

A helminth community in breeding Yellow-legged Gulls (*Larus cachinnans*): pattern of association and its effect on host fitness

Marc Bosch, Jordi Torres, and Jordi Figuerola

Abstract: We studied the community of helminths parasitizing adult Yellow-legged Gulls (*Larus cachinnans*) sampled during three consecutive breeding seasons in a western Mediterranean colony. The helminth community was depauperate, probably because of the high trophic dependence of the gullery on waste food from refuse dumps. The prevalences of two helminth species varied both among years and between the sexes of gulls, while the intensity of parasitism did not vary significantly for any helminth species. No clear pattern of association between helminth species was detected, showing an unstructured helminth community in which the occurrence of any species was not restricted or favoured by the occurrence of any other species. The lack of associations might be influenced by the fact that only one core species occurred in the helminth community. Negative relationships were found between occurrence of certain helminths and body condition of hosts. Gulls infected by *Tetrabothrius* (*Tetrabothrius*) *erostris* were leaner than uninfected gulls; interestingly this negative relationship varied with the presence/absence of *Cosmocephalus obvelatus*. Moreover, body condition of gulls infected by *C. obvelatus* varied according to the year of sampling, while that of uninfected individuals showed no variability. High intensities of the parasites *Eucoelus contortus* and *Brachylaima* sp. were associated with poorer body condition of the host. In the case of *E. contortus*, this negative relationship with gulls' body condition was more pronounced in male than in female gulls. The results show that helminth pathogenicity can be affected by helminth community structure, environmental factors, and traits of the host.

Résumé : On trouvera ici les résultats d'une étude sur la faune des helminthes adultes parasites des Goélands leucophées (*Larus cachinnans*) échantillonnés pendant trois saisons consécutives de reproduction au sein d'une colonie de l'ouest de la Méditerranée. La communauté des helminthes s'est révélée appauvrie, probablement parce que les goélands se nourrissent abondamment de déchets qu'ils récoltent dans les dépotoirs. La prévalence de deux espèces d'helminthes a varié d'une année à l'autre et elle différait chez les mâles et les femelles, mais l'intensité des infections n'a pas varié significativement chez aucune des espèces d'helminthes. Les associations entre les espèces d'helminthes ne suivaient pas de pattern bien défini, ce qui indique qu'il s'agit d'une communauté non structurée dans laquelle la présence d'une espèce donnée n'est ni restreinte ni favorisée par la présence d'une autre. L'absence d'association peut être attribuable à la présence d'une seule espèce-clé dans la communauté des helminthes. Des corrélations négatives ont été trouvées entre certains helminthes et la condition physique des goélands. Les oiseaux infectés par *Tetrabothrius* (*Tetrabothrius*) *erostris* étaient plus maigres que les goélands sains; curieusement, cette corrélation négative variait avec la présence/absence de *Cosmocephalus obvelatus*. En outre, la condition physique des goélands infectés par *C. obvelatus* variait d'année en année, alors que celle des individus sains ne variait pas. Les infections graves causées par *Eucoelus contortus* ou par *Brachylaima* sp. étaient associées à une mauvaise condition physique. Dans le cas d'*E. contortus*, cette corrélation négative avec la condition physique des goélands était plus marquée chez les mâles que chez les femelles. Les résultats démontrent que les propriétés pathogènes des helminthes peuvent être affectées par la structure de la communauté, par des facteurs environnementaux et par les caractéristiques de l'hôte.

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Introduction

Certain helminths parasitizing birds have been described as reducing host survival and breeding success, and consequently, they can affect the population dynamics of their

hosts whenever their presence does not compensate for other mortality factors (Minchella and Scott 1991; Hudson et al. 1992b). Helminths may affect host fitness by increasing morbidity (Rausch 1983), increasing predation risk (Hudson et al. 1992a; Murray et al. 1997), reducing both clutch size

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and breeding success (Hudson 1986; Saumier et al. 1986), weakening body condition (Keymer et al. 1991; Delahay et al. 1995), or altering metabolic rates (Connors and Nickol 1991; Delahay et al. 1995). Yet other helminth species have been described as having no discernible adverse effect on the biology of their avian hosts (Williams and Harris 1965; Dick and Burt 1971; Moore and Bell 1983; Thomas 1986; Gray et al. 1989; Clinchy and Barker 1994).

The pathogenicity of a helminth species can vary considerably, depending on several factors. Host resistance determines whether a helminth is detrimental to certain host species but not to others (Watson et al. 1988). Even within the same host species, the pathogenicity of a helminth can vary according to the sex or age of the host (Bakke and Barus 1976; Wallace and Pence 1986; Connors and Nickol 1991; McKindsey et al. 1994; Poulin 1996). Surprisingly, although pathogenicity might also be affected by parasite community structure (Holmes 1983), this subject has received virtually no attention (Moore and Clayton 1997).

The pathogenicity of helminths can depend on the intensity of parasitism, so in some cases higher intensity results in greater pathogenicity (Lemly and Esch 1984; Holmes and Price 1986). In turn, parasite intensity can be influenced by other parameters, including parasite prevalence (Bakke 1972*b*; Bakke and Barus 1976) and the density of definitive and (or) intermediate hosts (Kennedy et al. 1986; Gray et al. 1989; Price 1990; Drózd and Dudzinski 1993). Moreover, both intensity and prevalence of helminths may depend on the simultaneous occurrence of other parasites on the host (Bush and Holmes 1986*b*; Sousa 1994). In this way, competition between parasites limits, or even precludes, the occurrence of other parasites (Sousa 1993; Kuris and Lafferty 1994). Alternatively, the physiological responses of a host to a certain parasite may favour the establishment of other parasites (Richie 1988; Sousa 1992, 1994).

The study of helminth pathogenicity to avian hosts, therefore, far from requiring a simple approach, demands that the analysis of the effects of helminths on a host be integrated with several parameters, such as prevalence and intensity of the helminth and associations with other helminth species parasitizing the host.

Gulls are a cosmopolitan group of birds with abundant, large populations, which are often associated with human activities (Spaans and Blockpoel 1991; Burger and Gochfeld 1996). This has facilitated the publication of a large number of studies of this avian group and its helminth parasites (e.g., see references in Rausch 1983; Bakke 1985; Kennedy and Bakke 1989). However, most of these studies are faunistic, in that they focus on identification of the helminth species of a specific gull population, and only a few deal with the ecological relationships between parasites and their host group. To our knowledge, none focus on the interactions of the species of the parasite community in relation to their pathogenicity.

In this paper we study the community of helminths parasitizing adult Yellow-legged Gulls sampled during three consecutive breeding seasons in a western Mediterranean colony, and address the following questions: (i) Do the prevalence and intensity of helminths vary according to the year, sex of gulls, or occurrence of other parasite species? (ii) Are gulls infected by a helminth species in worse body condition

than uninfected or less parasitized gulls? How are these relationships affected by the occurrence or intensity of other helminth species? As body condition of breeding gulls correlates positively with clutch size (Houston et al. 1983; Bosch et al. 1997), it can be assumed that factors affecting body condition also influence the breeding performance of gulls and, consequently, their life-history and population dynamics.

Methods

Study area

The study was performed in the Yellow-legged Gull colony of the Medes Islands, a limestone archipelago with a total area of 20 ha located 0.9 km off the coast of northeastern Spain (42°0'N, 3°13'E). The gullery, with ca. 13 500 pairs in 1993 (Bosch et al. 1994*b*), depends mainly on waste food from refuse dumps, but also on fish discards and terrestrial invertebrates (Bosch et al. 1994*a*). From 1992 to 1996 the colony was periodically culled by the regional nature conservation agency (Departament d'Agricultura, Ramaderia i Pesca (DARP)) because of the gulls' possible role in transmitting microbial contamination and therefore their potentially harmful effect on other bird species (but see Bosch 1996; Bosch and Muniesa 1996). As a result, the density of breeding pairs has been progressively reduced (Bosch et al. 2000). Three main habitats in the Medes Islands are distinguished according to vegetation distribution: shrubs, grass, and bare soil (for details see Bosch and Sol 1998).

Sampling hosts and parasites

One hundred and twenty-two incubating Yellow-legged Gulls were sampled for helminth parasites in 1993, 1994, and 1995 (19, 77, and 26 individuals, respectively). In all 3 years, sampling was conducted during the last 2 weeks of April, at the end of incubation (when the conservation agency culled the gulls), thus avoiding a seasonal effect on the helminth load of birds (e.g., Bakke 1972*a*; Kennedy and Bakke 1989). Gulls were sampled from a same breeding area (grassy habitat) to preclude a spatial influence on their parasite load (Bakke 1972*a*; Bosch et al. 1997). Birds were collected from their own nests immediately after culling, then their body mass and tarsus length were measured and their alimentary tract (from the oesophagus to the cloaca), including the mesenteric vessels, was quickly removed, labelled, and frozen until helminthological examination. The sex of gulls was determined by dissection. Body condition of each gull was estimated as the ratio of body mass to tarsus length (Bosch et al. 1997; Bosch and Figuerola 1999). In the laboratory each intestinal tract was thawed at ambient temperature and the oesophagus, stomach, and small and large intestines were removed. Each section was immediately placed in an individual container filled with tap water to prevent desiccation of the tissue. Each section was split longitudinally and the mucosa scraped using the blunt handles of dissecting scissors. All helminths were removed by forceps or pipetting into vials containing fixative and sorted into Trematoda, Cestoda, and Nematoda. The fixative used for Platyhelminthes was a mixture of 85% ethanol, 10% glacial acetic acid, and 5% formalin and for Nematoda was 70% ethanol. Later, helminths were processed following general helminthological methods according to the species, identified, and counted. Platyhelminthes were stained with Semichon's acetic carmine, dehydrated, and permanently mounted in Canada balsam. Large individual tapeworms were cut into several pieces before being processed and mounted, and the number was determined by counting scolices. Nematodes were studied using lactophenol wet mounts in depression slides. Previous descriptions were used to identify helminth species, as follows: Niewiadomska (1984) for *Diplostomum pseudospathaceum* (Niewiadomska, 1984); Prevot and Bartoli (1980) for *Cardiocephalus longicollis* (Szidat, 1928); Macko (1963) and Witenberg and Lengy

(1967) for *Ornithobilarzia canaliculata* (Rudolphi, 1819); Cribb (1990, 1992) for *Brachylaima* sp.; Timon-David (1955) for *Aporchis massiliensis* (Timon-David, 1955); Zdzitowiecki et al. (1989) for *Cryptocotyle lingua* (Creplin, 1825); Macko (1964) and Hoberg (1994a) for *Tetrabotrius (Tetrabotrius) erostris* (Loennberg, 1889); Barus and Sergejeva (1989) for *Eucoleus contortus* (Creplin, 1839); Anderson and Wong (1981) for *Cosmocephalus obvelatus* (Creplin, 1825), and Wong and Anderson (1982a) for *Paracuarria adunca* (Creplin, 1846). All helminths are preserved in the collection of the Laboratori de Parasitologia at the University of Barcelona.

Terminology and statistics

The terms prevalence and mean intensity are used according to the definitions provided by Margolis et al. (1982), recently reviewed by Bush et al. (1997). Following Fedynich and Pence (1994), we consider "core" species to be those with prevalences greater than 70%, "secondary" species as those with prevalences between 20 and 70%, and "satellite" species as those with prevalences below 20%.

Several authors have shown that core and secondary species (common species) provide the basic structure of a helminth community, while satellite species represent more random elements in the community that tend to obscure overall patterns (Bush and Holmes 1986a, 1986b; Stock and Holmes 1987). For this reason, in many cases we have only included for analysis the four most commonly occurring helminth species (see Results), while data for the remaining six (satellite) species have been combined to form a single variable.

The effects of sex of gulls and year on the prevalence of helminths were analyzed by three-dimensional contingency tables (Zar 1996); analyses were performed as separate contingency tables for each common helminth species and also in total, as a contingency table summarizing overall helminth prevalences. Variations in helminth intensities among years and between the sexes were analyzed simultaneously by two-way ANOVA for each common species. As parasite intensities were not normally distributed (Kolmogorov-Smirnov test, $D_n = 0.28-0.44$, $P \leq 0.01$ in all cases), analyses were performed using ranked intensities (see Conover and Iman 1981; Marden and Muyot 1995).

Possible overall associations between helminths were studied in parasitized gulls using Schluter's variance-ratio test (see Schluter 1984; Ludwig and Reynolds 1988; Forbes et al. 1994). Association analyses were performed on the whole sample but also independently for each sex and year so as to control the effect of both variables (see Forbes et al. 1994). Furthermore, the pattern of association was analyzed within all helminth species using the same site (oesophagus or intestine) in the host and within the group of common helminth species. These last two sets of analyses included only data from gulls examined in 1994 because of the large size of the sample collected that year.

The relationship between body condition of the host and prevalence of helminths was studied by ANOVA, considering seven factors and their two-way interactions: sex of gulls, year, occurrence of each of the four common species, and a last variable indicating the occurrence of any of the satellite species. The relationship between body condition and intensity of helminths was studied for individuals parasitized by at least one species. Given that individuals were simultaneously infected by some but not all of the species considered, this could have resulted in a confusing effect of prevalence when the effects of parasite intensity were examined. However, we used this approach instead of separate analyses for each helminth species because of the high potential for interactions between parasite species (Holmes 1983). Body condition was modelled by general linear regression, considering as independent variables the intensities of each of the four common helminth species and the sum of the intensities of the six satellite species. Furthermore, sex and year of sampling were included in the model as

Table 1. Prevalences of helminth species parasitizing breeding Yellow-legged Gulls of the Medes Islands colony in relation to sex of gulls and year.

	n	<i>D. pseudo-spathaceum</i>										Total									
		<i>C. longicollis</i>	<i>O. canaliculata</i>	<i>Brachylaima</i> sp.	<i>A. massiliensis</i>	<i>C. lingua</i>	<i>T. (T.) erostris</i>	<i>E. contortus</i>	<i>C. obvelatus</i>	<i>P. adunca</i>											
1993																					
Males	12		8 (1)	25 (3)	8 (1)	25 (3)	58 (7)	33 (4)													92 (11)
Females	7	14 (1)		43 (3)	29 (2)		86 (6)	14 (1)													86 (6)
Combined	19	5 (1)	5 (1)	32 (6)	16 (3)	16 (3)	68 (13)	26 (5)													90 (17)
1994																					
Males	45	2 (1)	4 (2)	36 (16)	9 (4)	38 (17)	69 (31)	24 (11)													91 (41)
Females	32	3 (1)	3 (1)	59 (19)	19 (6)	47 (15)	91 (29)	25 (8)													100 (32)
Combined	77	3 (2)	4 (3)	46 (35)	13 (10)	42 (32)	78 (60)	25 (19)													95 (73)
1995																					
Males	14	7 (1)		7 (1)		57 (8)	14 (2)	43 (6)													79 (11)
Females	12	50 (6)		42 (5)	8 (1)	92 (11)	50 (6)	33 (4)													100 (12)
Combined	26	4 (1)		23 (6)	4 (1)	73 (19)	31 (8)	39 (10)													89 (23)
Grand total	122	0.8 (1)	11.5 (14)	38.5 (47)	10.7 (13)	44.3 (54)	66.4 (81)	27.9 (34)	0.8 (1)												92.6 (113)

Note: Numbers in parentheses are observed frequencies.

Table 2. Intensity of helminth species parasitizing breeding Yellow-legged Gulls of the Medes Islands colony in relation to sex of gulls and year.

	<i>D. pseudospathaceum</i>	<i>C. longicollis</i>	<i>O. canaliculata</i>	<i>Brachylaima</i> sp.	<i>A. massiliensis</i>	<i>C. lingua</i>	<i>T. (T.) erostris</i>	<i>E. contortus</i>	<i>C. obvelatus</i>	<i>P. adunca</i>	Total
1993											
Males			5.0±0.0 (1)	16.7±19.3 (3)	4.0±0.0 (1)		2.7±2.4 (3)	2.6±1.7 (7)	1.0±0 (4)		8.1±14.3 (11)
Females	1.0±0.0 (1)			4.3±2.5 (3)	5.0±3.0 (2)			6.5±5.1 (6)	1.0±0.0 (1)		10.7±4.5 (6)
Combined	1.0±0.0 (1)		5.0±0.0 (1)	10.5±15.1 (6)	4.7±2.5 (3)		2.7±2.4 (3)	4.4±4.1 (13)	1.0±0.0 (5)		9.0±11.9 (17)
1994											
Males			11.0±9.0 (2)	10.7±13.4 (16)	7.0±9.8 (4)		1.9±0.9 (17)	6.2±5.4 (31)	1.6±1.1 (11)	2.0±0.0 (1)	15.9±30.1 (41)
Females	14.0±0.0 (1)		1.0±0.0 (1)	7.9±7.3 (19)	2.3±1.8 (6)		2.0±1.1 (15)	13.1±16.5 (29)	1.6±1.3 (8)	1.3±0.4 (4)	19.0±17.4 (32)
Combined	98.5±84.5 (2)		7.7±8.7 (3)	9.2±10.6 (35)	4.2±6.8 (10)		2.0±1.0 (32)	9.6±12.6 (60)	1.6±1.2 (19)	1.4±0.5 (5)	17.2±25.3 (73)
1995											
Males	1.0±0.0 (1)			5.0±0.0 (1)			2.4±1.6 (8)	2.0±1.0 (2)	2.0±1.8 (6)		5.5±3.0 (11)
Females				28.8±40.6 (5)		1.0±0.0 (1)	3.0±1.7 (11)	3.7±3.1 (6)	1.5±0.5 (4)	1.0±0.0 (1)	18.1±32.7 (12)
Combined	1.0±0.0 (1)			24.8±38.1 (6)		1.0±0.0 (1)	2.7±1.6 (19)	3.3±2.9 (8)	1.8±1.5 (10)	1.0±0.0 (1)	12.0±24.5 (23)
Grand total	1.0±0.0 (1)		7.0±7.6 (4)	11.4±18.0 (47)	4.3±6.1 (13)	1.0±0.0 (1)	2.3±1.4 (54)	8.1±11.3 (81)	1.6±1.2 (34)	1.3±0.5 (6)	14.9±23.9 (113)

Note: Values are given as the mean ± standard deviation, followed by the sample size in parentheses.

discrete factors. Normal error and identity link functions were used in the linear models. A first complete model was fitted that included all variables and their two-way interactions. Afterwards, the variables and interactions were removed one by one from the model to determine the loss of fitting associated with each, as judged from *F* tests. The least influential variable that resulted in a nonsignificant loss of fitting was excluded and the model was recalculated with all the remaining variables. A final model was obtained when exclusion of any factor resulted in a significant loss of fitting (for a detailed description of this procedure see Crawley 1993).

Results

Helminth prevalences

Ten helminth species were found: *D. pseudospathaceum*, *C. longicollis*, *O. canaliculata*, *Brachylaima* sp., *A. massiliensis*, *C. lingua* (Trematoda), *T. (T.) erostris* (Cestoda), *E. contortus*, *C. obvelatus*, and *P. adunca* (Nematoda). Four of these (*Brachylaima* sp., *T. (T.) erostris*, *E. contortus*, and *C. obvelatus*) had prevalences higher than 27%, while the others had prevalences below 12% (Table 1). This allowed us to differentiate two groups: the first comprised one core and three secondary species (common species) and the second comprised six satellite species. The relationship between helminth prevalence and intensity was positive but not significant (Spearman's rank correlation: $r_s = 0.6$, ns, $n = 10$ species). Of the 122 gulls sampled, only 9 were uninfected (=7%). Taken as a whole, parasite prevalence did not depend on sex or year ($\chi^2_7 = 8.33$, ns). When the species were considered separately, the prevalences of neither *C. obvelatus* nor *Brachylaima* sp. depended on sex or year (*C. obvelatus*: $\chi^2_7 = 3.19$, ns; *Brachylaima* sp.: $\chi^2_7 = 12.90$, ns). However, overall independence between prevalence, sex, and year was rejected for both *E. contortus* ($\chi^2_7 = 27.66$, $P \leq 0.001$) and *T. (T.) erostris* ($\chi^2_7 = 21.05$, $P \leq 0.005$), there being significant partial dependences of both species on sex and year (*E. contortus*: $\chi^2_5 = 28.54$, $P \leq 0.001$; *T. (T.) erostris*: $\chi^2_5 = 20.09$, $P \leq 0.002$). *Eucoleus contortus* showed a greater prevalence in females than in males ($\chi^2_1 = 7.70$, $P \leq 0.006$) and a significant variation in prevalence among years ($\chi^2_1 = 19.41$, $P \leq 0.001$). Thus, in 1994 its prevalence was greater than expected and in 1995 was lower than expected (residuals). In the case of *T. (T.) erostris*, only interyear differences were significant ($\chi^2_1 = 15.22$, $P \leq 0.001$), owing to a lower prevalence in 1993 and a higher prevalence in 1995 than expected (residuals).

Helminth intensities

Table 2 shows the mean intensities of each parasite for each sex of infected gulls and year of sampling. No significant effect of sex or year was detected in the intensities of any of the common helminth species (for ANOVA results see Table 3).

Associations between helminths

No significant association was detected between helminths in the sample as a whole. When years or sexes were differentiated, only one significant positive association corresponding to the 1995 sample was detected; the remaining associations were not significant, six of them tending to be positive and four negative (Table 4). When the 1994 sample was separated

Table 3. Results of ANOVA testing differences in infection intensity between the sexes of gulls and years (1993–1995).

	Sex			Year			Interaction		
	df	F	P	df	F	P	df	F	P
<i>E. contortus</i>	1,75	3.29	ns	2,75	4.97	ns	2,75	0.13	ns
<i>C. obvelatus</i>	1,28	0.00	ns	2,28	0.85	ns	2,28	0.12	ns
<i>Brachylaima</i> sp.	1,41	0.03	ns	2,41	0.11	ns	2,41	0.08	ns
<i>T. (T.) erostris</i>	1,47	0.48	ns	1,47	1.81	ns	1,47	0.55	ns

Note: For *T. (T.) erostris*, only data from 1994 and 1995 were included because of the lack of infected females in the 1993 sample.

into groups of helminths occupying the same location in the hosts, a significant negative association was detected only in the intestinal helminths sampled in females; the remaining associations were not significant, four tending to be positive and one negative (Table 4). With regard to the group of common species, associations were also not significant, and they tended to be positive (Table 4).

Relationship between body condition of hosts and prevalence of helminths

Table 5 shows the body condition of Yellow-legged Gulls, both parasitized and unparasitized with helminths, that were sampled in the present study. Gulls' body condition varied according to the prevalence of *T. (T.) erostris*, infected individuals having poorer body condition than uninfected ones (Table 6). Body condition also varied significantly between the sexes and among years of sampling (Table 6). A significant interaction between *C. obvelatus* and *T. (T.) erostris* prevalences was detected on body condition. It was because gulls infected by *T. (T.) erostris* were leaner when *C. obvelatus* was also present, even though the latter helminth had no significant effect on body condition. Another significant interaction was detected between prevalence of *C. obvelatus* and year of sampling, because the body condition of uninfected individuals altered little during the 3 years of study (range of least square means = 15.36–15.84), while that of infected individuals was highly variable (range of least square means = 14.43–17.42). No significant interaction between sex and the prevalence of any individual helminth species was detected.

Relationship between body condition of hosts and intensity of helminths

Significant negative effects of both *E. contortus* and *Brachylaima* sp. intensities were detected on body condition of gulls (Table 7). Sex of gulls and year of sampling also had a significant effect on body condition, as was detected in previous analyses using prevalences. Thus, both males and birds sampled in 1995 showed a higher body condition. Analyses showed a significant interaction between year and sex of gulls, though not when prevalences were used. This interaction was due to the fact that differences in body condition between the sexes were lower in 1993 than in 1994 and 1995. Another significant interaction was detected between intensity of *E. contortus* and sex of gulls, because *E. contortus* intensity had a more detrimental effect on body condition of males than on that of females.

Discussion

Yellow-legged Gulls from the Medes Islands colony harboured a community of helminths that was relatively poor in

Table 4. Variance ratios, Schluter's test statistics (*W*), and the direction of associations among helminth species parasitizing Yellow-legged Gulls of the Medes Islands colony, according to sex of gulls, year, and location in the host and within the group of common helminth species ("core" and "secondary" species).

	Variance ratio	<i>W</i>	Direction of the association
Overall	1.12	136.76	Positive
Overall males ^a	1.08	76.75	Positive
Overall females ^a	0.96	35.60	Negative
1993			
Males	0.92	10.99	Negative
Females	1.20	8.40	Positive
Combined ^b	0.96	18.26	Negative
1994			
Males	1.12	50.39	Positive
Females	0.86	27.39	Negative
Combined ^b	1.10	84.90	Positive
1995			
Males	1.55	21.77	Positive
Females	1.37	16.47	Positive
Combined ^b	1.63	42.44	Positive*
Location in the host ^c			
Oesophagus ^d			
Males	1.16	52.08	Positive
Females	1.02	32.65	Positive
Combined	1.13	86.87	Positive
Intestine ^e			
Males	1.02	45.71	Positive
Females	0.68	21.50	Negative*
Combined	0.91	69.86	Negative
Common helminth species ^c			
Males	1.08	48.66	Positive
Females	1.37	43.88	Positive
Combined	1.24	95.63	Positive

Note: Associations between helminth species in the mesenteric vessels were not tested, as only one species (*O. canaliculata*) was found.

^aIndividuals sampled in the 3 years are pooled.

^bMales and females are pooled.

^cData from gulls examined in 1994 only.

^dGroup consists of *E. contortus*, *C. obvelatus*, and *P. adunca*.

^eGroup consists of *D. pseudospathaceum*, *C. longicollis*, *Brachylaima* sp., *A. massiliensis*, *C. lingua*, and *T. (T.) erostris*.

*A significant net association at $P \leq 0.05$.

species compared with those in many other populations of gulls, which may harbour up to 41 helminth species (see a review in Kennedy and Bakke (1989), although Hair and Holmes (1970) described only seven helminth species parasitizing a population of Bonaparte's Gulls, *Larus philadelphia*). This

Table 5. Body condition (expressed as the ratio between body mass and tarsus length) of parasitized and non-parasitized Yellow-legged Gulls of the Medes Island colony in relation to sex of gulls and year.

	<i>Brachylaima</i> sp.		<i>T. (T.) erostris</i>		<i>E. contortus</i>		<i>C. obvelatus</i>		Others		Total	
	Parasitized	Non-parasitized	Parasitized	Non-parasitized	Parasitized	Non-parasitized	Parasitized	Non-parasitized	Parasitized	Non-parasitized	Parasitized	Non-parasitized
1993												
Males	16.01±0.53	16.40±1.04	15.50±0.83	16.56±0.84	16.30±1.13	16.30±0.64	15.80±0.46	16.55±1.04	16.23±0.05	16.31±1.05	16.24±0.97	17.00±0.00
Females	15.53±0.68	15.88±0.74	15.50±0.73	15.73±0.73	15.51±0.56	17.01±0.00	15.71±0.00	15.73±0.79	15.39±0.44	15.86±0.78	15.51±0.56	17.01±0.00
Combined	15.77±0.66	16.24±0.99	15.50±0.83	16.20±0.90	15.94±0.99	16.42±0.64	15.78±0.42	16.20±1.02	15.81±0.52	16.16±0.99	15.98±0.92	17.01±0.01
1994												
Males	16.28±1.16	16.31±0.95	16.32±1.15	16.29±0.94	16.33±1.14	16.25±0.70	16.22±0.91	16.33±1.06	16.16±0.43	16.33±1.10	16.31±1.03	16.24±0.98
Females	14.71±1.00	14.22±0.83	14.61±1.12	14.47±0.80	14.57±0.99	13.90±0.18	14.36±1.01	14.56±0.95	14.34±0.68	14.61±1.09	14.51±0.97	16.24±0.98
Combined	15.43±1.33	15.67±1.33	15.52±1.42	15.58±1.27	15.48±1.39	15.83±1.10	15.44±1.32	15.60±1.34	15.01±1.06	15.74±1.37	15.52±1.34	16.24±0.98
1995												
Males	17.03±0.00	17.48±1.05	17.34±0.70	17.59±1.31	17.03±0.63	17.52±1.05	17.77±0.85	17.20±1.06	17.72±0.42	17.24±1.26	17.52±0.83	17.16±1.49
Females	15.03±0.61	15.52±1.93	15.20±1.56	16.66±0.00	14.79±1.61	15.85±1.28	15.88±1.45	15.04±1.52	15.52±1.94	15.03±0.55	15.32±1.54	17.16±1.49
Combined	15.37±0.93	16.79±1.70	16.10±1.65	17.46±1.26	15.35±1.72	16.96±1.38	17.01±1.46	16.12±1.70	16.54±1.82	16.39±1.50	16.37±1.67	17.16±1.49
Grand total	15.46±1.23	16.07±1.47	15.72±1.51	15.92±1.33	15.54±1.38	16.41±1.29	15.95±1.45	15.79±1.39	15.65±1.52	15.91±1.36	15.76±1.41	16.72±1.16

Note: Values are given as the mean ± standard deviation.

Table 6. Results of ANOVA of effects of helminth prevalences, sex of gulls, and year of sampling on body condition of gulls.

	df	F	P
Main effect			
<i>Brachylaima</i> sp.	1,86	0.33	ns
<i>T. (T.) erostris</i>	1,86	4.95	≤ 0.05
<i>E. contortus</i>	1,86	2.28	ns
<i>C. obvelatus</i>	1,86	0.05	ns
Others	1,86	0.61	ns
Sex of gulls	1,86	8.05	≤ 0.01
Year	2,86	4.53	≤ 0.01
Interaction			
<i>Brachylaima</i> sp. × <i>T. (T.) erostris</i>	1,86	3.39	ns
<i>Brachylaima</i> sp. × <i>E. contortus</i>	1,86	0.47	ns
<i>Brachylaima</i> sp. × <i>C. obvelatus</i>	1,86	0.28	ns
<i>Brachylaima</i> sp. × others	1,86	2.18	ns
<i>Brachylaima</i> sp. × sex of gulls	1,86	0.53	ns
<i>Brachylaima</i> sp. × year	2,86	0.88	ns
<i>T. (T.) erostris</i> × <i>E. contortus</i>	1,86	0.28	ns
<i>T. (T.) erostris</i> × <i>C. obvelatus</i>	1,86	6.31	≤ 0.01
<i>T. (T.) erostris</i> × others	1,86	0.01	ns
<i>T. (T.) erostris</i> × sex of gulls	1,86	0.00	ns
<i>T. (T.) erostris</i> × year	2,86	2.17	ns
<i>E. contortus</i> × <i>C. obvelatus</i>	1,86	0.07	ns
<i>E. contortus</i> × others	1,86	0.89	ns
<i>E. contortus</i> × sex of gulls	1,86	0.02	ns
<i>E. contortus</i> × year	2,86	0.87	ns
<i>C. obvelatus</i> × others	1,86	2.01	ns
<i>C. obvelatus</i> × sex of gulls	1,86	0.36	ns
<i>C. obvelatus</i> × year	2,86	4.45	≤ 0.01
Others × sex of gulls	1,86	0.08	ns
Others × year	2,86	0.09	ns
Sex of gulls × year	2,86	1.40	ns

might be due, in part, to the high trophic dependence of this gullery on refuse dumps, since waste food constitutes more than 60% of the biomass consumed by the gulls of the colony (Bosch et al. 1994a), and this resource has not been described to be involved in the life cycles of helminths. While the numbers of helminth species were similar among years, the prevalences of two, *T. (T.) erostris* and *E. contortus*, varied. This variation did not show any clear tendency, and did not appear to result from the progressive reduction in gull density due to culling of the colony. Several authors suggest that many temporal variations in helminth prevalences are due to changes in the availability or consumption of intermediate hosts (Bakke 1972b; Drobney et al. 1983; Rausch 1983). This would explain the variation in prevalence of *T. (T.) erostris* but not of *E. contortus* if we assume that the latter helminth only has a direct life cycle (Anderson 1992). However, Madsen (1952) pointed out that earthworms could be occasionally involved as paratenic hosts of this helminth. In that case, variation in the consumption of earthworms might explain the temporal variation in the prevalence of *E. contortus*, as well as the greater prevalence observed in females, if we take into account the fact that females of the related Herring Gull (*Larus argentatus*) consume more earthworms than males (Pons 1993). On other hand, intensity of infection with any helminth did not vary among years or

Table 7. ANODEV and slopes for the significant variables related to body condition of gulls in the linear regression model.

Explanatory variable	Deviance	df	F	Significance	Slope (mean ± SE)
Year	20.56	4,104	19.43	$P < 0.001$	
1994					0.245±0.361
1995					1.147±0.441
Sex	84.82	4,104	80.17	$P < 0.001$	
Females					-0.959±0.529
<i>E. contortus</i> intensity	6.33	2,104	5.98	$P < 0.005$	-0.058±0.030
<i>Brachylaima</i> sp. intensity	4.98	1,104	4.71	$P < 0.05$	-0.017±0.008
Year × sex	5.19	1,104	4.91	$P < 0.05$	
1994 × females					-1.295±0.587
1995 × females					-1.101±0.687
Sex × <i>E. contortus</i> intensity	5.82	1,104	5.50	$P < 0.05$	
Females × <i>E. contortus</i> intensity					0.074±0.032

Note: For the variables analyzed as factors, different slopes are reported for each factor score, or are equal to zero if not reported in the table ($R^2 = 0.51$).

between the sexes. This contrasts with other vertebrate populations subjected to culls, where a reduction in helminth intensities has resulted from a reduction in host densities (Drózd and Dudzinski 1993; Drózd et al. 1994).

No clear pattern of association between helminth species was detected. Most analyses failed to reveal any significant association, while there was no common tendency towards a given type of interaction (positive or negative) within the nonsignificant associations. May (1984) considered a group of species lacking any statistical association to be unstructured; the more a community differs from a random association of species, the more structured it is. Consequently, the helminths of the gulls in the Medes Islands colony constituted an unstructured community in which the occurrence of any species was neither restricted nor favoured by the occurrence of any other species. Our results contrast with those of most studies, which show interactive communities of helminths in avian hosts (see the review in Bush 1990). Holmes and Price (1986) stated that the number of core species within a component community is an indication of the potential for biotic interactions. Accordingly, the occurrence of only one core species in the helminth community in the present study could explain its low interactive rate. If we consider just the group of common species, significant associations also were not detected. Bush and Holmes (1986a) observed that the positive associations between the most frequently occurring helminths are due to the same intermediate host constituting an important item in the diet of the definitive host. However, in the present study all the common helminth species have life cycles with different paths of transmission. *Brachylaima* sp. is transmitted by terrestrial snails (Cribb 1990); *T. (T.) erostris* involves crustaceans, cephalopods, and (or) teleosts as intermediate and paratenic hosts (Hoberg 1994b); *E. contortus* has a direct cycle (Anderson 1992); and *C. obvelatus* is transmitted by amphipods, although freshwater fish may act as paratenic hosts (Wong and Anderson 1982b). Therefore, this disparity in the mode of transmission impede the appearance of a positive association.

Negative relationships were found between certain helminths and host body condition: gulls infected by *T. (T.) erostris* were leaner than noninfected individuals; also, gulls with

higher intensities of *E. contortus* and *Brachylaima* sp. were leaner. As some helminths have been shown to cause lesions and disruptions in the alimentary tract of their hosts (Rausch 1983; Tuggle and Crites 1984; Watson et al. 1987; Connors and Nickol 1991), or to remove resources from their hosts (Price 1980, 1990), it can be assumed that an increase in occurrence and intensity of helminths led to reduction in body condition rather than vice versa. In that case, the occurrence or intensity of these helminths would negatively affect the breeding performance of gulls, since body condition of breeding gulls correlates positively with clutch size (Houston et al. 1983; Bosch et al. 1997). Interestingly, the negative relationship between the occurrence of *T. (T.) erostris* and gull body condition varied with the occurrence/absence of *C. obvelatus*. Thus, gulls infected by *T. (T.) erostris* were in poorer body condition if they were simultaneously infected by *C. obvelatus*. This result supports Holmes (1983), who pointed out that pathogenicity can be affected by parasite community structure. *Cosmocephalus obvelatus* had no significant effect on body condition of gulls as a whole, but body condition of gulls infected by this helminth varied according to the year of sampling, while noninfected gulls showed no such variability. Furthermore, the negative effect of *E. contortus* intensity on body condition of gulls was greater for males than for females. These findings emphasize that variability in helminth pathogenicity depends on several factors, including helminth community structure, environmental factors, and traits of the host. This study demonstrates that in determining the effects of helminths on their host, each species should not be studied in isolation but rather in relation to the whole helminth community.

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