FLOCKING BEHAVIOUR DOES NOT FAVOUR HIGH CHEWING LICE LOAD IN SHOREBIRDS

EL TAMAÑO DE BANDO NO SE RELACIONA CON LA CARGA DE ECTOPARÁSITOS EN AVES LIMÍCOLAS

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SUMMARY.—*Flocking behaviour does not favour high chewing lice load in shorebirds.*

As shorebirds show a high variability in the flocking behaviour among species from solitary ones to species forming flocks of hundreds of individuals, they offer a good opportunity to test if the proximity of individuals in highly gregarious species increases the risk of horizontal ectoparasite transmission in comparison with solitary species. We investigate whether there exists a higher ectoparasite load in gregarious shorebirds compared to solitary ones at Salinas del Cabo de Gata, Almeria, Spain. Seven species of shorebirds (Scolopacidae and Charadriidae) were captured with mist-nets during the night. Ectoparasites were estimated by means of visual examination of seven body regions and differentiated in five levels of infestation. Flock size was divided into three categories: solitary species, species forming flocks up to 99 individuals and species forming flocks of more than one hundred. Based on the application of a phylogenetic comparative method, our results show that the abundance of chewing lice is not related with flocking behaviour.

Key words: chewing lice, flock behaviour, shorebirds species.

RESUMEN.—*El tamaño de bando no se relaciona con la carga de ectoparásitos en aves limícolas.*

Las aves limícolas se pueden distribuir tanto en bandos de cientos de individuos como de forma solitaria. Esta variabilidad en el tamaño de los bandos permite poner a prueba la hipótesis que supone que una mayor aproximación entre individuos favorece el riesgo de transmisión horizontal de ectoparásitos móviles respecto a las especies solitarias. En el presente estudio se investigó si existe una mayor cantidad de ectoparásitos en aves limícolas más gregarias respecto a aquellas que son solitarias. Se capturaron siete especies de limícolas (Scolopacidae y Charadriidae) mediante redes japonesas durante la noche en las Salinas del Cabo de Gata, Almería, España. Los ectoparásitos se estimaron visualmente en siete regiones diferentes del cuerpo de cada ave. Las estimaciones se clasificaron en cinco niveles de infestación. Según el tamaño de bando, las especies se clasificaron en tres categorías: (i) solitarias,

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(ii) con bandos de hasta 99 individuos y (iii) con bandos de más de 100 individuos. Aplicando el método comparativo, los resultados encontrados indican que la abundancia de piojos de la pluma en estas aves no estaría relacionada con el tamaño de bando.

Palabras clave: aves limícolas, ectoparásitos, tamaño de bando.

INTRODUCTION

Parasites produce a large variety of effects on the ecology of their hosts, such as effects on reproductive success (see Møller, 1997), sexual selection (Hamilton and Zuk, 1982), dispersal (Brown and Brown, 1992), habitat selection (Chapman and George, 1991) and behaviour (Barbosa *et al*., 2002) among others.

These effects may be sensitive to the degree of social aggregation, as it has been shown in colonial birds (Brown and Brown, 1986). Since parasite transmission is usually positively density-dependent (Anderson and May, 1979; McCallum *et al*., 2001) and animals living in groups will generally experience higher local densities of conspecifics than those living solitarily, they are expected to also experience higher rates of parasite transmission (Freeland, 1979; Dobson, 1988; Côté and Poulin, 1995). Therefore, highly social bird species should be more affected by parasites than non social ones, as host aggregation promotes transmission of parasites. Although some studies have supported this prediction (Hoogland, 1979; Brown and Brown, 1986; Moore *et al*., 1988; Côté and Poulin, 1995 among others) some authors found results showing that no relationship exists between social behaviour and parasite abundance (Poiani, 1992; Rózsa, 1997). Explanations of these contradictory results include differences in the mobility of the parasites, with more mobile parasites such as like ticks, flea mites and flies being more likely to be transmitted between hosts than relatively less mobile parasites such as chewing lice (Rózsa, 1997, but see Moore *et al*., 1988,

who obtained the same result studying gastrointestinal parasites). Another explanation includes the lack of use of phylogenetically controlled analyses in interspecific comparisons (Poiani, 1992; Rózsa, 1997; but see Arneberg *et al*., 1998).

One expression of sociality is the formation of foraging flocks. Flocking behaviour has benefits in terms of reduction of predation risk (Hamilton, 1971; Pulliam, 1973) and increase of foraging efficiency (Beauchamp, 2003). However, there are also some costs associated with sociality, such as the increase of competition for resources (Goss-Custard, 1980). One of the likely costs accruing to flocking species is the increase in the risk of ectoparasite transmission, exacted by the close proximity of hundreds or thousands of individuals. Such individual proximity can favour parasite transmission in comparison with solitary species (Whiteman and Parker, 2004). Therefore, it is expected that more gregarious birds have higher parasite loads than solitary birds.

Shorebirds show a high variability in the flocking behaviour among species. Even their flock sizes could be sometimes influenced by location, activity (roosting, foraging), presence or absence of predators, food availability and environmental variables like temperature, winds and tide (Burger and Gochfeld, 1983; Myers, 1984; Barbosa, 1997), shorebirds offer a good opportunity to test the hypothesis because their flocks vary from solitary species to species forming flocks of hundreds of individuals (Barbosa, 1995; Barbosa and Moreno, 1999).

Therefore, the objective of this study was to investigate whether higher ectoparasite load, specifically of chewing lice, are charac-

teristic of solitary species, species forming small flocks and species forming large flocks of hundreds individuals.

MATERIAL AND METHODS

The work was carried out during September and October of 2004 in the Salinas of Cabo de Gata, southeastern Spain (36º 46' N, 2º 14' W). Seven species of waders were captured (table 1) by means of mist-nets during the night. Each individual was identified and banded with a metal ring.

Ectoparasites were estimated by means of visual examination. This method is a good predictor of the abundance of body lice and a fair predictor for wing lice (Clayton and Drown, 2001). Seven body regions were examined (head, throat, back, rump, belly, ventral lower surfaces of wing feathers and ventral lower surfaces of tail feathers). Five levels of infestation were differentiated (level 0 for no visible lice, level 1 for less than 5 lice, level 2 for 6 to 10, level 3 for 11 to 20 and level 4 for more than 21 individual lice). The ranking score protocol is an attempt to cover the variation from no ectoparasites

TABLE 1

Shorebirds species captured at Salinas. It is specified the common name and family and acronym (ID), N = sample size captured. Flock category (FC) was classified according to Barbosa (1995) as 0 solitary species, 1 species forming flocks between 40 and 99 individuals and 2 = species forming flocks of more than 100 individuals. Body mass (BM) is shown in grams ± standard deviation (SD) and ectoparasites scores (ES) are showed as an average per species ± standard deviation (SD).
[Aves limícolas capturadas en Salinas. En la tabla se especifica el nombre común y el acrónimo (ID) de cada especie, N = tamaño de muestra. El tamaño de bando (FC) se clasificó según la bibliografía de Barbosa (1995) como: 0 especies solitarias, 1 especies que forman bandos entre 40 y 99 individuos, y 2 especies que forman bandos de más de 100 individuos. El peso (BM) se muestra en gramos ± desviación estándar (SD) y los registros de ectoparásitos (ES) se muestran como la media ± desviación estándar (SD) por especie.]

Species	Common Name	Family	ID	N	FC	BM ± SD	ES ± SD
Calidris alpina	Dunlin	Scolopacidae	Cap	37	2	44.7 ± 6.5	2.59 ± 1.04
Calidris alba	Sanderling	Scolopacidae	Cb	4	1	47.5 ± 3.0	2 ± 1.15
Calidris minuta	Little Stint	Scolopacidae	Cm	15	1	25.8 ± 4.8	0.93 ± 1.10
Tringa totanus	Redshank	Scolopacidae	Tt	2	2	126.3 ± 29.8	1 ± 1.41
Calidris ferruginea	Curlew Sandpiper	Scolopacidae	Cf	2	2	56.23 ± 5.7	2 ± 0.0
Charadrius alexandrinus	Kentish Plover	Charadriidae	Chx	9	0	38.66 ± 9.2	1.11 ± 0.93
Charadrius hiaticula	Ringed Plover	Charadriidae	Chh	2	0	49.85 ± 1.4	1 ± 0.0

to high infestation, and provides a straight-forward approach to reducing processing time for each bird (Dietsch, 2002). Body mass was taken by means of a spring balance to the nearest 5 grams and was expressed by grams for each species as shown in table 1.

Flock size for each species was taken from the literature (Barbosa, 1995) because birds were caught at the night and thus it was impossible to infer the flock size at the moment of study and also, to minimize the ecological and environmental variables that were not considered and could influence the size and distribution of birds at the beach (Burger and Gochfeld, 1983; Myers, 1984). Flock sizes were divided into three categories:

(i) Solitary species.
(ii) Species forming flocks between 40 and 99 individuals.
(iii) Species forming flocks of more than 100 individuals, see table 1.

Interspecific comparisons should be carried out using a phylogenetic approach, due to issues of statistical non-independence of species resulting from common ancestry effects (Felsenstein, 1985). To analyse differences between ectoparasites load in relation to flock size, a phylogenetic analysis of variance was performed (PDANOVA; Garland *et al*., 1993) in which each species was assigned to one of the three flock size
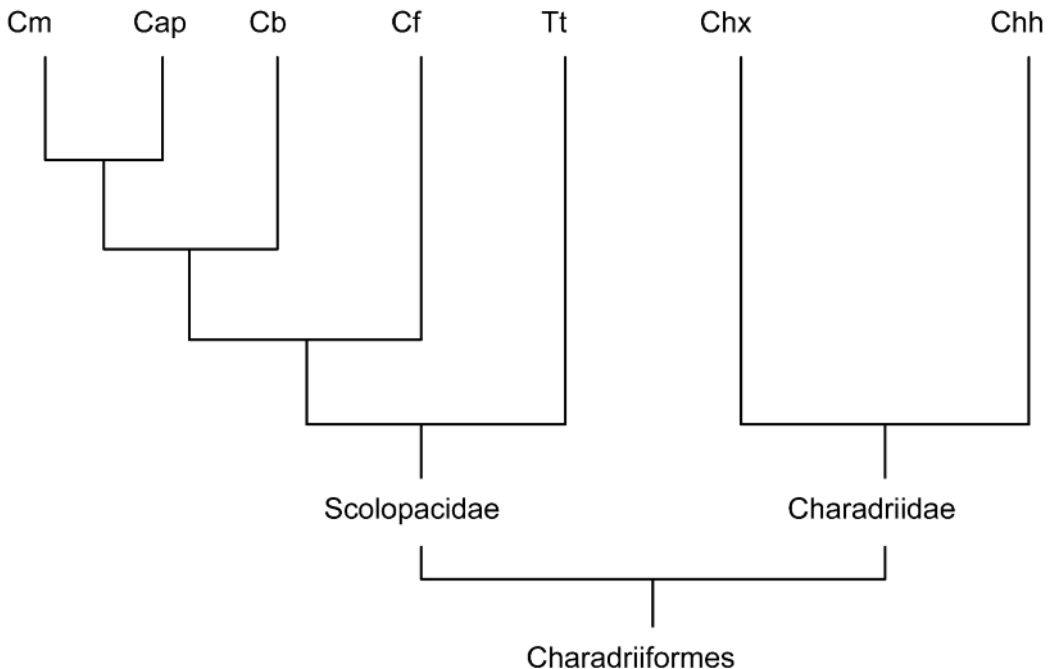

FIG. 1.—Phylogeny of the shorebirds following Thomas *et al.* (2004). The model assumes length branches in the phylogeny equal to one. It is used when exact information of branch length is unknown.
[Árbol filogenético de aves limícolas de acuerdo a la descripción de Thomas et al. (2004). El modelo asume que la longitud de cada rama en la filogenia es igual a 0. Esta suposición se utiliza cuando no se conoce la longitud exacta de cada rama.]

categories (table 1). This method uses Monte Carlo simulations of a trait of interest (ectoparasites loads in this case) along the phylogeny to create a phylogenetically correct and empirically scaled null distribution of F statistics. A conventional ANOVA is then performed on the data with the critical value derived from the 95th percentile of the simulated F distribution (Garland *et al.*, 1993). Using PDSIMUL program, 1,000 simulations were performed under a speciation model of evolutionary change. This model assumes length of branches in the phylogeny to be all equal to one and should be used when exact information of branch length is unknown. The phylogeny (fig. 1) has been taken from Thomas *et al.* (2004).

Relationship between the estimated ectoparasites loads and body mass of shorebird species were analysed using the PDAP software (Garland *et al.*, 1992).

RESULTS

Seventy one individuals of seven species of waders were captured and classified into three flock categories (table 1). Ectoparasites found were chewing lice (Phthiraptera, formerly known as Mallophaga) but they could not be identified at species level. Of those 71 individuals checked for ectoparasites, 84.5% carried ectoparasites at different levels of abundance measured as percentage per level: 22.5% showed level 1, 29.5% level 2, 19.7% level 3 and 12.6% level 4. Ringed Plover (*Charadrius hiaticula*) was the species that showed the highest abundance of chewing lice (table 2).

One-way ANOVA shows differences in the abundance of chewing lice in relation to flock size, with species forming the larger flocks also displaying the highest levels of abundance ($F_{2, 68} = 13.9$, $P < 0.001$). Interspe-

TABLE 2

Percentage of ectoparasites at different levels of abundance carried by each shorebirds species. Level 0 for no visible lice, level 1 for less than 5 lice, level 2 for 6 to 10, level 3 for 11 to 20 and level 4 for more than 21 individual lice.
[Porcentaje de los ectoparásitos clasificados en niveles de abundancia que fueron encontrados en las especies de aves limícolas. Nivel 0: no detección de ectoparásitos, nivel 1: menos de 5 ectoparásitos, nivel 2: entre 6 y 10, nivel 3: entre 11 y 20, y nivel 4: más de 21 ectoparásitos.]

Common Name	ID	0	1	2	3	4
Dunlin	Cap	2.7	10.8	32.4	32.4	21.6
Sanderling	Cb	0	50	50	0	0
Little Stint	Cm	40	40	13.3	0	6.7
Redshank	Tt	50	0	50	0	0
Curlew Sandpiper	Cf	0	0	100	0	0
Kentish Plover	Chx	33.3	22.2	44.4	0	0
Ringed Plover	Ch	0	100	0	0	0

cific comparisons considering phylogenetic analysis of variance (PDANOVA, Garland *et al.*, 1993) showed non significant differences (PDANOVA, P = 0.06).

No significant relationship was found between body mass of shorebirds and chewing lice load (r = –0.16, n = 6, p = 0.73). Inclusion of body mass in the analysis did not affect the results of variation of chewing lice infestations (PDANOVA, P = 0.10).

DISCUSSION

Our results are different depending of whether we use conventional ANOVA without phylogenetic correction or phylogenetically corrected ANOVA (PDANOVA, Garland *et al.*, 1993). The former gives highly significant results suggesting that a close relationship can be established between the flocking behaviour and the abundance of chewing lice, while the later shows non significant results. Phylogenetically controlled methods should be used because closely related species share common traits due to their evolution from a common ancestor, then, species cannot be used as independent data for statistical analyses (Felsenstein, 1985). Therefore, our results show that the abundance of chewing lice is not related with the flocking behaviour of the species.

Several studies of the relationship between sociality and parasite abundance give contradictory results. Some studies support the prediction that birds living in aggregations should be highly parasitized (Hoogland, 1979; Brown and Brown, 1986; Moore *et al.*, 1988; Côte and Poulin, 1995 among others), while others did not find such an association (Poiani, 1992; Rózsa *et al.*, 1996; Rekasi *et al.*, 1997; Rózsa, 1997).

Some studies reporting positive results between social behaviour and parasite load have been carried out at the intraspecific level (Ezenwa, 2004), however when inter-specific comparative analyses are performed and phylogenetic control is used, as we did in the present study, negative results are obtained (see also Poiani, 1992). One potential explanation is that intraspecific studies whose results are negative may not published due to them being less likely to be accepted in a journal, the so-called "file drawer problem" (Csada *et al.*, 1996). Consequently, the perception of the relationship between group size and parasite load could be biased towards the existence of such relationship. In fact, in comparative analyses, including the present work, where several species are studied, results have shown that the relationship is not always found (Poiani, 1992; Rózsa, 1997).

Our results notwithstanding, we should caution against the easy generalization that a relationship between parasite load and sociality does not exist. Whiteman and Parker (2004) suggest that the relationship between host density and parasite abundance should be specific to each parasite taxon due to differences in the parasite biological traits such as transmissibility for instance. In this context, predictions on the relationships between parasite load abundance and host sociality can be fulfilled in more mobile parasites such as fleas, ticks or flies than less mobile parasites such as the chewing lice (Rózsa, 1997). Alternatively, differences in other biological traits than flocking behaviour could also explain differences in the predicted relationships. For example, the roosting behaviour could favour ectoparasite transmission more than flocking behaviour. This could explain why in our study, species like the Sanderling which roosts at migration stopover sites may contain several thousand individuals (Ferns, 1980), showed a high parasite load than expected from its flocking behaviour. In fact, collective roosting may facilitate the transfer of Mallophaga (Doyle *et al.*, 2005). But, in the other hand, variables related to the body conditions, such as body mass of shorebirds which in other studies showed relationships

to ectoparasites in birds (Booth *et al*., 1993; Rózsa, 1997) in the present work were not related. As other reports in fact, body mass did not explain the variation of chewing lice infestations (Lee and Clayton, 1995; Darolova *et al*., 2001; Doyle *et al*., 2005; Hughes and Page, 2007), the inclusion of body mass in the analyses did not modify the ectoparasite results.

In summary, our results derived from an interspecific analysis that controlled for phylogenetic effects, do not support a positive relationship between group size and ectoparasite load at least in the chewing lice. However, our results should be interpreted cautiously mainly, since the number of shorebird species and individuals sampled were relatively low.

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