, d.f. = 1, $P > 0\cdot96$). However, rooks did not harbour significantly larger subpopulations of *Myrsidea* and *Philopterus* (Mann–Whitney, two tailed, $U = 286\cdot0$, $P > 0\cdot33$; $U = 340\cdot5$, $P > 0.56$, respectively). Subpopulation sizes were not compared for *Brueelia*, *Menacanthus* and *Allocolpocephalum* because of the small number of subpopulations.

2. Louse species richness (Fig. 1). The average number of louse species was $0\cdot81$ on individual hooded crows and $2\cdot08$ on rooks. The frequency distribution of the hooded crows and those of the rooks among the species richness pools differed significantly ($\chi^2 = 32\cdot59$, d.f. = 4, $P < 0\cdot001$).

3. Louse diversity. There were 21 (24%) hooded crows and 24 (65%) rooks harbouring two or more species of lice. The average Shannon–Wiener diversity of these loads was $0\cdot67$ (SD = $0\cdot20$) in the hooded crow and $0\cdot81$ (SD = $0\cdot26$) in the rook. This difference proved to be significant (Mann–Whitney, one-tailed, $U = 165\cdot5$, $P < 0\cdot03$).

Table 1. Sample size and sex ratio of adult lice collected from the hooded crow and the rook. The sex ratio was the fraction of males. P refers to a binomial test of sex ratio skewness (comparison of the actual ratio to an equal sex ratio)

|	Number (%) of infested birds	Number of adult lice	Sex ratio	P
Hooded crow ($n = 89$)				
Myrsidea cornicis	26 (29%)	178	0·27	0·001
Philopterus ocellatus	34 (38%)	299	0·26	0·001
Brueelia uncinosa	4 (4%)	8	—	
Menacanthus cornicis	7 (8%)	18	—	
Allocolpocephalum fregili	1 (1%)	1	—	
Rook ($n = 37$)				
Myrsidea isostoma	26 (70%)	413	0·41	0·001
Philopterus atratus	22 (59%)	369	0·39	0·001
Brueelia tasniamae	17 (46%)	529	0·32	0·001
Menacanthus laticeps	3 (8%)	15	—	
Allocolpocephalum fregili	9 (24%)	36	—	

—Sample size too small to be informative.
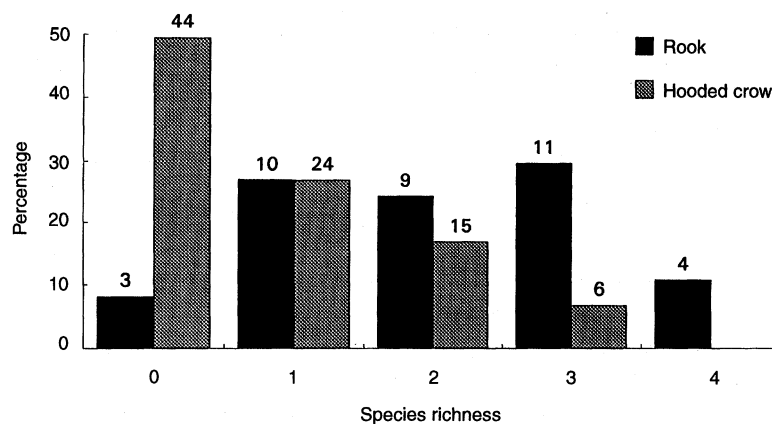
Fig. 1. Louse species richness on hooded crows and rooks. Numbers of birds are shown above the bars.

4. Frequency distributions of *Myrsidea* and *Philopterus* (Figs 2 and 3). The degree of aggregation was $k = 0.10$ (d.f. = 8) for *M. cornicis* and $k = 0.11$ (d.f. = 8) for *P. ocellatus*, from the hooded crow, and $k = 0.19$ (d.f. = 8) for *M. isostoma* and $k = 0.16$ (d.f. = 8) for *P. atratus* from the rook. The difference between *Myrsidea* distributions on the two host species was significant ($\chi^2 = 29.05$, d.f. = 7, $P < 0.001$), while the same difference for *Philopterus*

lice was not significant ($\chi^2 = 12.87$, d.f. = 7, $P < 0.08$).

5 & 6. Sex ratios of *Myrsidea* and *Philopterus*. The sex ratios of both genera were biased towards females on both hosts (Table 1). Sex ratio increased significantly with subpopulation size (Figs 4 and 5, $F = 5.41$, d.f. = 1, 52, $P < 0.02$). Sex ratios were significantly more skewed in the solitary hooded crow than in the colonial rook ($F = 4.15$, d.f. = 1, 52, $P < 0.05$).
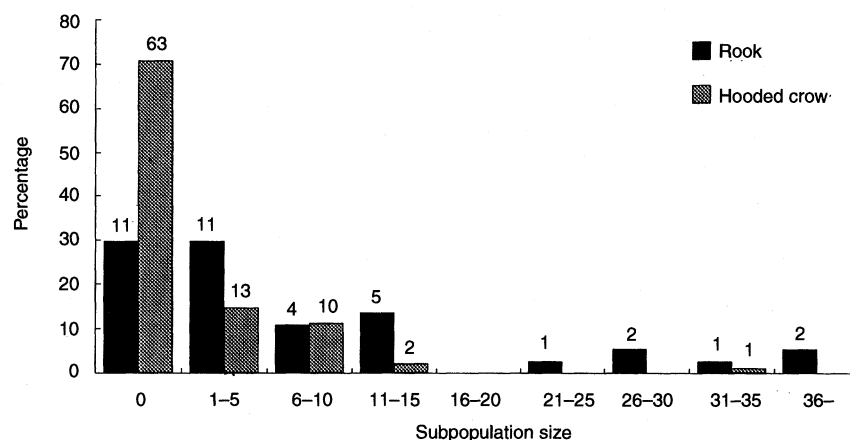

Fig. 2. The frequency distribution of *Myrsidea cornicis* among hooded crows and *M. isostoma* among rooks. Numbers of birds are shown above the bars.
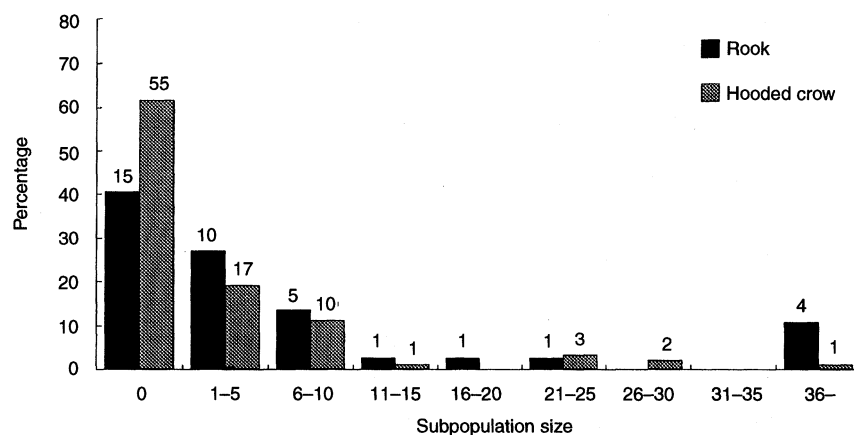
Fig. 3. The frequency distribution of *Philopterus ocellatus* among hooded crows and *P. atratus* among rooks. Numbers of birds are shown above the bars.
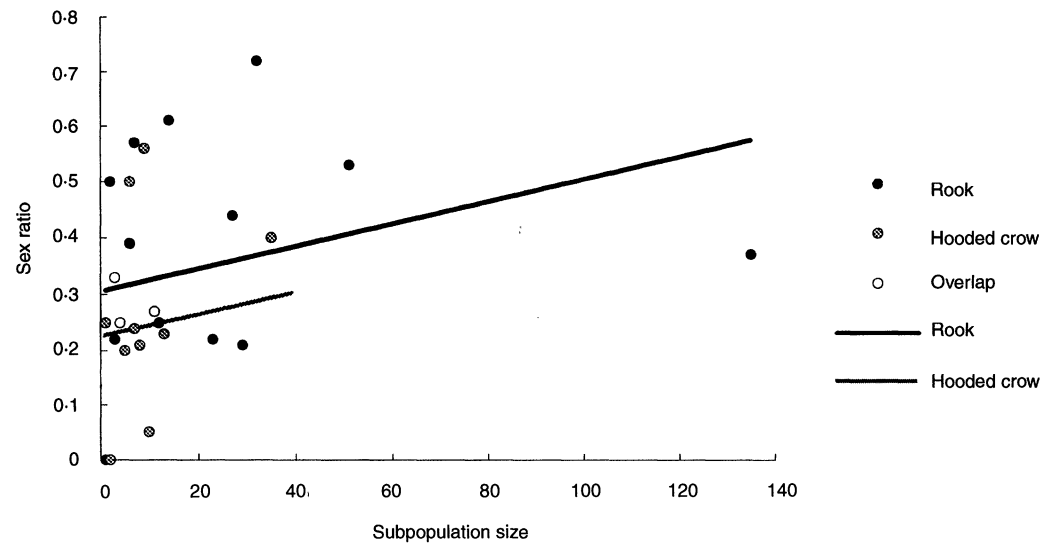
Fig. 4. *Myrsidea* subpopulations of equal size (the same number of adult lice) and conspecific hosts were pooled together. The subpopulation size and the observed sex ratio of the louse pools of the hooded crow and of the rook are indicated by dots. The correlations computed by a variance-covariance analysis are shown by the two lines. The sex ratio was the fraction of males in the pools.

Neither louse genus, nor the interaction between louse genus and host species was found to be significant factor ($F = 0.98$, d.f. $= 1, 52, P > 0.32$; and $F = 0.03$, d.f. $= 1, 52, P > 0.86$, respectively). After pooling, the significance levels remained unchanged. The residuals are regarded as normally distributed ($\chi^2 = 4.65$, d.f. $= 5, P > 0.46$). Removing the large subpopulations (> 40) did not change significance. Therefore, the effect of host species is not an artefact of a few, very large subpopulations.

Discussion

More rooks had lice than crows, in accordance with the prediction that colonial species of hosts should

have more parasites than solitary species (Møller *et al.* 1993). Furthermore, the territorial hooded crow harboured louse loads which were less species-rich, less diverse and characterized by more aggregated frequency distributions than those of the colonial rook. The results are in accordance with the view that louse subpopulations are less isolated on colonial hosts than on solitary hosts. Coloniality is known to increase the intraspecific competition for critical resources like mates, food, nest sites and materials (Alexander 1974). Consequently, it probably results in an increased frequency of body-to-body contacts, e.g. extra-pair copulation (Møller 1987). Although it is not known whether lice can transfer from one bird to another during a fight, Hillgarth (1996) recently showed exper-
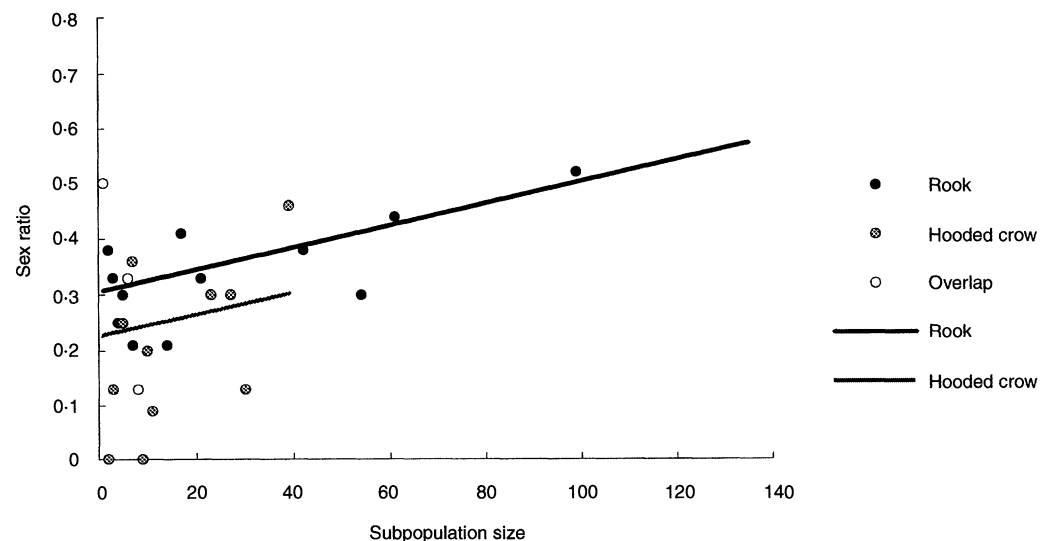
Fig. 5. *Philopterus* subpopulations of equal size (the same number of adult lice) and conspecific hosts were pooled together. The subpopulation size and the observed sex ratio of the louse pools of the hooded crow and of the rook are indicated by dots. The correlations computed by a variance-covariance analysis are shown by the two lines. The sex ratio was the fraction of males in the pools.

imentally that bird lice transfer during host copulation. Our results suggest that the rate of direct contact among hosts had rarely been considered as a factor increasing ectoparasite abundance and diversity in avian colonies (but see Møller 1987, 1991).

Our results on skewed sex ratios are consistent with the view that LMC is responsible for the observed biases, and that differences reflect different levels of isolation. Amblyceran (*Myrsidea*) and Ischnoceran (*Philopterus*) lice exhibited the same sex ratio pattern. However, three alternative hypotheses should also be mentioned.

SAMPLING ERROR

As lice have larger females than males, and so females are easier to collect, female-biased sex ratios may result from sampling error. On the other hand, louse mortality, caused partially by preening and grooming, may also be sexually biased because of the size difference and may result in male-biased sex-ratios (Kim 1985). If sex ratio bias is caused by sampling error or differential mortality, no correlations with subpopulation size and host social system can be expected.

Local resource competition (LRC) may also be argued to cause skewed sex ratios in cases where the subpopulation growth is resource-limited and one sex is more likely to disperse than the other (Clark 1981). Like LMC, LRC could explain the correlation between subpopulation size and sex ratio, and the correlation between coloniality and sex ratio. However, there are no published data to suggest that lice are resource limited (Marshall 1981; Clayton 1991).

UNEQUAL COSTS

Sex ratio theory predicts an equal investment in production of male and female offspring (Fisher 1930). Whether this results in an even sex ratio, partially depends on the relative cost of producing sons vs. daughters. Differential parental investment seems to be absent in avian lice as sexual size dimorphism in the egg phase is not known. There is no parental investment after laying eggs. If sexual differences exist at the egg phase, male-biased sex ratios would be expected.

Given the shortcomings in the fit of these hypotheses to the present data and lice in general, it seems reasonable to argue that LMC might be responsible for the sex ratio patterns of lice. There is a problem remaining unsolved. Though the original LMC model (Hamilton 1967) predicted female-biased sex ratios in isolated and inbred subpopulations, altered versions of the model suggest that sex ratio bias can only be selected if there is a differential dispersal between the sexes, with a sex ratio bias in favour of the dispersive sex (Bulmer & Taylor 1980; Leigh, Herre & Fisher

1985). LMC favours the sex less affected by intra-sex competition within the subpopulation. The degree of the bias will also depend on the degree of difference in the dispersal abilities. Therefore, LMC fits our present findings only if we presume that female lice disperse more effectively than males and there are no major differences in the sexually differential dispersal among the species involved.

This study is the first to compare the ecological measures of lice of territorial vs. colonial birds. The results indicate an increased rate of transmission in colonial birds. Theoretically, two forms of transmission may reduce the level of isolation among subpopulations. Vertical transmission is the dispersal of lice from parents to offspring. We have no reason to suppose differences in the vertical transmission of lice between the two host species. Horizontal transmission is the dispersal of lice between unrelated host individuals. Our results indicate increased horizontal transmission in colonial birds. The existence of horizontal louse transmission among colonial birds is significant because the mode of transmission (vertical vs. horizontal) plays a major role in host–parasite coevolution (Anderson & May 1982) including bird–ectoparasite coevolution (Clayton & Tompkins 1994).

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