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Ectoparasite community structure on three closely related seabird hosts: a multiscale approach combining ecological and genetic data

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Parasite communities can be structured at different spatial scales depending on the level of organization of the hosts; hence, examining this structure should be a multiscale process. We investigated ectoparasite community structure in three closely related seabird hosts, the Mediterranean Cory's shearwater *Calonectris diomedea diomedea*, the Atlantic Cory's shearwater *C. d. borealis* and the Cape Verde shearwater *C. edwardsii*. This community was composed of three lice (*Halipeurus abnormis*, *Austromenopon echinatum* and *Saemundssonia peusi)* and one flea species (*Xenopsylla gratiosa*), and was considered at the infra-, component and regional community levels. We examined temporal and spatial structuring of the infracommunities, the influence of host aggregation and body condition on the component community, and the effect of genetic and geographic connectivity among host populations on the regional community. Ectoparasite infracommunities showed substantial species overlaps in temporal patterns of abundance, but species were spatially segregated within the host body. Within component communities, all ectoparasite species showed an aggregated distribution in abundance. However, aggregation patterns and their relationships with the spatial distribution of hosts within the breeding colony differed among ectoparasite species, mainly reflecting ecological differences between fleas and lice. At the regional scale, similarity in ectoparasite communities correlated with geographic distances among host colonies, but not with genetic distances. This result suggests differences in climate and habitat characteristics among host localities as a major determinant of regional communities, rather than host connectivity. Taken together, our results highlight the importance of the geographic distribution of host breeding colonies and the spatial segregation within the host body as key factors in determining ectoparasite community structure in *Calonectris* shearwaters.

Parasite assemblages interact with their hosts at different spatial scales. The structure of parasite communities may result from the interplay between the intrinsic characteristics of each parasite species, the extrinsic features of their habitat patch (i.e. the host, Poulin 2006), the off-host environment (i.e. host habitat, Krasnov et al. 2002, 2005b), as well as the connectivity among host populations (Poulin and Morand 1999, Morand and Guégan 2000). However, the influence of each factor remains poorly understood and greatly depends on the level of organization being considered. Three hierarchies have been commonly defined for parasite assemblages in which different spatial and temporal factors may act: infra-, component, and regional communities (Guégan et al. 2004).

Infracommunities include all parasite populations within an individual host. They can be temporally and spatially structured. Temporal variation in parasite infracommunities can be coupled with the breeding cycle of the host (Figuerola 2000, Clayton and Walther 2001). Spatial segregation is promoted by resource heterogeneity within the host body, to avoid competition and favouring coexistence among parasite species (Mouillot et al. 2003).

Component communities include all infracommunities within the same host population. Their structure may result from differences in host susceptibility to infestation or from differences in parasite exposure among individual hosts (Poulin 1998). Susceptibility to infestation has been shown to correlate with host traits, such as body size and condition (Whiteman and Parker 2004a). Likewise, host sex can also affect the ability to cope with parasite infestation, for example owing to immunological or body size differences between males and females (Poulin 1996). Exposure can be mediated by the spatial aggregation of hosts because it affects the probability of parasite transmission, leading to differences in parasite infestation (Rózsa et al. 1996, Rózsa 1997, Rékási et al. 1997, Tripet et al. 2003).

The regional community is composed of all component communities within a host species. At this level, structure is mainly determined by habitat characteristics (Krasnov et al. 1997, 2004a, b, 2005b), host population size and density

(Rózsa et al. 1996, Rózsa 1997, Rékási et al. 1997, Arneberg et al. 1998, Calvete et al. 2003, Lopez 2005), and host connectivity (Poulin and Morand 1999, Morand and Guégan 2000). For example, climate has been shown to play an important role in shaping ectoparasite species distributions (Krasnov et al. 2005a). Host connectivity among populations can favour parasite dispersal promoting the homogenization of parasite communities (Poulin and Morand 1999, Proctor and Jones 2004). Geographic distance among host populations has often been used as a proxy for host connectivity (Goüy de Bellocq et al. 2002, Krasnov et al. 2005b). However, hosts do not necessarily disperse according to distance due to geographic barriers or other factors acting on specific routes, such as stopover areas or prevailing winds. Moreover, climate and habitat characteristics also change with geographic distances. In this context, genetic similarity among host populations can offer a complementary perspective on host connectivity to disentangle the effect of each factor and thus help us understand the forces structuring parasite communities.

Seabirds, and especially petrels, offer a useful model to investigate factors influencing the structure and composition of parasite communities at different scales. Seabird feathers provide a heterogeneous environment which many taxa of ectoparasites have colonized (Janovy Jr 1997). Petrels are particularly amenable to studying the effects of host isolation, as parasite dispersal can be temporally limited to the reproductive periods and spatially structured among remote oceanic islands where they breed, grouped into archipelagos and oceans. In addition, monogamous breeding is widespread among petrels and most species show natal and breeding site fidelity (Brooke 2004), which can limit opportunities for parasite transmission. As a consequence, connectivity among seabird populations is expected to influence the structure of their ectoparasite communities at different scales.

In the present study, we examine temporal and spatial structure of three lice species (*Halipeurus abnormis*, *Austromenopon echinatum* and *Saemundssonia peusi*) and one flea species (*Xenopsylla gratiosa*) at three different levels of parasite organization on three closely related seabird taxa, the Mediterranean Cory's shearwater *Calonectris diomedea diomedea*, the Atlantic Cory's shearwater *C. d. borealis* and the Cape Verde shearwater *C. edwardsii*. In particular, we aim; 1) to evaluate the degree of temporal and spatial segregation among parasite species within parasite infracommunities, 2) to assess the influence of host aggregation, sex and body condition on the structure of the component community, and 3) to investigate the effect of climate and host connectivity, as indicated by both geographic distance and genetic similarity among populations, on the regional ectoparasite community structure throughout the entire geographic range of the three seabird taxa.

Material and methodology

Host-parasite system

Cory's shearwater *Calonectris diomedea* is a colonial and monogamous seabird breeding on islands along the Mediterranean Sea and Macaronesic archipelagos (Azores, Canary Islands, Madeira Island and Cape Verde). It comprises two subspecies that can be differentiated morphologically, the Atlantic *C. d. borealis* and the Mediterranean *C. d. diomedea* subspecies. Formerly, the species *C. edwardsii*, from Cape Verde Islands, was also considered a subspecies but it is now regarded as a full species (Gómez-Díaz et al. 2006). Cory's and Cape Verde shearwaters begin moulting at the end of the chick-rearing period, before departing from the breeding grounds to the wintering areas (Monteiro and Furness 1996, unpubl.). Despite the fact that the all three taxa exhibit segregated breeding distributions, recent work indicates a substantial degree of mixing among *Calonectris* breeding populations in the wintering areas (González-Solís et al. 2007), suggesting a potential for ectoparasite transmission (Gómez-Díaz et al. 2007).

Cory's and Cape Verde shearwaters share three louse species, known only from these taxa (Price et al. 2003): *Halipeurus abnormis* (Ischnocera: Philopteridae), *Saemundssonia peusi* (Ischnocera: Philopteridae), and *Austromenopon echinatum* (Amblycera: Menoponidae) (all lice identified by R. Palma). Cory's and Cape Verde shearwaters also share one species of flea *Xenopsylla gratiosa* (Siphonaptera: Pulicidae) (identified by J. C. Beaucournu), which is recorded from the seabird genera: *Calonectris*, *Puffinus,* and *Hydrobates* (Beaucournu et al. 2005). In addition, one species of soft tick *Ornithodoros maritimus* (Hoogstraal et al. 1979) (Acarina, Ixodoidea, Argasidae) (identified by A. Estrada-Peña) has also been recorded from *Calonectris* and, at least five species of mites have been identified: *Microspalax brevipes*, *Brephosceles puffini*, *Zachvatkinia puffini*, *Brephosceles* sp. and *Zachvatkinia* sp. (Acari: Alloptidae and Avenzoariidae; identified by H. Proctor and S. Mironov). Due to relative prevalence and abundance; we only considered the louse and flea species in the present study.

Chewing lice are permanent ectoparasites which complete their entire life cycle on the host where they feed mainly on feathers, dead skin, blood or secretions. As they are incapable of independent mobility, transmission occurs during periods of direct contact between hosts (Clayton and Tompkins 1994, Lee and Clayton 1995). On the contrary, fleas are obligatory blood feeders closely associated with the host's breeding environment (nest). In most fleas, all stages of the breeding cycle occur off of the host body, except for the adults, which feed on the host (Marshall 1981).

Study sites and field methods

We sampled breeding birds from 15 localities of the three *Calonectris* taxa across Mediterranean and NE Atlantic regions from 2001 to 2005 (Fig. 1). We estimated the total number on a bird from one minute visual counts on six body regions: belly, breast, head, left wing, mantle and tail. We recorded 3 lice (*H. abnormis, A. echinatum* and *S. peusi*) and 1 flea species (*X. gratiosa*) (Table 1). To assess whether visual counts reflected the total abundance of parasites, we fully removed ectoparasites from a sample of 30 birds using the dust-ruffling method described by Clayton and Walther (1997), as this method has been shown to be an accurate predictor of total abundance of ectoparasites (Clayton and Drown 2001). We compared

Table 1. Abundance and prevalence of three louse and one flea species on *Calonectris* hosts in relation to the breeding colony. Values are means ± SD. Numbers of shearwaters sampled in each breeding colony are shown in brackets. N refers to the number of sampled colonies for each host taxa.

Host Taxa	Island population	Archipelago/ area	Geographic coordinates		Lice						Flea	
					Halipeurus abnormis		*Austromenopon echinatum*		*Saemundssonia peusi*		*Xenopsylla gratiosa*	
			Latitude	Longitude	Mean abundance	Prevalence	Mean abundance	Prevalence	Mean abundance	Prevalence	Mean abundance	Prevalence
C.d. borealis	St. Maria (Vila) (90)	Azores Is.	36°94′N	25°17′W	27.20 ± 12.52	100.0	2.92 ± 2.85	82.2	3.36 ± 3.09	88.9	2.38 ± 4.96	46.5
	S. Miguel (8)	Azores Is.	37°71′N	25°44′W	14.38 ± 7.60	100.0	3.38 ± 2.39	87.5	4.25 ± 4.20	75.0	2.13 ± 1.96	62.5
	Faial (15)	Azores Is.	38°52′N	28°75′W	18.87 ± 11.10	100.0	0.80 ± 1.21	40.0	2.20 ± 3.05	53.3	0.20 ± 0.56	13.0
	Graciosa (34)	Azores Is.	39°05′N	27°95′W	30.24 ± 19.86	100.0	3.56 ± 6.82	73.5	1.97 ± 2.33	67.6	0.38 ± 1.74	8.8
	Corvo (25)	Azores Is.	39°67′N	31°11′W	17.60 ± 10.52	100.0	1.32 ± 2.06	52.0	2.32 ± 2.72	68.0	0.20 ± 0.81	8.0
	G. Canaria (107)	Canary Is.	27°85′N	15°79′W	10.07 ± 7.74	97.2	0.34 ± 0.76	22.9	0.33 ± 0.75	20.2	3.39 ± 6.67	56.9
	Lanzarote (35)	Canary Is.	29°29′N	13°54′W	31.49 ± 21.17	100.0	7.31 ± 7.90	88.6	0.77 ± 1.46	37.1	2.94 ± 4.44	74.3
	Tenerife (9)	Canary Is.	28°45′N	16°23′W	20.22 ± 7.90	100.0	3.67 ± 3.00	88.9	3.11 ± 3.30	88.9	2.00 ± 1.58	88.9
	Almeria (31)	Mediterr. coast	37°35′N	1°65′W	39.26 ± 20.80	100.0	4.19 ± 5.13	71.0	1.65 ± 2.51	45.2	0.48 ± 1.00	25.8
N = 9	Total				23.26 ± 9.36	99.69 ± 0.93	3.05 ± 2.11	67.40 ± 23.86	2.22 ± 1.24	60.5 ± 23.4	1.57 ± 1.26	42.7 ± 30.1
C.d. diomedea	Mallorca (29)	Balearic Is.	39°58′N	2°37′E	16.66 ± 9.97	100.0	1.17 ± 1.20	65.5	0.41 ± 0.73	31.0	0.41 ± 0.78	27.6
	Ibiza (47)	Balearic Is.	38°96′N	1°20′E	26.38 ± 11.87	100.0	0.45 ± 0.80	29.8	0.97 ± 2.17	36.2	1.34 ± 1.85	51.1
	Cabrera (20)	Balearic Is.	39°20′N	2°98′E	25.20 ± 12.28	100.0	0.50 ± 1.10	25.0	0.95 ± 1.43	50.0	0	0
	Menorca (47)	Balearic Is.	39°80′N	4°29′E	19.74 ± 11.38	100.0	0.32 ± 0.73	21.3	0.66 ± 1.09	36.2	0.15 ± 0.63	8.5
N = 4	Total				22.00 ± 4.58	100.0	0.56 ± 0.38	35.4	0.75 ± 0.27	38.3	0.48 ± 0.60	21.8
C. edwardsii	Raso (47)	Cape Verde	16°61′N	24°59′W	17.89 ± 10.47	100.0	5.57 ± 4.37	91.4	1.74 ± 2.31	62.9	0.26 ± 0.61	20.0
	Boavista (35)	Cape Verde	15°98′N	22°78′W	28.57 ± 21.26	100.0	8.23 ± 7.75	93.6	0.74 ± 1.13	46.8	1.11 ± 1.82	40.4
N = 2	Total				23.23 ± 7.55	100.0	6.90 ± 1.88	92.5	1.24 ± 0.71	54.8	0.69 ± 0.60	30.2

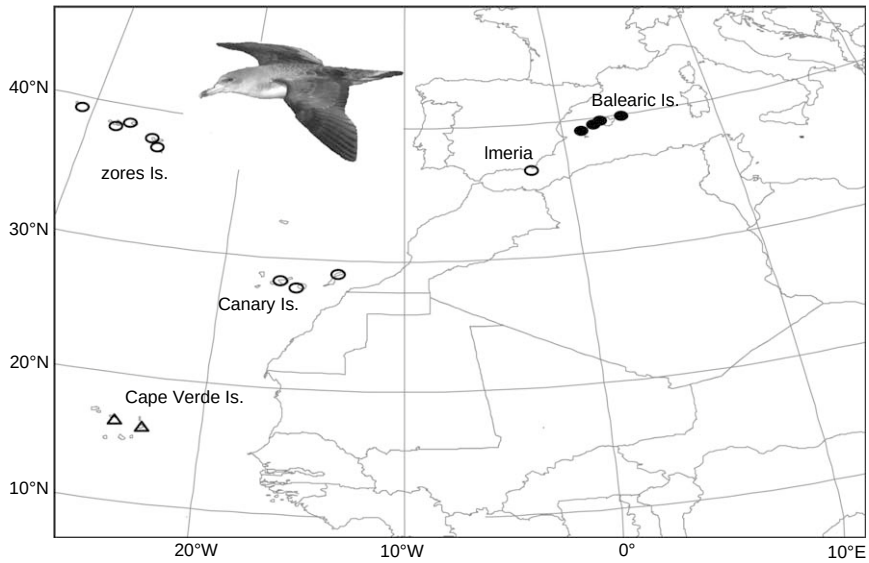

Figure 1. Breeding colonies of Mediterranean (●) and Atlantic (○) Cory's shearwaters and Cape Verde shearwaters (Δ) sampled across their geographic distribution.

dust-ruffling and visual counts using a least square linear correlation.

Genetic analysis

Genetic analyses were performed on 38 Mediterranean Cory's, 75 Atlantic Cory's and 20 Cape Verde shearwaters from 11 breeding colonies. DNA was isolated from ethanol-preserved whole blood using the salting-out extraction protocol from Bruford et al. (1998). We amplified a 293 bp fragment of Domain I of the mitochondrial control region of all three *Calonectris* taxa using three specific primers previously designed for the species (Gómez-Díaz et al. 2006): either CAL2H (5′CATCCCATCCAACTTA AG3′) or CAL4H (5′AGCCTATGTATGGATGTGC AT3′) was used in conjunction with CAL1L (5′GGTC CTGAAGCTAGTAATAC3′). Reaction conditions and automated sequencing followed those described by Gómez-Díaz et al. (2006).

We estimated Φ_{ST} genetic distances among *Calonectris* breeding colonies using ARLEQUIN 3.0 (Excoffier et al. 2005). To visualize the genetic relationships among colonies, we generated a population similarity tree using the neighbour-joining analysis of the Φ_{ST} pairwise distances using NTSYSpc package ver. 2.1 (Rohlf 1997).

Parasite distribution

Prevalence was calculated as the proportion of birds infected by a given parasite species. Mean abundance was calculated as the average number of ectoparasite individuals of a given species per individual host or body area (Bush et al. 1997). For subsequent analyses, mean abundance data were log transformed ($\log_{10}(x+1)$) to approach normality. Mean abundance values are reported as mean number of parasites $\pm$ standard error and prevalence values are reported as percentages of occurrence. We restricted all analyses on infra-, component and regional community levels (except those on seasonal abundance or were otherwise indicated) to visual counts performed during the incubation period. We selected this period to avoid a potential effect of the moult on the detection ability of ectoparasites (Moyer et al. 2002), to homogenize the sampling period and to optimize our probability of detection by focusing on a period when ectoparasites are generally abundant (see results on the seasonal abundance of parasites).

Infracommunity

At the infracommunity level, we first examined spatial patterns of ectoparasite infestation (all parasites on a host individual) for 109 Atlantic Cory's shearwaters from one breeding colony (Veneguera, Canary Is.), following procedures described by Reed et al. (2000). We measured the surface (in cm^2) of each of the six body areas considered in the visual counts of parasites. Assuming a null model of uniform ectoparasite distribution, we compared the ectoparasite counts of each area against the expected number of ectoparasite individuals of each species for each area based on the size of that area using a chi-square test. To test for parasite exclusion, that is, whether the presence of one parasite interferes with that of a competing species, we measured correlations of mean abundances for each pair of ectoparasite species for each host body area. Next, we investigated temporal patterns of ectoparasite abundance in a subset of 17 Cory's shearwaters from Veneguera (Canary Is.) using a MANOVA test. For this analysis, the same 17 individuals were monitored at 5 different periods covering the entire breeding season: pre-laying (scored between 20 and 30 d before laying), egg-laying (scored between 0 and 10 d after laying), mid-incubation (scored between 15 and 20 d after laying), egg-hatching (scored between 0 and 5 d after hatching) and chick-rearing (scored between 50 and 60 d after egg-hatching).

Component community

At the component community level, we investigated the effects of host aggregation by quantifying differences in mean abundance of infestation for each ectoparasite species among shearwater individuals from one Atlantic breeding colony (90 birds from Vila, Azores Is.) using ANOVA. To test for differences between sexes, we compared ectoparasite abundances in 37 and 43 breeding mates from Vila islet (Azores) and Veneguera (Canary Is.), respectively, using paired t-tests. Within the Vila colony, we examined aggregation patterns for each ectoparasite species using Green's coefficient of dispersion (Krebs 1989). In addition, we tested the effects of nest density on mean infestation in 39 birds breeding at this same colony. That is, we correlated the mean abundance of each ectoparasite species with nest density, as measured by the number of nests within 1, 3, 5 and 10 m radii. Finally, we examined spatial patterns in ectoparasite prevalence and mean abundance within the component community. We investigated whether proximity among host breeding pairs could explain similarity in their infracommunities. At one breeding colony (Vila, Azores Is.), we tested the relationship between distance among nests and similarity in ectoparasite infracommunities of breeding birds using the Mantel test (Mantel 1967, Mantel and Valand 1970) implemented in the zt program (Bonnet and Van de Peer 2002). The significance test of the r statistic was determined by a nonparametric randomization procedure. Similarity in prevalence was measured using both the Jaccard and Morisita-Horn indices. Similarity in mean abundance was calculated as a Euclidean distance.

Secondly, at this level, we examined the effect of host body condition on mean infestation in 54 breeding birds from the Vila colony (Azores Is.), using ANCOVA (the model considered weight and body size as covariables and sex as a factor). Birds were sexed using molecular methods described by Fridolfsson and Ellegren (1999). For birds of known sex, a body size covariable was calculated as the first axis of a principal component analysis (PC1 which accounted for 90% of the total variance) on 5 body measurements (tarsus, wing length, cranium-bill length, bill height and bill-height at nostril).

Regional community

At the regional level, we examined differences in infestation parameters among component communities from 11 out of 14 host breeding colonies (those sampled during the incubation period) distributed across the host geographic range. As breeding colonies were sampled in different years and annual availability of host resources may affect ectoparasite abundance, we first assessed temporal repeatability at the component community level. We compared the mean abundance of each ectoparasite species between two consecutive years (2004 and 2005) in a subset of 33 individuals sampled at the same breeding period (pre-laying) and used the Wilcoxon paired test to control for host individual effects.

We calculated prevalence and mean abundance at two spatial levels: for each breeding colony and for each host taxa. To test whether ectoparasite abundance differs among species and across the breeding range of their host we conducted MANOVA tests at two spatial levels; among host taxa and among host breeding colonies. To account for inter-individual variability in body size, initial models included a body size covariable (PC1 calculated as described above). Since no significant effect was detected (see results), further models did not include the body size covariable.

To examine similarity in parasite communities among host breeding colonies, we calculated a dissimilarity matrix from the chi-square distances based on the mean abundance of each parasite species at each breeding colony for all pairwise combinations of breeding colonies. We constructed a cladogram from the dissimilarity matrix using the neighbour-joining clustering analysis implemented in the NTSYSpc package ver. 2.1 (Rohlf 1997). Cladograms based on Morisita similarity indices were also built and gave similar results (data not shown). Similarity of parasite communities were also calculated for prevalence data, using Euclidean distances among all pairwise breeding colonies and building a cladogram with UPGMA clustering analysis (NTSYSpc package ver. 2.1 (Rohlf 1997)). Neighbour-joining cladograms based on Rekonen similarities were also built for prevalence data and gave similar results (data not shown).

To investigate whether genetic relationships among host colonies were related to similarity patterns of prevalence and mean abundance of the ectoparasite component communities, we used two proxies of population connectivity: 1) genetic distances among host breeding colonies; and 2) by sea geographic distances among host breeding colonies. To examine the correlation between the two indexes of population connectivity and patterns of mean abundance and prevalence, we applied a partial Mantel test analysis using the program zt (Bonnet and Van de Peer 2002). The goal was to test the correlation between matrices A and B while controlling the effect of a third matrix C, in order to remove spurious correlations (Smouse et al. 1986). First, we correlated ectoparasite abundance and prevalence with by-sea geographic distances while controlling for host genetic distances. Second, we correlated abundance and prevalence with host genetic distances while controlling for by-sea geographic distances among colonies. A permutation approach was applied that was developed by Anderson and Legendre (1999).

Results

Ectoparasite species and visual vs dust-ruffling counts

We sampled parasites from 585 individual birds from 9 Atlantic Cory's, 4 Mediterranean Cory's and 2 Cape Verde shearwaters breeding colonies (Table 1). Correlations between visual counts of the four ectoparasite species and the number of parasites obtained after applying the dust-ruffling method on 30 shearwaters were highly significant (all $p < 0.001$ for the four ectoparasite species). The R^2 of those correlations ranged from 0.61 to 0.78, indicating that visual counts provide a reliable estimate of total mean abundance of ectoparasites.

Temporal and spatial ectoparasite infracommunity structure

We found significant differences in distribution and mean abundance among ectoparasite species in relation to host

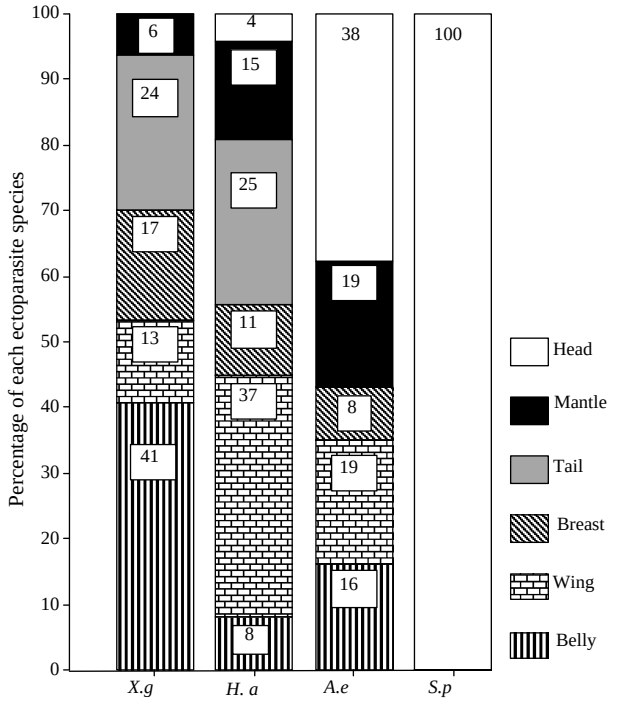

Figure 2. Mean percentage of ectoparasite species on each of 5 host body regions for 109 Cory's shearwaters from Gran Canaria (Canary Is.) sampled during the incubation period. *X.g.* = *Xenopsylla gratiosa*, *A.e.* = *Austromenopon echinatum*, *S.p.* = *Saemundssonia peusi* and *H.a.* = *Halipeurus abnormis*.

body area (*H. abnormis*: $\chi^2 = 3567.97$, $p < 0.001$, *A. echinatum*: $\chi^2 = 82.86$, $p < 0.001$, *S. peusi*: $\chi^2 = 11.82$, $p < 0.001$, *X. gratiosa*: $\chi^2 = 862.35$, $p < 0.001$). All four ectoparasite species occurred in specific areas on the host body (Fig. 2). Fleas were mainly distributed on the belly, tail and breast; the louse *H. abnormis* mostly appeared on the wings, mantle and tail; *S. peusi* appeared to be head specific and *A. echinatum* mainly occurred on the head, mantle and wings. We found a significant and positive correlation between the mean abundances of *A. echinatum* and *H. abnormis* ($R_s^2 = 0.09$, $p < 0.01$). For each body area, mean abundance of *A. echinatum* correlated with abundances of *H. abnormis* on the mantle ($R_s^2 = 0.04$, $p < 0.05$) and *S. peusi* on the head ($R_s^2 = 0.05$, $p < 0.05$).

We found significant changes in the mean abundance of the ectoparasite species over the breeding season (Fig. 3). Among the 17 shearwaters monitored during the entire breeding cycle, *H. abnormis* and *A. echinatum* abundances significantly decreased from pre-laying to chick rearing periods (Fig. 3A–B, *H. abnormis*: $F_{4,13} = 21.79$, $p < 0.001$; *A. echinatum*: $F_{4,13} = 5.16$, $p < 0.02$). The mean abundance of the flea species *X. gratiosa* also decreased from the beginning to the end of the breeding season (*X. gratiosa*: $F_{4,13} = 7.90$, $p < 0.05$), but the peak of greatest mean abundance for this species corresponded to the egg-laying period (Fig. 3D). On the contrary, *S. peusi* mean abundance showed no significant differences throughout the study period (Fig. 3C, *S. peusi*: $F_{4,13} = 0.49$, $p = 0.74$).

Spatial structure in the ectoparasite component community

At Vila islet (Azores Is.), the most prevalent and abundant parasite species was *H. abnormis*, which was observed in 100% of the birds and had high abundances representing 77.8% of the parasite individuals observed (prevalence; *A.e*: 82.2%, *S.p*: 88.9%, *X.g*: 45.6%, relative abundance; *A.e*: 7.6%, *S.p*: 8.8%, *X.g*: 5.9%). However, differences in abundance of each ectoparasite species were not homogeneous among individual hosts, as indicated by a significant interaction between individual host and parasite species ($F_{1,89} = 717.85$, $p < 0.001$). In fact, the abundance distribution among Cory's shearwaters for all ectoparasite species was aggregated (Green's index > 1), but the degree greatly differed among ectoparasite species. Green's index of dispersion values for the flea *X. gratiosa* were the greatest (9.32), whereas among louse species, *S. peusi* and *A. echinatum* showed lower values than *H. abnormis* (*H.a* = 4.76, *A.e* = 1.77 and *S.p* = 1.85). The correlation between the spatial distribution of nests, as measured by the distance among host nests, and the similarity in ectoparasite communities was not significant (Mantel: $r_{1,2} = 0.04$, $p = 0.32$). Nevertheless, host nest aggregation, as measured by number of neighbouring nests within 3 m, was correlated with the mean infestation of nesting birds for the flea species (flea: $R^2 = 0.15$, $p < 0.05$; lice species all $R^2 < 0.01$, all $p > 0.10$).

Overall, ectoparasite mean abundances of male and female Cory's shearwaters from Vila islet (Azores) and Veneguera (Canary Is.) were similar for all species (t-student, all $p > 0.05$). However, only the mean abundance of fleas (*X. gratiosa*) and the louse *A. echinatum* were significantly correlated between breeding mates of Vila islet (Azores Is.) (*X. gratiosa*: $R^2 = 0.59$, $p < 0.001$; *A. equinatum*: $R^2 = 0.14$, $p < 0.01$; *H. abnormis*: $R^2 = 0$, $p = 0.96$; *S. peusi*: $R^2 = 0.03$, $p = 0.34$). This pattern changed in the Veneguera colony where the correlations were significant (*X.g.*: $R^2 = 0.37$, $p < 0.001$; *H.a*: $R^2 = 0.17$, $p < 0.01$; *A.e.*: $R^2 = 0.01$, $p = 0.59$; *S.p.*: $R^2 = 0.01$, $p = 0.59$). Thus, correlations in ectoparasite abundance between males and females were only consistent for *X. gratiosa*.

Finally, body condition did not correlate with the mean abundance of infestation for any of the four ectoparasite species considered (*X.g.*: $F_{1,50} = 0.17$, $p = 0.68$; *H.a*: $F_{1,50} = 1.03$, $p = 0.32$; *A.e.*: $F_{1,50} = 1.64$, $p = 0.21$; *S.p.*: $F_{1,50} = 0.93$, $p = 0.34$). In addition, there was no relationship between breeding mates in body condition or body size in either of the two localities examined (all $p > 0.05$).

Spatial structure in ectoparasite regional community

At Veneguera (Canary Is.), ectoparasite abundance on 33 shearwaters scored during the pre-breeding period in two consecutive years differed only for *A. equinatum* (*H. abnormis*, year 2004 = 9.33 ± 1.0, year 2005 = 14.76 ± 1.64; *S. peusi*, year 2004 = 4.45 ± 0.58, year 2005 = 7.85 ± 1.11; *X. gratiosa*, year 2004 = 4.27 ± 1.12, year 2005 = 2.21 ± 0.51; student's t tests, all $p > 0.05$; *A. equinatum*, year 2004 = 0.24 ± 0.12, year 2005 = 0.85 ± 0.26, $p = 0.01$). Although a year effect can not be ruled

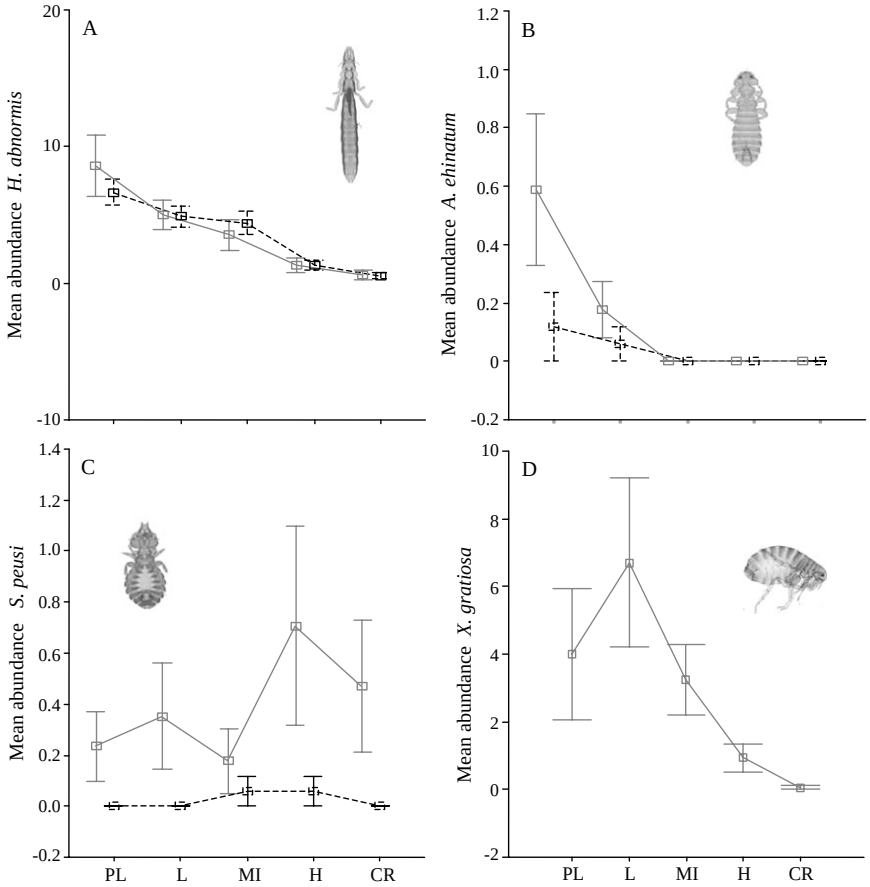

Figure 3. Ectoparasite abundance in 17 Cory's shearwaters from Veneguera (Canary Is.) throughout the breeding season: (A) *Halipeurus abnormis*, (B) *Austromenopon echinatum*, (C) *Saemundssonia peusi* and (D) *Xenopsylla gratiosa*. PL: pre-laying, EL: egg-laying, MI: mid-incubation, H: hatching, and CR: chick-rearing stages. Lines indicate mean values for adult (continuous and grey line) and nymphal ectoparasites (discontinuous lines). Bar intervals indicate standard errors.

out, our results suggest a relatively low interannual variability in parasite abundances, suggesting that different sampling years for different breeding colonies should not significantly bias results. Thus, to test whether ectoparasite mean abundance differs among parasite species and host taxa, we conducted a multivariate analysis of variance (MANOVA). We found a significant interaction between ectoparasite species and host taxa (Wilks' $\lambda = 0.44$, $F_{5.6,1101} = 29.93$, $p < 0.001$), which indicates that the mean abundance of each ectoparasite species differs depending on the host taxa. Therefore, we tested for differences in ectoparasite mean abundance among host colonies for each host taxa separately. We found significant differences in mean abundance among ectoparasite species for the three host taxa and among host colonies for the Mediterranean Cory's shearwater. However, in all cases we found a significant interaction between ectoparasite species and host breeding colony, suggesting that differences in the abundance of each ectoparasite species are not homogeneous among host breeding colonies (Fig. 4, Atlantic Cory's shearwater: species, $F_{2.6,443} = 162.70$, $p < 0.001$; host colony, $F_{4,168} = 1.75$, $p = 0.14$; species × host colony, $F_{10.5,1078} = 7.76$, $p < 0.001$; Mediterranean Cory's shearwater: species, $F_{2.8,391} = 705.62$, $p < 0.001$; host colony, $F_{3,139} = 7.60$, $p < 0.001$; species × host colony, $F_{8.4,391} = 12.28$, $p < 0.001$; Cape Verde shearwater: species, $F_{2.7,218} = 225.24$, $p < 0.001$; host colony, $F_{1,80} = 2.52$, $p = 0.12$; species × host colony, $F_{2.7,218} = 5.37$, $p < 0.05$).

Geographic distances among host breeding colonies were significantly correlated with the similarity index of ectoparasite communities, based on both mean ectoparasite abundance and prevalence (Fig. 5, partial Mantel test on mean abundance data: $r_{1,2} = 0.71$, $p < 0.001$; partial Mantel test based on prevalence data: $r_{1,2} = 0.04$, $p < 0.05$). Conversely, we did not find a correlation between either ectoparasite mean abundance or prevalence and host genetic distances (mean abundance: $r_{1,2} = -0.022$, $p = 0.497$; prevalence: $r_{1,2} = 0.073$, $p = 0.297$).

Discussion

Infracommunity structure

Ectoparasite infracommunities were spatially and temporally structured in relation to the host body and the host breeding cycle, respectively. Spatially, the flea and the three louse species showed a noticeable and consistent segregation within the host body (Fig. 2). Fleas concentrated mainly on the belly area, probably because the brood patch offers a feather-free surface where fleas can easily bite. Regarding the two Ishnoceran species; *S. peusi* was nearly exclusively

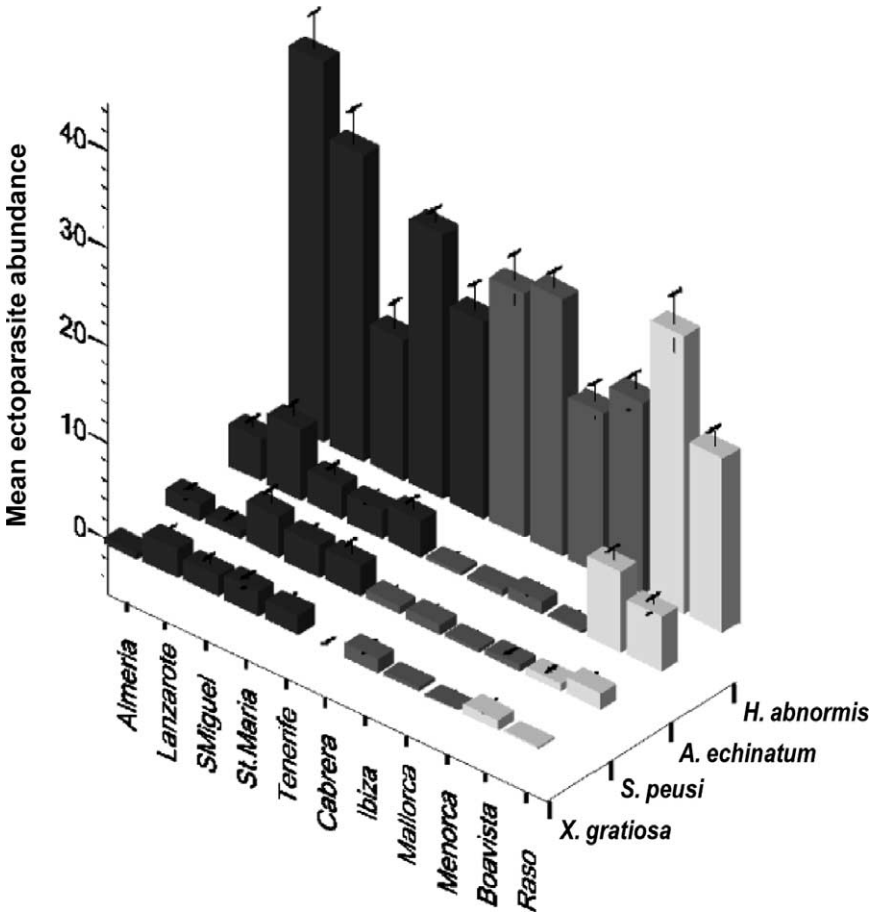

Figure 4. Histograms showing the mean abundances of each ectoparasite species per colony and host taxa. Bars corresponding to Mediterranean and Atlantic Cory's shearwaters and Cape Verde shearwaters are indicated in black, grey and white, respectively. Bar intervals indicate standard errors.

distributed on the head, whereas *H. abnormis* mostly occurred on other regions. Parasites that share resources can reduce competition by being spatially segregated (Mouillot et al. 2003). Spatial segregation probably resulted from exploitation rather than interference competition among parasites, since there were no negative correlations found between ectoparasite abundances within an individual host. Differences in the size and shape of the feathers seem to provide the necessary habitat heterogeneity for parasites to segregate (Crompton 1997). Indeed, most studies suggest that feather morphology and the ability of lice to escape preening are the major factors determining the distribution of lice on birds (Bush et al. 2006). Preening is the main defensive behaviour of birds against harmful ectoparasites (Clayton et al. 2005). Long thin forms, e.g. *H. abnormis*, are able to insert into the feather barbs to escape preening. In contrast, wider forms, e.g. *S. peusi*, are restricted to areas the host can not reach, such as the head. The distribution of food resources may also play a role on the distribution of lice. Ischnoceran, e.g. *H. abnormis* and *S. peusi*, are usually associated with feathers and mainly feed on the non-living keratin of feather barbules (Møller and Rózsa 2005). In the present study, *H. abnormis* was particularly abundant on the tail and wing feathers which can be related to the feeding preferences of this louse species, though other reasons such as mating, egg laying or escaping host defences can not be excluded. Amblyceran lice, e.g. *A. equinatum*, tend to occur in contact with the host skin where they feed on host secretions or chew the emerging tips of developing feathers to obtain blood (Møller and Rózsa 2005). In petrels, the skin as a whole acts as a sebaceous secretory organ possibly linked with the musty smell (Warham 1996, Stettenheim 2000). In accordance with this, *A. equinatum* was more widely distributed on areas with a greater proportion of skin, such as the belly, breast and mantle areas. This species was also abundant on the head area, which in this case is probably linked to its ability to feed on lachrymal secretions (Mey et al. 2006, unpubl.).

Temporally, ectoparasite abundance within infracommunities varied consistently among individuals throughout the breeding cycle of the host (Fig. 3). This pattern is probably related to changes in host behaviour and opportunities for parasite dispersal. In fact, these results provide some evidence of synchronicity of the parasite life cycle to the host in that some of the parasites appear to increase loads prior to host reproduction. This would allow them to move to the nestlings during the chick-rearing period. During the pre-laying period shearwaters mate on the breeding grounds. From laying to hatching, male and female shearwaters share incubation duties and spend approximately half of their time on the nest. In contrast,

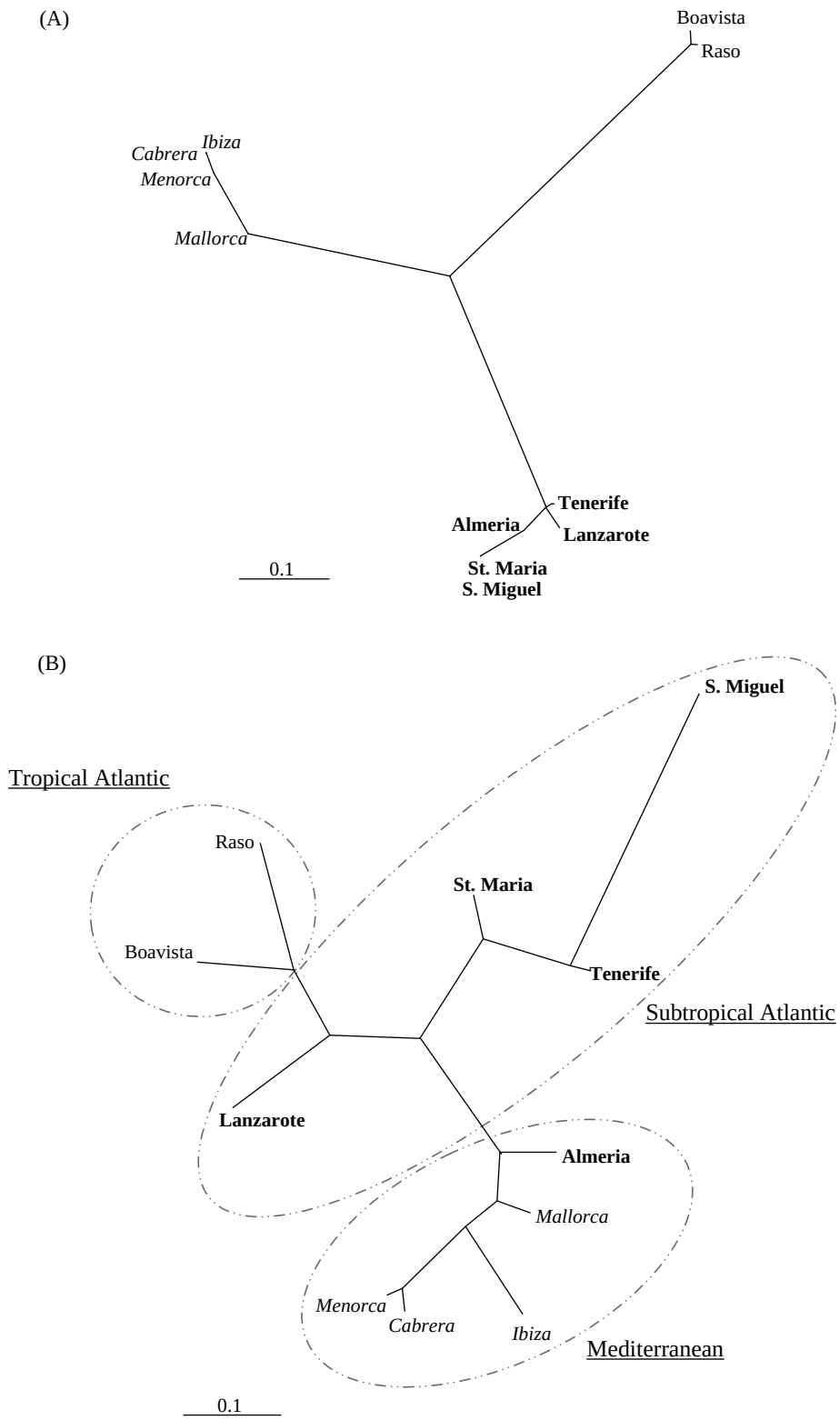

Figure 5. Neighbour-joining cladogram showing relationships among Cory's and Cape Verde shearwaters breeding colonies based on genetic data of hosts (A) and ectoparasite mean abundance data of component communities (B). Groups corresponding to Atlantic and Mediterranean Cory's shearwater and Cape Verde shearwaters are indicated in bold, italics and normal font, respectively. Localities belonging to tropical Atlantic, subtropical Atlantic and Mediterranean regimes are indicated. The Lanzarote population, although geographically belonging to the Canary archipelago within the subtropical Atlantic region, is much drier than Tenerife due to the absence of mountains, and thus climatically closer to the tropical Islands from the Cape Verde archipelago. The genetic cladogram (A) is based on Φ_{ST} pairwise genetic distances among colonies. The ectoparasite mean abundance cladogram (B) is based on chi-squared pairwise distances among host breeding colonies.

during chick-rearing period shearwaters only visit the nest intermittently for a few hours at a time to feed the chick and spend most of their time foraging at sea (Thibault et al. 1997). This behaviour may favour infestation by more opportunistic ectoparasites, such as fleas, at the beginning of the breeding period, when birds are easier to reach on the ground. Likewise, physical contact between birds during host mating also provides opportunities for parasite exchange. Accordingly, a great abundance of adult and nymphal lice of *A. equinatum* and *H. abnormis* during pre-laying and laying likely reflects ectoparasite reproduction. At the chick rearing period, however, the abundance of these two species dropped probably due to vertical transmission of ectoparasites from parents to the chick. Similarly, the abundance of the louse *S. peusi* also decreased from hatching to chick-rearing, but in this species the abundance was lower from pre-laying to mid-incubation (Fig. 3). This contrasting pattern may be related to the inability of *S. peusi* to escape allopreening of shearwater mates; a behaviour which is thought to be restricted to the pre-laying period. For example, until incubation, pairing shearwaters typically spend many days together at the burrow and often engage in allopreening (Warham 1996), which beyond the ritual meaning, may also be a defence against ectoparasites.

Component community structure

Ectoparasite abundance commonly shows an aggregated distribution, with higher parasite abundances occurring on a few host individuals (Anderson and May 1978, Lindell et al. 2002). This aggregation pattern can be particularly important in colonial nesting species, such as most seabirds, due to the aggregated nest distribution and the physical proximity of birds (Rózsa et al. 1996, Tripet et al. 2003). In the present study, the distribution of parasites among individual hosts matched a clumped pattern, but the degree of aggregation differed among lice and the flea, being by far greater in fleas than in lice. The aggregated distribution of parasites can result from the spatial aggregation of hosts, i.e. host density (Whiteman and Parker 2004b), but the effect of host density on parasite abundance also differed among parasite species.

In fleas, we found a positive effect of nest density on parasite abundance, as reported in previous studies (Krasnov et al. 2002). In addition, the mean abundance of these ectoparasites was correlated between breeding mates. These results indicate a relatively good dispersal capability and suggest horizontal transmission as the main dispersal mechanism. In fact, fleas are primarily associated with the nest, rather than with the host itself, suggesting a potential lower specificity and a more active dispersal ability compared with lice.

In lice, parasite abundance was less aggregated, especially among the less abundant species (*S. peusi* and *A. echinatum*), and there was no relationship with host density. Previous studies on birds found similar louse loads on pair mates (Potti and Merino 1995). We also found significant correlations in the mean abundances of *H. abnormis* and *A. echinatum* between mates, although there were conflicting patterns in different locations. Similarity in the mean abundance of ectoparasites between mates was only consistently significant for fleas, presumably due to horizontal transmission. Alternatively, similarity between mates could also arise from assortative mating based on characters that correlate with parasite loads, e.g. body size and condition. However, in this study neither body condition nor body size correlated with ectoparasite infestation. Moreover, there was no evidence of assortative mating based on either of these two traits. The conflicting patterns found for the abundance of *H. abnormis* and *A. echinatum* between mates probably reflects a lower rate of horizontal transmission compared to vertical transmission in these species, although differential susceptibility of individual birds to parasites cannot be excluded.

Differences in aggregation patterns and in the effects of host density and mating between fleas and lice could be linked to differences in parasite mobility and host-specificity (Clayton et al. 2004). The three louse species showed limited mobility. On the contrary, the flea species *X. gratiosa* is more vagile and mainly associated with the host nest. In fact, this flea parasitizes several seabird species that share habitat and nest sites with *Calonectris* (Beaucournu et al. 2005, unpubl.). Although data on infestation levels of fleas on other sympatric seabirds are not available, horizontal transmission can occur among different host species due to the higher mobility and infestation ability of fleas.

Host body size and condition can sometimes explain differences of mean abundance within the component community since this factors can determine the resources and niches available for parasites (Clayton and Walther 2001). Further, host condition can have a notable influence on susceptibility to parasite infestation (Potti and Merino 1995, Rózsa 1997, Morand et al. 1999, Clayton and Walther 2001, Whiteman and Parker 2004a). However, we did not detect a significant relationship between host size or condition and ectoparasite mean abundance. Nevertheless, previous studies were based on interespecific comparisons or focused on fish species of undetermined growth. In fish, intraspecific differences in body size can be large compared to the relatively low within-population variability of body size in Cory's shearwaters. Likewise, as seabirds often feed from the same resource patch (Croxall 1987), body condition might not vary enough among individuals to detect effects on parasite mean abundance. Alternatively, sexual inequalities in size and condition, e.g. morphological, behavioural and immunological differences can lead to one sex to being more prone to parasitism than the other (Poulin 1996). Cory's shearwater males could be expected to have greater parasite loads than females, since they are larger and spend more time in the burrow (Jouanin et al. 2001). However, there were no significant differences in ectoparasite loads between mates from the same pair. Either, sexual inequalities in Cory's shearwaters are irrelevant regarding parasite loads or parasite transmission among mates obscures sexual differences.

Regional community structure

Successful infestation by a parasite requires passing through an encounter filter to reach a potential host (Combes 2001). This includes appropriate spatial and temporal overlap and

the ability to locate and enter the potential host. When dispersal of a parasite is host-dependent, connectivity of host populations may act as a dispersal filter for parasites and shape the parasite regional community (Guégan et al. 2004). In the present study, ectoparasite communities differed significantly among host taxa and host colonies within each taxon. As the connectivity among host populations is typically influenced by geographical distances to some extent, differences in ectoparasite communities are often spatially structured (Poulin and Morand 1999, Goüy de Bellocq et al. 2002, Poulin 2003, Krasnov et al. 2005b). Accordingly, we found that similarity in parasite communities among Cory's shearwater colonies decreased with increasing geographic distance. However, if this relationship reflects host connectivity, we should expect to find even stronger relationships between the similarity of parasite communities and host genetic distances. The rationale for this is that geographic distance alone may not always reliably reflect connectivity because shearwater dispersal over large distances is influenced by other factors that may obscure the relationship, such as the distribution of land masses, prevailing winds and oceanographic features, such as productivity and sea surface temperature (González-Solís et al. 2007). In this context, if similarity in parasite community structure is mediated by host connectivity, genetic similarity among host populations should be associated with the structure of parasite communities. However, we found no such association. For example, in the Almeria population, although the hosts group genetically with the Atlantic Cory's shearwaters, this colony is located within the Mediterranean and its parasites group with the rest of Mediterranean localities (Fig. 5B). Therefore, factors other than host connectivity must explain the increasing similarity in parasite communities with decreasing distance among localities.

Climate and differences in habitat characteristics among host localities, can also explain spatial patterns in parasite community structure (Krasnov et al. 1997, 2004a, 2005a, Cumming 2002). Indeed, previous findings show that weather conditions, e.g. ambient temperature and rainfall, can influence patterns of abundance and prevalence of ectoparasites (Merino and Potti 1996). However, geographically close localities usually show similar climatic regimes. Nevertheless, we suggest in this case climate may be a more important factor than host connectivity in explaining the relationship with geographic distance because host genetic distances were not correlated with similarity. Moreover, one locality (Lanzarote), geographically located within the subtropical Atlantic region, showed greater similarity in the component community to distant localities within the tropical region (Raso and Boavista) than to neighbouring localities within its own region (Tenerife) (Fig. 5B). We interpret this unexpected affinity as a stronger role of climate versus geographic distance. Indeed, the local climatic regime of Lanzarote is probably closer to tropical localities such as Cape Verde, due to the lack of mountains, which makes Lanzarote much drier than its neighbouring subtropical colonies. An appropriate test of this hypothesis will require further examination of climatic variables (e.g. temperature and precipitation), as well as detailed habitat characteristics (e.g. vegetation and altitude) of each breeding colony.

In summary, we could detect the influence of several factors on the structure of parasite communities at different community levels. Ectoparasite species showed significant spatial segregation within the host body. At the component community level, host density and mating influenced patterns of abundance of the most mobile ectoparasite, i.e. the flea. Regional community structure was influenced by geographic distances among host breeding colonies, but similarity was probably mediated by climatic resemblance rather than by host-dependent parasite dispersal. Although host susceptibility and temporal factors can have a limited effect, our results highlight the role of spatial factors as the main determinants shaping ectoparasite communities.

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