

Intracolony differences in the infestation by *Haemoproteus lari* on Yellow-legged Gulls *Larus cachinnans*

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The prevalence and intensity of *Haemoproteus lari* infestation were studied in a colony of Yellow-legged Gulls (*Larus cachinnans*) on the Medes Islands (NE Spain) during 1994 and 1995. Prevalence did not differ between years, sexes, clutch sizes or nesting habitats. More heavily infected females tended to lay smaller clutches and to be in a leaner body condition; in males, intensity of parasites was unrelated to their clutch size and their body condition. These results are partially consistent with the detrimental effect of blood parasites, but also with a tendency for stressed birds to relapse. Intensity of parasitemia differed both between years and among nesting habitats of the gullery, probably as a result of differences in bird quality at the time of sampling. We suggest that these effects should be controlled for in studies dealing with parasites in colonial nesting birds.



1. Introduction

Several hypotheses propose that various life-history characteristics of birds could be modelled through their interaction with parasites: population regulation (e.g. Anderson & May 1978, 1979), behavioural ecology (Keymer & Read 1991, Weatherhead et al. 1995), determination of clutch size (Poiani 1993) or sexual selection (Hamilton & Zuk 1982, Borgia & Collins 1990). Some of these hypotheses have been supported by comparative studies that correlate the levels of parasites recorded in different species with the variable supposedly affected by parasites. However,

differences in parasite levels have been detected not only between different species but also within the same species according to the age, sex, locality or habitat of the individuals sampled, as well as with the month and year of sampling (e.g. Atkinson & van Riper 1991, Korpimäki et al. 1993, Allander & Bennett 1994, Bennett et al. 1995, Ruiz et al. 1995, Tella et al. 1996). All factors affecting parasite levels in a species, even when not directly related to the hypothesis being tested, need to be identified and accounted for in further comparative analyses (Weatherhead & Bennett 1991, 1992).

Hypotheses of parasite-mediated selection assume that parasites reduce the fitness of their hosts.

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Although debilitating effects have been reported in birds infested by ectoparasites (Moller et al. 1990), evidence of the effects of Haematozoa in wild birds is contradictory. Some studies have reported positive associations between variables related to reproductive output and parasite loads in wild populations (Korpimäki et al. 1993, Norris et al. 1994, Allander & Bennett 1995, Richner et al. 1995, Dufva 1996, Oppliger et al. 1996), while others have reported negative or non-significant results (e.g. Davidar & Morton 1993, Dale et al. 1996, Tella et al. 1996). This disparity of results does not necessarily imply a contradiction. Some parasites may be detrimental to the host under stressful conditions but not in favourable conditions (Korpimäki et al. 1993), or they may only have a negative impact on a segment of the population (i.e., females as opposed to males, or juveniles as opposed to adults; Atkinson & van Riper 1991).

In this study we test whether an association between levels of parasitemia and clutch size occurs in breeding Yellow-legged Gulls. We also investigate possible differences in parasite prevalence and intensity in birds breeding in different nesting habitats within a colony, and discuss the use of colonial bird species in comparative tests of parasite-mediated selection.

2. Material and methods

2.1. Study area

The study was performed in the Yellow-legged Gull colony of the Medes Islands (42°0'N, 3°13'E; NE Spain), which are calcareous rocks with a total area of 20 ha, just 0.9 km off the coast. The gullery, with ca. 13 500 pairs in 1993 (Bosch et al. 1994), has been periodically culled by the regional nature conservancy agency (DARP) since 1992, because of possible harmful effects both on other bird species and on the bacteriological quality of natural reservoirs of water (however, see Bosch 1996, Bosch & Muniesa 1996). The distribution of vegetation on the Islands allowed us to distinguish three main nesting habitats: shrubby habitat, dominated by *Atriplex halimus*, a dense shrub which reaches a height of 60–100 cm in the archipelago; grassy habitat, mainly dominated by

Hordeum murinum; and bare habitat, with no vegetation, bare soil and scattered rocks (for a more detailed description of the vegetation, see De Bolòs & Vigo 1984).

2.2. Sampling parasites

Blood smears from 68 and 87 incubating Yellow-legged Gulls were sampled in the last two weeks of April both in 1994 and 1995. In both years, sampling occurred at the end of incubation, during the conservation agency's culling program. However, since gulleries exhibit intracolony laying asynchrony (Burger 1979, Pierotti 1982), some birds could have been sampled at slightly different stages of incubation. Birds were sampled only in the grassy habitat in 1994, while in 1995 they were sampled in the three nesting habitats described above. Gulls were collected in their own nests immediately after culling, and then their body masses and tarsus lengths were measured. Sex was determined by dissection. Additionally, the clutch size was recorded in 1995 for most of the gulls sampled. One drop of blood from the jugular vein of each gull was taken and smeared on a glass slide. Smears were air-dried and fixed with absolute methanol in the field and subsequently stained with the Giemsa technique (Bennett 1970).

Blood smears were screened for *Haemoproteus* sp. under oil emersion ($\times 1\ 000$). We focused on this group because no other Haematozoa have been previously reported in Laridae (Peirce 1981, Bennett et al. 1992, Ruiz et al. 1995). Examination was 'blind', i.e., the person who examined the smears knew nothing about the sampled gulls. For each smear, 10 000 erythrocytes were examined to detect the presence of parasites. Haemoparasite prevalence was estimated as the percentage of infested individuals in the sample. Intensity of infestations was established by counting the number of parasites per 4 000 erythrocytes. The reliability of parasite-intensity estimations obtained by this method has been established by a high repeatability, both intra-observer ($r_i = 0.93$, Ruiz et al. 1995) and inter-observer ($r_i = 0.81$, $F_{64,65} = 9.04$, $P < 0.001$; authors unpublished).

The effects of sex, year, nesting habitat, and clutch size on the prevalence of Haemoparasites

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were tested using three-dimensional contingency tables (Zar 1984). The possible effects of sex, year, nesting habitat, and clutch size on the intensity of parasitemia were tested in infested birds by two-way and three-way ANOVA. The data on intensity of parasitemia were previously square-root transformed (Zar 1984) to attain normality. Potential variations in the body condition of infested birds between sexes, years, nesting habitats, and clutch sizes were assessed by two-way and three-way ANOVA. The relationship between the body condition of infested gulls (expressed by the ratio of body mass/tarsus length; see Ruiz et al. 1995) and their parasite load was assessed separately for each sex by partial correlations, controlling the effect of clutch size. Tests analyzing the effect of sampling year used only data from gulls sampled in the grassy vegetation habitat, while those analyzing nesting habitat, body condition and clutch size effects only used data from 1995.

3. Results

3.1. Parasite prevalence

Haemoproteus lari was the only blood parasite found in the smears of the gulls. Its prevalence

was 89% (occurring in 138 of the 155 samples), in contrast to other species of gulls or Charadriiformes whose infestation by Haematozoa seems to be very rare (Peirce 1981, Atkinson & Van Riper 1991, Bennett et al. 1992, Earlé & Underhill 1993, Figuerola et al. 1996; but see Ruiz et al. 1995). Overall dependence among parasite prevalence, sex and year was not detected (three-dimensional contingency table, $\chi^2_4 = 4.7$, $P = 0.32$) (Table 1). Similarly, overall dependence among prevalence, sex and nesting habitat was not detected ($\chi^2_7 = 4.3$, $P = 0.37$) (Table 1). Parasite prevalence did not vary between clutch sizes when the sex of the birds was considered ($\chi^2_4 = 8.0$, $P = 0.33$) (Table 2).

3.2. Intensity of Parasitemia

Intensity of parasites in infested gulls from the grassy habitat varied significantly between years but not between sexes (two-way ANOVA, factor year: $F_{1,93} = 8.82$, $P = 0.004$; factor sex: $F_{1,93} = 2.05$, $P = 0.155$; interaction: $F_{1,93} = 0.135$, $P = 0.718$). Multiple range analyses showed that the parasite load was lower in 1994 than in 1995 (Table 3).

Breeding habitat had a significant effect when sex and clutch size of gulls sampled in 1995 were

Table 1. Prevalence of *Haemoproteus lari* in breeding Yellow-legged Gulls of the Medes Islands colony in relation to sex, year and nesting habitat. N = number of gulls sampled.

	N	Males		Females		Combined	
		Para-sitized (%)	Non-parasitized	Para-sitized (%)	Non-parasitized	Para-sitized (%)	Non-parasitized
1994							
Grassy habitat	68	36 (90.0)	4	26 (92.9)	2	62 (91.2)	6
1995							
Grassy habitat	40	14 (77.8)	4	21 (95.5)	1	35 (87.5)	5
Shrubby habitat	25	15 (88.2)	2	8 (100)	0	23 (92.0)	2
Bare habitat	22	11 (84.6)	2	7 (77.8)	2	18 (81.4)	4

Table 2. Prevalence of *Haemoproteus lari* in breeding Yellow-legged Gulls of the Medes Islands colony in 1995, according to sex and clutch-size. N = number of gulls sampled.

	N	Males		Females		Combined	
		Para-sitized (%)	Non-parasitized	Para-sitized (%)	Non-parasitized	Para-sitized (%)	Non-parasitized
2-egg clutches	26	13 (86.7)	2	11 (100)	0	24 (92.3)	2
3-egg clutches	33	12 (80.0)	3	17 (94.4)	1	29 (87.9)	4

condition, age, immunity, status, etc.) varied between 1994 and 1995, leading to a reduction in parasite intensity in infested birds in the second year. The absence of differences in parasite prevalence between both years in the same area does not support the first hypothesis, if we assume that the probability of being infested depends on vector abundance (see Allander & Bennett 1994, Bennett et al. 1995). The better body condition of infested gulls in 1995 than in 1994 also seems an unlikely explanation of the increase in the intensity of parasite infestation, if we consider the negative relationship between body condition and parasite load described above (see Results). Studies in other colonies have shown that continuous culling programmes progressively reduce the mean age of breeding individuals (Duncan 1978, Coulson et al. 1982), and a lower intensity of infestation has been reported in older individuals than in younger ones (Allander & Bennett 1994, Sundberg 1995; but see Dale et al. 1996, Tella et al. 1996 and references therein). Such age-related patterns of parasite infestation might explain the increase in the intensity of infestations in 1995, but further research is needed to understand the annual variations in parasite loads (Bennett et al. 1995).

Differences in parasite levels among nesting habitats resembled those found in body condition. These differences in parasite levels within the colony could have at least two possible explanations: 1) haematzoa vectors were more abundant in some areas of the colony than in others, and 2) the 'quality' of breeding birds differed among nesting habitats at the time of sampling. The lack of differences in the prevalence of parasites among nesting habitats does not support the first hypothesis. Inter-habitat differences in the 'quality' of birds seems to be the most likely explanation. In this way, non-random patterns in the distribution of different 'quality' individuals have been described within colonies of gulls (Coulson 1968, Pierotti 1982, Aebischer & Coulson 1990). Furthermore, laying asynchrony among different zones occur within large gulleries (Burger 1979, Pierotti 1982), which might promote the appearance of spatial differences in body condition and parasite load of gulls at a given time.

Our results suggest that the comparison of levels of parasitemia among different colonies or spe-

cies could be complicated by the heterogeneity in the spatial distribution of parasite intensities. Data on intensity of infestation by parasites in colonial nesting birds might not be suitable in comparative analyses testing hypotheses of parasite mediated selection, unless the spatial distribution of the sampled individuals within the colony is accounted for.

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Selostus: *Haemoproteus lari-veriloisen* esiintyminen keltajalkalokilla

Kirjoittajat tutkivat *Haemoproteus lari-veriloisen* esiintymistä keltajalkalokin koloniassa, joka pesii luoteisspanjalaisella saarella. Loisten esiintymisen yleisyys (loisittujen lintujen osuus) ei vaihdellut kahden tutkimusvuoden eikä eri pesimähabitaattien (pensaikko, ruohikko ja täysin kasviton) välillä. Myöskää sukupuolten välillä ei ollut eroa loisten esiintymisessä. Vuosien välillä oli kuitenkin selkeä ero loisinnan voimakkuudessa: vuonna 1995 loisia oli enemmän loisittua yksilöä kohti kuin 1994. Naarailta, joilla oli paljon veriloisia, pesyekoko oli pienempi ja ne olivat huonommassa fyysisessä kunnossa kuin vähemmän loisitut naaraat; koirailta ei vastaavia eroja löytynyt. Jälkimmäisenä tutkimusvuonna havaittiin lisäksi, että ruohikolla pesivien lintujen loisinnan voimakkuus oli korkeampi kuin muilla habitaateilla pesivillä. Loisinnan voimakkuuden vaihtelu vuosien, eri pesimähabitaattien ja lintujen kunnan mukaan kolonian sisällä vaikeuttaa vertailujen tekemistä eri kolonioiden välillä loisten merkityksestä ellei em. tekijöitä pystytä kontrolloimaan.

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examined simultaneously (three-way ANOVA, breeding habitat: $F_{2,41} = 5.93$, $P = 0.006$). Multiple range analysis showed that individuals from the grassy habitat had a higher parasite load than those from the other nesting habitats (Table 3). Sex and clutch size did not have a significant effect on parasite load, but a significant interaction between both factors was detected (sex: $F_{1,41} = 0.79$, $P = 0.390$; clutch size: $F_{1,41} = 3.75$, $P = 0.061$; interaction: $F_{1,41} = 6.938$, $P = 0.012$). *A posteriori* t-tests showed that this interaction was due to the higher, marginally significant, parasite load of females with two-egg clutches compared with that of both males with two-egg clutches ($t_{22} = 2.03$,

$P = 0.055$) and females with three-egg clutches ($t_{26} = 1.7$, $P = 0.089$) (Table 4). No other significant interaction was detected between nesting habitat, sex and clutch size.

3.3. Body condition of gulls

Body condition of infested gulls from the grassy habitat varied both between years and sexes (two-way ANOVA; factor year: $F_{1,93} = 27.20$, $P < 0.001$; factor sex: $F_{1,93} = 62.65$, $P < 0.001$; interaction: $F_{1,93} = 0.37$, $P = 0.550$) (Table 5). Multiple range analyses showed that body condition was poorer

Table 3. Intensity of *Haemoproteus lari* parasitemia in infested breeding Yellow-legged Gulls of the Medes Islands colony in relation to sex, year and nesting habitat. Mean = mean number of *Haemoproteus* per 4 000 erythrocytes, S.E. = standard error, N = number of gulls sampled.

	Males		Females		Combined	
	Mean \pm S.E.	N	Mean \pm S.E.	N	Mean \pm S.E.	N
1994						
Grassy habitat	20.6 \pm 3.0	36	15.3 \pm 2.2	26	18.0 \pm 2.3	62
1995						
Grassy habitat	31.6 \pm 4.8	14	26.2 \pm 3.9	21	28.9 \pm 3.1	35
Shrubby habitat	16.5 \pm 4.0	15	33.3 \pm 7.3	8	24.9 \pm 4.5	23
Bare habitat	13.8 \pm 6.0	11	17.9 \pm 7.8	7	15.8 \pm 4.9	18

Table 4. Intensity of *Haemoproteus lari* parasitemia in infested breeding Yellow-legged Gulls of the Medes Islands colony in 1995, according to sex and clutch. Mean = mean number of *Haemoproteus* per 4 000 erythrocytes, S.E. = standard error, N = number of gulls sampled.

	Males		Females		Combined	
	Mean \pm S.E.	N	Mean \pm S.E.	N	Mean \pm S.E.	N
2-egg clutches	14.2 \pm 5.1	13	32.9 \pm 5.5	11	23.5 \pm 3.8	24
3-egg clutches	16.2 \pm 5.3	12	17.1 \pm 4.5	17	16.6 \pm 3.5	29

Table 5. Body condition (expressed by ratio of body mass/tarsus length) of infested breeding Yellow-legged Gulls of the Medes Islands colony, in relation to sex, year and nesting habitat. S.E. = standard error, N = number of gulls sampled.

	Males		Females		Combined	
	Mean \pm S.E.	N	Mean \pm S.E.	N	Mean \pm S.E.	N
1994						
Grassy habitat	16.2 \pm 0.2	36	14.4 \pm 0.2	26	15.3 \pm 0.2	62
1995						
Grassy habitat	17.7 \pm 0.3	14	15.5 \pm 0.3	21	16.6 \pm 0.2	35
Shrubby habitat	17.5 \pm 0.3	15	15.3 \pm 0.5	8	16.4 \pm 0.3	23
Bare habitat	18.3 \pm 0.4	11	16.1 \pm 0.5	7	17.2 \pm 0.3	18

both in females and in individuals sampled in 1994. Body condition of infested individuals sampled in 1995 varied significantly between clutch sizes and between sexes (three-way ANOVA; factor clutch-size: $F_{1,41} = 8.79$, $P = 0.005$; factor sex: $F_{1,41} = 25.60$, $P < 0.001$), with a poorer body condition being recorded in both females and gulls with two-egg clutches (multiple range analyses) (Table 6). A significant effect of nesting habitat was not detected (three-way ANOVA; $F_{2,41} = 2.95$, $P = 0.06$), although infested gulls from the grassy habitat had a significantly poorer condition than those from the bare habitat (multiple range analysis, $P = 0.024$). No significant interaction among clutch size, sex or nesting habitat was found (in all cases, $P > 0.3$). When controlling the effect of clutch size, intensity of infection was negatively related to body condition in females (partial correlation: $r_{26} = -0.43$, $P = 0.029$) but not in males ($r_{23} = -0.26$, $P = 0.80$).

4. Discussion

A basic assumption of the theories that describe the effect of parasites on behaviour and ecology of birds is that parasites have a detrimental effect on the fitness of their hosts (see Loye & Zuk 1991). The results of our study are partially consistent with this assumption, in that females with smaller clutch size had a higher intensity of *Haemoproteus* infestation than the other females. However, no such relations were found in males. Since *Haemoproteus* have prepatent periods between 14 and 32 days (Fallis & Bennett 1961, Atkinson & van Riper 1991, Bennett et al. 1995), the differences detected here in the intensity of infestation should reflect the varying susceptibility of birds to *Haemoproteus* during the egg-laying stage. At this stage, females, but not males, reduce their body mass greatly as a result of their energetic investment in egg production (Hario et al. 1991). A relationship between female body condition and clutch size has been proved for gulls and other birds (Jones & Ward 1976, Houston et al. 1983). In the present study, females with two-egg clutches were in poorer condition than those with three-egg clutches. The poorer body condition and the lower clutch size of some females might be a consequence of the energetic cost of the intense para-

site load, since blood parasites may inhabit not only blood cells but also the tissues of several organs of the hosts (Atkinson & van Riper 1991), and may compete for the resources allocated to egg formation (Korpimäki et al. 1993, Norris et al. 1994). Alternatively, some females might have a reduced ability to cope with the energetic costs of reproduction, which might place their immune system under stress, favouring a relapse of the parasitic infestation (Atkinson & van Riper 1991, Weatherhead & Bennett 1991, Sundberg 1995). In this way, a clear effect of breeding effort on haemoparasite loads has been experimentally demonstrated in the Great Tit (Richner et al. 1995, Oppliger et al. 1996). In our study, females in poorer body condition (i.e., females with two-egg clutches) might be under greater egg-laying stress than females with better body condition (able to produce a clutch of three eggs), and consequently be more vulnerable to *Haemoproteus* infestation relapse. Nevertheless, breeding asynchrony gives rise to another explanation that cannot be ignored. The relationship found in females between clutch size and intensity of parasitemia could result from breeding asynchrony within the gullery. Females could reinforce their immune system after egg laying, during the incubation period, when breeding effort would be reduced. If female gulls breeding later lay small clutches (Parsons 1972, 1975, Kilpi 1990), they would have a shorter period to combat the infection, and thus they should be more heavily parasitized at the time of sampling. This is one of the possible reasons why causality cannot be inferred from the data presented here.

The increase in parasite levels between 1994 and 1995 within the same nesting habitat could have two possible explanations: 1) the abundance of haematozoa vectors in this habitat increased in 1995, and 2) the 'quality' of breeding birds (body

Table 6. Body condition (expressed by ratio of body mass/tarsus length) of infested breeding Yellow-legged Gulls of the Medes Islands colony in 1995, in relation to sex and clutch size. S.E. = standard error, N = number of gulls sampled.

	Males		Females	
	Mean \pm S.E.	N	Mean \pm S.E.	N
2-egg clutches	17.5 \pm 0.4	13	15.2 \pm 0.4	11
3-egg clutches	18.3 \pm 0.4	12	15.9 \pm 0.3	17