Acquisition of parasites correlated with social rank and behavioural changes in a fish species

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Abstract

A survey of parasites was conducted on 258 *Symphodus ocellatus* (Teleostei: Labridae) collected in Corsica National Park (west Mediterranean). In addition, the total length, sex and social status were recorded for each individual fish. Three species of trematodes were found in the digestive tract. One of the parasites, *Genitocotyle mediterranea*, was only present, with one exception, in males of large size, and principally in the individuals that had the highest status and that were involved in nest construction. Two hypotheses are suggested to explain this particular distribution of a parasite: the immunocompetence handicap and the changing trophic behaviour as the fish grows.

Introduction

The question of the relationship between behaviour and parasitism arises in two forms. On one hand, heavy parasitic loads can modify the behaviour of individuals within populations. These changes can favour transmission of the parasite (Poulin, 1994, 1998). In some cases, it has been demonstrated that the social status of animals can be altered (Delahay *et al*., 1995). Avoidance behaviours can also be initiated by the hosts in response to selective pressures of the parasites (Christe *et al*., 1994; Loehle, 1995).

On the other hand, the relationship between behaviour and parasitism may take an alternative form in which individual behavioural patterns influence the subsequent acquisition of parasites. In primates, Freeland (1981) showed the importance of social status on the level of parasite infection. In the mallard, *Anas platyrhynchos,* populations are composed of mated and solitary males; the mated males are dominant and occupy the most favourable habitats. Gray *et al*. (1989) have demonstrated that solitary males are more heavily parasitized than mated males. Most surveys of parasites in humans, conducted in countries where the hygiene standards are deficient, demonstrate that low social status is correlated with behaviours leading to high levels of parasitism, especially by intestinal nematodes (see Combes, 1995). Conversely, in reindeer, the highest prevalences of the nematode *Elaphostrongylus rangiferi,* whose intermediate hosts are terrestrial gastropods, are observed in dominant individuals, especially in the calves of dominant females (Halvorsen, 1985). These examples illustrate how the host social status and the parasite exposure may be related (Folstad *et al*., 1994).

We report on the relationship between behaviour and parasitism in one population of a coastal fish of the western Mediterranean, *Symphodus ocellatus*, a common labrid fish. This species is sedentary, usually living in rocky areas covered with algae. They are most abundant at depths of 5 to 15 m. Sexual maturity is reached during the second year of life (Lejeune, 1985) with an average lifespan of three years.

In *S. ocellatus,* as in many labrids, there exists a social hierarchy of adult males, which has been divided into

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https://doi.org/10.1017/S0022149X00701040 Published online by Cambridge University Press

three distinctive ranks, each characterized by a specific behaviour and colour pattern (Lejeune, 1985; Michel *et al*., 1987): i.e. terminal males (also called territorial or nesting), helpers, and sneakers. All male fish start as sneakers and end as terminals (Lejeune, 1985). Terminal males are brightly coloured, especially on the operculum, fins and ventral portion of the head. Helpers are less bright and sneakers even less. Our results indicate that terminal males are more heavily infected by certain parasites.

Materials and methods

Sampling was carried out in the Parc Naturel Régional de Corse in July and August of 1992, 1993 and 1994 during the host reproductive period. It was not possible to collect a sufficiently large sample within a single year. Fish were caught by hand net (by scuba-diving). The three types of males were identified by their behaviour and localization with respect to nests. Confirmation of this identification was made by examining the colour pattern. A total of 258 fishes was caught, briefly kept in an aquarium, then killed and necropsied. They were classified as follows (age was determined by size, following Lejeune, 1985):

1. Immature: n = 12
   first year of life: total length (TL): < 4 cm
2. Female: n = 83
   juvenile (end of first year; TL: 4–5 cm): 12
   adult (second year; TL: 5.1–6.5 cm): 34
   adult (third year; TL: 6.6–7.3 cm): 24
   adult (end of third year; TL: > 7.4 cm): 13
3. Male: n = 163
   juvenile (end of first year; TL: 4.1–5.1 cm): 7
   adult (second year; TL: 5.2 - 7.5 cm): 82: sneakers, 68; helpers, 14
   adult (third year; TL: 7.6–9.0 cm): 47: sneakers, 17; helpers, 22; terminals, 8
   adult (end of third year; TL: > 9.1 cm): 27: helpers, 3; terminals, 24

Symphodus ocellatus is rarely infected by ectoparasites. For example, there is no ectoparasitic monogenean reported on this host in the Mediterranean Sea (Sasal *et al*., 1997). Intestinal helminths were exhaustively collected, counted and the position in the gut of each recorded. Parasites were then removed, gently flattened in Bouin-Holland fixative, washed, stained with Grenacher borax carmine, and finally mounted in Canada balsam on permanent slides. All specimens were individually identified to the species level, and each species characterized according to its mean intensity (mean number of parasites per host) and prevalence (percent of infected hosts).

In order to stabilize variances, ANCOVA was performed on transformed variables; i.e. host size by ln and parasite intensities by ln (x + 1).

Homogeneity of variances was assessed by Bartlett's test. Post-hoc tests (Scheffé) were used to demonstrate differences in parasitic infection among males of different status.

By comparison with related species of Hemiuridae for which some information is available, it is possible to propose some hypotheses regarding the life cycles of trematodes infecting *S. ocellatus*. The intermediate host of *Lecithaster stellatus* could be a calanoid copepod of the genus *Acartia*, since this was found to be the case for two related species of *Lecithaster*, according to Hunninen & Cable (1943) and Køie (1989). Similarly, a shrimp related to the genus *Crago* may serve to transmit *Genitocotyle mediterranea*, since this is the host for an American species of *Genitocotyle* (Pratt, 1970). However, for *Macvicaria alacris*, no comparable information is currently available.

In our sampling area, no other fish species was found harbouring *L. stellatus*. We thus assume that *L. stellatus* exploits only *S. ocellatus* as its definitive host. In contrast, *G. mediterranea* was found in the apogonid fish *Apogon imberbis*, and *M. alacris* was found to be common in three labrids living in sympatry, *Symphodus rostratus*, *S. tinca* and *S. cinereus*.

Results

Parasites and site of recovery

Three species of adult trematodes were collected in the digestive tract of *S. ocellatus*. *Macvicaria alacris* (Looss, 1901) Gibson & Bray (1982), and *Genitocotyle mediterranea* Bartoli, Gibson & Riutort (1994), were located in the intestine (Bartoli *et al*., 1994), the third, *Lecithaster stellatus* Looss 1907, in the rectum.

Mean intensity and prevalence of the three species were analysed with the aim of determining the relationships of parasitism with the following host parameters: (i) size (without considering sex or social status), (ii) size classes within each sex, and (iii) social rank of males. No differences in level of infection between years were detected, which allowed pooling data for analysis.

Size and parasitism

In general, for fish greater than 6 cm, parasitism increased with size, whether measured as intensity (fig. 1a) or prevalence (fig. 1b). Parasites were always absent in fish less than 6 cm in length. Furthermore, for fishes > 6 cm, the increase in parasitism differed between parasite species; for fishes between 8 and 9 cm, the increase appeared to be 'explosive' for *G. mediterranea*, with a decrease for sizes above 9 cm, whereas it remained moderate in *M. alacris* and *L. stellatus*. There is a positive correlation between host size and overall parasite intensity ($r = 0.49$; $P < 0.0001$, $df = 1, 244$). Positive relationships were also found for each parasite species: *M. alacris* ($r = 0.28$; $P < 0.0001$, $df = 1, 244$), *G. mediterranea* ($r = 0.40$, $P < 0.0001$, $df = 1, 244$) and *L. stellatus* ($r = 0.18$, $P = 0.004$, $df = 1, 244$).

Sex, size and parasitism

The relationship between size and parasitism was analysed separately in males and females because of the differences in growth rates between the sexes. Males have significantly more parasites than females (t test, $P = 0.0007$). In females, *M. alacris* and *L. stellatus* were present in fishes > 6 cm length, whereas the occurrence of *G. mediterranea* was rare whatever their size. We found this trematode (nine individuals) in a single large female

https://doi.org/10.1017/S0022149X00701040 Published online by Cambridge University Press

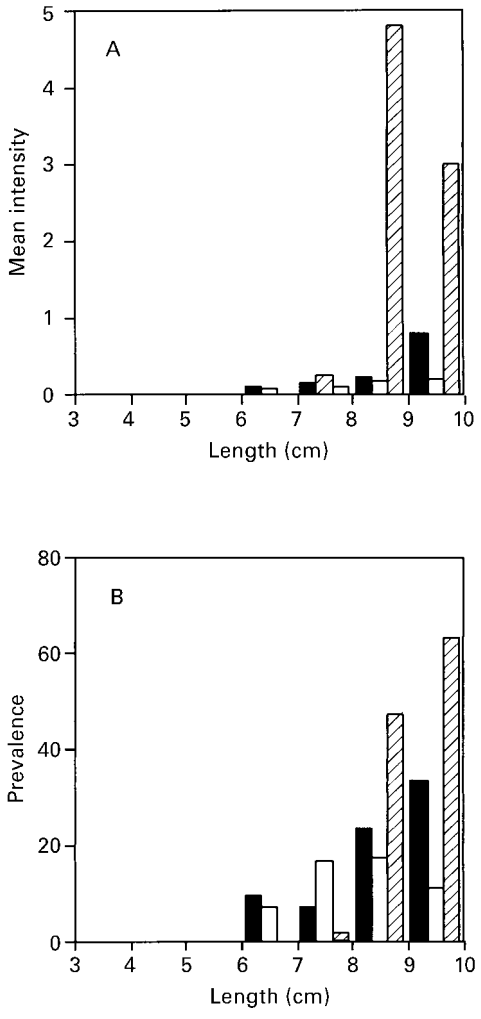

Fig. 1. (a) Relationship between fish size and parasite mean intensity and (b) relationship between fish size and parasite prevalence. (■, *Macvicaria alacris*; □, *Lecithaster stellatus*; ▨, *Genitocotyle mediterranea*).

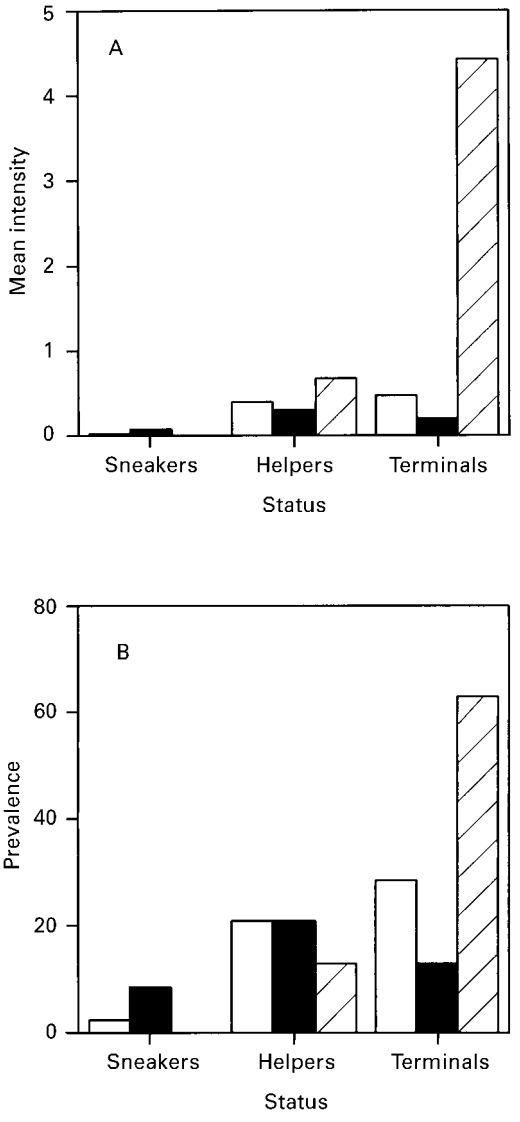

Fig. 2. (a) Relationship between social status of male fish and parasite mean intensity and (b) relationship between social status of male fish and parasite prevalence. (■, *Macvicaria alacris*; □, *Lecithaster stellatus*; ▨, *Genitocotyle mediterranea*).

(TL: 7.7 cm). Females >7.9 cm were free of infections. In males, *M. alacris* and *L. stellatus* were recruited at more than 7 cm and increased in prevalence and mean intensity with size. *Genitocotyle mediterranea* showed a distinctive distribution pattern, being absent in 2-year-old hosts, and becoming frequent and abundant during the third year of life.

Male social rank and parasitism

This analysis was based on the entire male sample, i.e. 163 individuals, classified according to their social status (fig. 2). Intensities were compared using Kruskal-Wallis one-way analysis of variance by ranks. With respect to *M. alacris* and *L. stellatus*, there was a moderate significant difference between sneakers and the other males ($P < 0.05$). On the contrary, a very marked difference ($P < 0.001$) appeared in the case of *G. mediterranea*. There was also a marked difference (chi-square test, $P < 0.0001$) in prevalence.

The ANCOVA showed a significant effect of male status when host size was controlled ($F_{3,158} = 33.213$, $P < 0.00001$; regression result: effect of covariate $F_{1.158} = 4.31$, $P = 0.039$).

Discussion

The terminal males occupy the highest social rank, first acquired at the end of the third (and last) year of life (Lejeune, 1985). Their total length is 8.4–10 cm. During the breeding period (May to August), a terminal male constructs a nest in which several adult females deposit

https://doi.org/10.1017/S0022149X00701040 Published online by Cambridge University Press

unfertilized eggs, which are then fertilized, aerated and protected against predators by the male. During a single breeding season, a terminal male can build several nests successively and so ensure several reproductive cycles.

Helpers have a lower social rank, which is also acquired during the third year (Lejeune, 1985). They are usually smaller than terminal males (7.0–9.3 cm), although their density is similar. These males do not build nests. Each helper is closely associated with a terminal male during the period of sexual activity of the latter and functions to attract females and repel males of lower status (Michel *et al*., 1987). When a terminal male is away from its nest for a brief period and a female comes to the nest, then the helper fertilizes the eggs.

Sneakers are also adult males, but have the lowest rank. Most are two years old and smaller than helpers (5.0–7.8 cm) (Lejeune, 1985). They are the most abundant and stay near the nests, ready to fertilize some eggs if an opportunity occurs (Lejeune, 1985).

Most studies showed positive relationships between parasite abundance (or parasite diversity) and fish length or fish age (Lo *et al*., 1998). The fact that the changes related to host size are markedly different for different parasites suggests that the prey which harbour the infective stages are different, and differently ingested by the fish. If this was not the case, the acquisition and abundance of these parasites would probably exhibit similar patterns in all species.

The analysis by social rank of males provides what seems to be the most important information. Whereas this analysis did not reveal anything special regarding *M. alacris* and *L. stellatus* infections, there was a close positive correlation between host social status and parasitism by *G. mediterranea*. Sneakers were never infected, helpers moderately so, and terminal fish heavily. Also, juveniles and females (one exception out of 83 individuals) were not infected. From a total of 176 *G. mediterranea* collected, 141 (80.1%) were found in terminal males, despite the fact that they represented only 14% of the sample. The ANCOVA confirmed the importance of male status in parasitism.

Social rank may affect parasite exposure and parasite resistance (Folstad *et al*., 1994). Parasite exposure is related to the trophic behaviour of fish. It may be that fish modify their diet as they grow in size, in such a way that the males ascending to the higher social rank (terminal males) ingest prey that the other smaller members of the population cannot capture, or ingest, or both. It is possible that the structure of the nest, built with a variety of plant materials gathered by the terminal male fish, creates a new niche in the environment, one which is then colonized by particular invertebrates, some of which are responsible for the transmission of *G. mediterranea* only in the immediate vicinity of the nest. This may also explain why one female became infected, if the transmission took place during its brief stay over the nest.

The dominant position may affect the immunocompetence of the host, perhaps based on the immunodepressive effects of testosterone in male vertebrates (Folstad & Karter, 1992; see also Møller & Saino, 1994). Increased testosterone appears to reduce the efficiency of the immune system. The phenomenon is well documented in mammals. For example, Barnard *et al*. (1994) have shown not only that dominant male mice have high serum concentrations of testosterone and corticosterone, but also that these males are less resistant to the parasitic protozoan *Babesia microti*. Other examples are reviewed by Barnard *et al*. (1994). In fish, Matty (1985) reviewed the relationships between ornamentation and sexual hormones, whereas Grossman (1985) demonstrated the effectiveness of an interaction between gonadal steroids and immunity. In the freshwater fish *Rutilus rutilus*, Wedekind (1992) found a positive correlation between parasitism and the expression of sexual characters, which are themselves under the control of steroids.

The hypothesis that the observed parasite distribution in *S. ocellatus* may be due to a hormone-mediated immunodepression is attractive because the social rank of fish is likely to be correlated with different levels of sex hormones and other steroids. However, these three trematodes have similar nutritional and physiological requirements, and provoke similar pathogenic effects. This makes it difficult to explain why the decrease in immune efficiency would facilitate the success of only one of the three trematode species so markedly, and not the other two. It cannot be excluded that terminals differ in susceptibility and that the most brightly coloured males would have least parasites (A.P. Møller, personal communication). This hypothesis should be tested.

Acknowledgements

This research was conducted under the control of the Comité Scientifique de la Réserve Naturelle de Scandola. The work was partly financed by grants from the Ministère de l'Environnement and from the Région Corse. We thank Professor T. Yoshino, University of Wisconsin, Professor J.C. Holmes, University of Alberta and Dr A.P. Møller, University of Paris VI for valuable helpful comments and suggestions on the manuscript.

References

Barnard, C.J., Behnke, J.M. & Sewell, J. (1994) Social behaviour and susceptibility to infection in house mice (*Mus musculus*): effect of group size, aggressive behaviour and status-related hormonal responses prior to infection on resistance to *Babesia microti*. *Parasitology* **108,** 487–496.

Bartoli, P., Gibson, D. & Ruitort, J.-J. (1994) *Genitocotyle mediterranea* n.sp. (Digenea, Opoecelidae) from *Symphodus ocellatus* (Teleostei, Labridae) in the Western Mediterranean. *Parasite* **1,** 365–370.

Christe, P., Oppliger, A. & Richner, H. (1994) Ectoparasite affects choice and use of roost sites in the great tit, *Parus major*. *Animal Behaviour* **47,** 895–898.

Combes, C. (1995) *Interactions durables*. Paris, Masson.

Delahay, R.J., Speakman, J.R. & Moss, R. (1995) The energetic consequences of parasitism: effects of a developing infection of *Trichostrongylus tenuis* (Nematoda) on red grouse (*Lagopus lagopus scoticus*) energy balance, body weight and condition. *Parasitology* **110,** 473–482.

Folstad, I. & Karter, A.J. (1992) Parasites, bright males, and the immunocompetence handicap. *American Naturalist* **139,** 603–622.

Folstad, I., Hope, A.M., Karter, A. & Skorping, A. (1994)

Sexually selected color in male sticklebacks: a signal of both parasite exposure and parasite resistance? *Oikos* **69,** 511–515.

Freeland, W.J. (1981) Parasitism and behavioral dominance among male mice. *Science* **213,** 461–462.

Gray, C.A., Gray, P.N. & Pence, D.B. (1989) Influence of social status on the helminth community of late-winter mallards. *Canadian Journal of Zoology* **67,** 1937–1944.

Grossmann, C.J. (1985) Interactions between the gonadal steroids and the immune system. *Science* **227,** 257–261.

Halvorsen, O. (1985) On the relationship between social status of host and risk of parasitic infection. *Oikos* **47,** 71–74.

Hunninen, A.V. & Cable, R.M. (1943) The life-history of *Lecithaster confusus* Odhner, 1905 (Trematoda: Hemiuridae). *Journal of Parasitology* **29,** 71–79.

Køie, M. (1989) On the morphology and life history of *Lecithaster gibbosus* (Rudolphi, 1802) Lühe, 1901 (Digenea, Hemiuroidea). *Parasitology Research* **75,** 361–367.

Lejeune, P. (1985) Le comportement social des Labridés méditerranéens. *Cahiers d'Ethologie Appliquée* **5,** 1–208.

Lo, C., Morand, S. & Galzin, R. (1998) Parasite diversity, host age and size relationships in three coral reef fishes from French Polynesia. *International Journal for Parasitology* **28,** 1695–1708.

Loehle, C. (1995) Social barriers to pathogen transmission in wild animal populations. *Ecology* **76,** 326–335.

Matty, A.J. (1985) *Fish endocrinology*. London, Croom Helm.

Michel, C., Lejeune, P. & Voss, J. (1987) Biologie et comportement des Labridés européens. *Revue Française d'Aquariologie* **14,** 1–80.

Møller, A.P. & Saino, N. (1994) Parasites, immunology of hosts, and sexual selection. *Journal of Parasitology* **80,** 850–858.

Poulin, R. (1994) Meta-analysis of parasite-induced behavioural changes. *Animal Behaviour* **48,** 137–146.

Poulin, R. (1998) *Evolutionary ecology of parasites*. London, Chapman & Hall.

Pratt, I. (1970) Life cycle and host specificity of the marine digenetic trematode, *Genitocotyle acirra* Park. *Journal of Parasitology* **56,** 273.

Sasal, P., Morand, S. & Guégan, J.-F. (1997) Determinants of parasite species richness in Mediterranean marine fish. *Marine Ecology Progress Serie* **149,** 61–71.

Wedekind, C. (1992) Detailed information about parasites revealed by sexual ornamentation. *Proceedings of the Royal Society of London, B Biological Sciences* **247,** 169–174.

(Accepted 15 March 2000)