

Pectoral fin size in a fish species with paternal care: a condition-dependent sexual trait revealing infection status

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SUMMARY

1. The three-spined stickleback, *Gasterosteus aculeatus* L., is a territorial fish with exclusive male parental care. Males oxygenate the eggs with fanning movements of their pectoral fins. The present authors investigated whether the apparent sexual differences in the functional demands of the pectoral fins have resulted in sexual differences in fin size. If males have relatively larger pectoral fins, females may use this as a signal to aid their mate choice for good fathers. Therefore, further objectives were to study the condition-dependency of relative pectoral fin size in males and the relationship with male parasite load.

2. Reproductively active males possessed relatively larger pectoral fins than females in both wild-caught and laboratory-bred fish.

3. In the field, caring males with relatively large pectoral fins were in better physical condition and had more food in their stomachs.

4. Relatively small pectoral fins and poor body condition were associated with infection by the intestinal parasite *Pomphorhynchus laevis* (Acanthocephala), the prevalent parasite species in the study population.

Keywords: condition, *Gasterosteus aculeatus*, pectoral fins, *Pomphorhynchus laevis*, sexual dimorphism

Introduction

Exclusive male parental care is quite common in teleost fishes with external fertilization (Ridley, 1978; Gross & Sargent, 1985). Paternal care often entails oxygenation of the developing embryos by fanning movements of the pectoral fins. Pectoral fins are paired fins which serve manoeuvring activities, and in labriform swimmers, locomotion as well. The use of the pectoral fins in fanning makes additional functional demands on the size and form of the pectoral fins. Larger pectoral fins would increase fanning efficiency because the volume of water which can be moved per unit of time will be greater, provided that

the fin rays are rigid enough and that the necessary musculature is present. Moreover, paternal males defend territories and forage in a limited area. This probably selects for increased manoeuvrability in paternal males, which is achieved by increased pectoral fin size. Because of the different functional demands of pectoral fins in males and females of species with exclusive male parental care, the present authors predicted a sexual dimorphism in pectoral fin size during the breeding season in species with paternal care. Furthermore, they predicted that only males in good physical condition are able to allocate the energy needed for extra fin growth. Lastly, the factors which debilitate male condition, such as reduced food intake or parasitization, are therefore predicted to be negatively associated with pectoral fin size.

Although there exist many examples of exaggerated fins in male fish, there is a lack of data on sexual differences in the pectoral fin size of fish with paternal

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care. The only study which the present authors were aware of at the time that they started the current study was that on the river sculpin, *Cottus hangiongensis* Mori, in which no sexual difference was found (Goto, 1984). It has been known for a long time that the pectoral fin muscles of males three-spined stickleback, *Gasterosteus aculeatus* L., are enlarged during the breeding season (Titschack, 1922; see also Guderley & Foley, 1990). Recently, Brønseth & Folstad (1997) described a sexual dimorphism in relative pectoral fin size in a Norwegian stickleback population in which males had relatively larger pectorals than females. In males, relative pectoral fin size was indeed positively correlated with condition, but contrary to expectation, positively correlated with the intensities of several parasites (Brønseth & Folstad, 1997).

Here the present authors report a study of sexual differences in pectoral fin size in a Swiss stickleback population which is parasitized by a different worm than in the population of Brønseth & Folstad (1997). Different samples of wild-caught fish as well as laboratory-reared fish were studied in order to avoid the confounding effects of parasite load. Sticklebacks are labriform swimmers which show exclusive male parental care (Wootton, 1976, 1984; Bell & Foster, 1994). During the breeding season in spring and early summer, typical male sticklebacks develop conspicuous breeding colouration. The males establish territories in shallow water where they build tunnel-shaped nests of plant materials. After spawning with several females, the males care for the eggs by defending the nest against territory intruders, which include cannibalistic conspecifics. The males also change the nest structure with increasing egg development, remove dead and diseased eggs, and provide the eggs with oxygen and remove waste products by fanning movements of the pectoral fins. The fanning activity can take up two-thirds of a male's time budget (e.g. Van Iersel, 1953).

In addition to studying sexual differences in pectoral fin size, the present authors also investigated the variation in male body condition and parasite infection – two factors potentially of importance for female mate choice (Andersson, 1994) – in relation to relative fin size. The great majority of sticklebacks in the present study population were infested by an orange-yellow worm, *Pomphorhynchus laevis* (Müller 1776) (Acanthocephala). It is transmitted by *Gammarus pulex* L. (Amphipoda) and resides in the posterior end

of the intestine. Because this parasite may affect a male's condition, the present authors looked for correlations among parasite load, relative pectoral fin size and condition.

Materials and methods

Study population

The study sites were three lengths of shallow banks (named Aumatt, Eymatt and Hasli) on the dammed Aare River (Wohlensee near Bern, Switzerland, 46° 57' N, 7° 28' E). The data were collected during the 1993 breeding season (first nest 13 April, last nest 20 August), and supplemented with some data from the 1991, 1992 and 1994 breeding seasons. Just before the beginning of the breeding seasons (April 1993 and 1994), samples of 200 fish were caught at the Hasli site and stocked in large (200-L) outdoor tanks with an inflow of cool (10–15 °C), running water from a well which kept the water temperature in the tank well below 20 °C when the outside air temperature rose above 30 °C in summer. The fish in the tank were fed daily with frozen chironomid larvae.

Pectoral fin size

The size of the pectoral fins was determined on dead fish by measuring the length of the longest ray of the left fin with a digitized vernier calliper. The appropriateness of this measure was checked by comparing maximal fin length with fin area in a sample of the left fins from 17 males. Fins were spread out and magnified with a binocular microscope, video-recorded and the outline (magnification = $\times 23$) was drawn from the monitor. The outline was scanned and measured with an image processing computer program (NIH Image Version 5.5, developed at the U.S. National Institutes of Health and available on the Internet at <http://rsb.info.nih.gov/nih-image/>). The maximal pectoral fin length correlated reasonably well with pectoral fin area [correlation between $\log(\text{length})$ and $\log(\text{area})$, $r = 0.64$, $n = 17$, $P < 0.01$].

The pectoral fin sizes of adult males and females were compared in three groups of fish. One group (D1) consisted of dead fish collected in the outdoor storage tank during the breeding season of 1993. A second group (L1) were males (fish with developing colouration) and females (fish with distended belly

and without red throat) caught and measured just before the breeding season of 1994 at the Hasli site. The third group (L2) was reared in the laboratory (fed with frozen blood worms) from eggs collected in the summer of 1992 from 13 different nests at the Aumatt, Eymatt and Hasli sites. The eggs were hatched in the laboratory (see Bakker, 1986), raised under summer conditions and put into winter-conditions at the age of 5 months (light:dark = 8:16 h, 8–10 °C) in sib groups of 10–30 individuals. At the age of 11 months, a random sample was transferred to summer conditions (L:D = 16:8 h, 15 °C) by putting the fish individually into 10-L tanks which were provided with nesting material and a Petri dish with sand. The males were regularly stimulated with enclosed ripe females to promote nest building. Nearly all the males built nests, and after 2.5 months under summer conditions, their pectoral fins were measured. Additionally, pectoral fin size was measured in males which were reproductively active at the Hasli site (group L3) and some from the other two breeding sites.

Male condition

Male condition and parasite load were determined at the Hasli site during the 1993 breeding season (group L3). In a small ($\approx 2 \text{ m}^2$) area in the littoral zone, a group of about 15 males settled within a few days in spring, and a second, similarly sized group settled after removal of the early group.

After the settlement of the first male in each group, males were checked daily for their willingness to show courtship against a dummy of a ripe female (for details, see Bakker & Mundwiler, 1994). After completion of the nest, the males were hand-netted, and their body size and mass were measured to calculate their condition factor:

$$100 \times \text{mass(g)} / \text{length(cm)}^b$$

where b is the slope of the regression of $\log(\text{mass})$ on $\log(\text{length})$ (Bolger & Connolly, 1989). In order to distinguish neighbouring males, the nearest neighbours were differentially marked by clipping the tip of the first and/or second dorsal spine. Thereafter, the males were released at their nests, caught again and their wet mass determined at the end of their breeding cycle, i.e. ≈ 3 weeks after settlement, just before hatching of the eggs. The male fish were transferred

to the laboratory and their wet mass was again determined after 2 days of starvation in order to quantify the stomach contents. The males were then killed by decapitation, their pectoral fins were measured and the males were dissected to determine macro-parasite load (see below). The data on pectoral fin size and parasites were supplemented with some data of males that cared for offspring during the same period at the other two sites.

Parasite load

The intensity of infection by the prevailing parasite, a spiny headed worm called *Pomphorhynchus laevis* (Acanthocephala), was determined by dissection of the fish and counting the number of live acanthocephalans in the intestine, and the number of dead or remnants of dead worms (whether encapsulated or not) outside the intestine by checking the body cavity and viscera. Dead worms were frequently located in the outer membranes of the intestinal canal. When not specified, the number of acanthocephalans refers to the total number of live and dead worms. The prevalence and intensity of infection were assessed from samples of reproductive males at various breeding sites during the 1991–1994 breeding seasons: dead fish were collected from the outdoor storage tank in 1993 (group D1) and fish which were found dead during the present authors' regular visits to the various breeding sites throughout the 1993 breeding season (group D2) were also studied.

Two other macroparasites were found in the study population, but with low prevalences (both $< 5\%$). One was another acanthocephalan species which could easily be distinguished from *P. laevis* because it was white, had fewer hooks on its proboscis and resided in the intestine just behind the stomach. Feeding experiments showed that it was transmitted by *Asellus aquaticus* L. (T. C. M. Bakker & B. Mundwiler, unpublished data). The other macroparasite was a trematode species which was located in the bladder.

Data analysis

When applying parametric statistics, variables were checked for normal distributions using the Kolmogorov–Smirnov test with Lilliefors' correction. The following transformations were applied to achieve

normality: $\log_{10}(x)$ transformation for pectoral fin length, body mass (minus liver mass) after starvation, liver mass and body size; $\log_{10}(1 + x)$ transformation for the mass of the stomach contents.

All statistical tests applied in this study were two-tailed.

Results

Sexual dimorphism in pectoral fin size

The relationship between standard body length and the length of the pectoral fins was allometric in both males and females, as illustrated for the dead fish in the outdoor storage tank (group D1) in Fig. 1. Males had significantly longer pectoral fins for a given body length than females (Fig. 1, Table 1). The allometric relationship between body length and pectoral fin size was similar for males which died in the outdoor storage tank (group D1, $n = 25$) and males which reproduced during the same period at the Hasli site (group L3, $n = 29$) (regression coefficients: ANCOVA, $F = 0.50$, d.f. = 1,50, $P = 0.48$; y-intercepts: ANCOVA, $F = 0.78$, d.f. = 1,51, $P = 0.38$). This similarity suggests that the males which died in the outdoor tank were an unbiased sample with respect to their pectoral fin sizes. In other groups, a similar sexual dimorphism in pectoral fin size was assessed (i.e. in groups L1 and L2; Table 1).

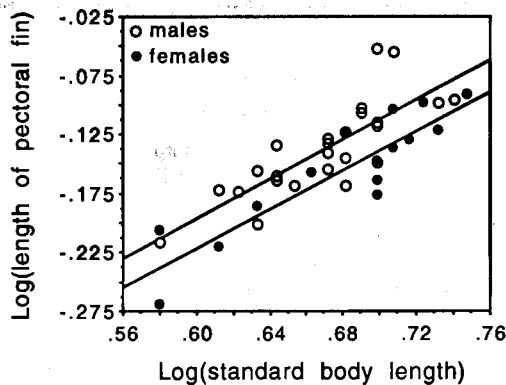


Fig. 1 Correlation between standard body length (log of length, cm) and the length of the pectoral fin (log of the length of the left fin, cm) of 25 males (○) and 15 females (●) which died in the outdoor storage tank during the 1993 breeding season (group D1). The lines are least-square regressions (males: $y = 0.844x - 0.703$, $r^2 = 0.64$, $F = 41.43$, d.f. = 1,23, $P < 0.0001$; females: $y = 0.829x - 0.719$, $r^2 = 0.81$, $F = 54.90$, d.f. = 1,13, $P < 0.0001$).

Condition-dependency of pectoral fin size

The condition-dependency of pectoral fin size was determined in reproductively active males at the 1993 Hasli site (group L3). The exponent in the formula for the condition factor was 2.782 for males during the egg-collection phase [regression of $\log(\text{mass})$ on $\log(\text{length})$: $y = 2.782x - 1.666$, $r^2 = 0.76$, $F = 109.07$, d.f. = 1,34, $P < 0.0001$]. The mean length of the pectoral fins of these males was standardized for differences in body length by taking the residuals of the regression of $\log(\text{fin length})$ on $\log(\text{body length})$. Standardized pectoral fin size was positively correlated with male condition, as determined at the end of the paternal phase ($r^2 = 0.18$, $F = 5.76$, d.f. = 1,27, $P < 0.03$).

The mass of the stomach contents relative to body mass correlated positively with standardized pectoral fin size ($r^2 = 0.25$, $F = 8.53$, d.f. = 1,26, $P < 0.01$). Thus, the fullness of the stomach may be partly responsible for the condition-dependency of relative pectoral fin size. In a multiple regression analysis, the simultaneous effect of components of condition on standardized pectoral fin length was tested (Table 2). The mass of the stomach contents was indeed most strongly correlated to pectoral fin size and pectoral fin size only tended to correlate with body mass (minus liver mass) after starvation.

Pectoral fin size, condition and survival of parasitized males

Dissection of samples of reproductively active males during the breeding seasons of 1991 through 1994 showed an overdispersed distribution of *P. laevis* (Fig. 2). The degree of overdispersion, as defined by the variance:mean ratio, was 4.6. The prevalence of infection was high (75.2%), with a median of three worms in infected males (range = 1–20).

The group D2 males had a significantly higher *P. laevis* load than males which were reproductively active during the same period of time (median number of parasites in 22 D2 males: 3, range 0–23; in 59 active males: 1, range 0–17; Mann-Whitney U-test, $z = 2.97$, $P = 0.003$). The difference may be indicative of the pathogenic effect that this acanthocephalan parasite has on its host. The live acanthocephalans in the intestine were responsible for the different parasite load of live and dead males (live parasites in 59 live males, median = 1, range 0–17; in

Table 1 Comparison of linear least-square regression of the length of the pectoral fin (\log_{10} of the length of left fins, cm) on standard body length (\log_{10} of length, cm) between males and females in various groups using ANCOVA

Group*	Regression coefficients			y-Intercepts		
	F-value	d.f.	P-value	F-value	d.f.	P-value
D1	0.01	1,36	0.92	11.67	1,37	0.002
L1	1.89	1,87	0.17	4.55	1,88	0.04
L2	2.43	1,56	0.13	5.98	1,57	0.02

*Key: (D1) dead adult fish (25 males, 15 females) in the outdoor storage tank during summer; (L1) adult fish (69 males, 22 females) caught shortly before the breeding season; and (L2) laboratory-raised, reproductively active fish (32 males, 28 females) from eggs collected in the field.

22 dead males, median = 2.5, range 0–21; Mann-Whitney *U*-test, $z = 3.81$, $P = 0.0001$. The number of dead parasites was similar in 59 live males (median = 0, range 0–4) and 22 dead males (median = 0, range 0–2; Mann-Whitney *U*-test, $z = 0.58$, $P > 0.50$). The number of live parasites was greater than that of dead ones in both live (Wilcoxon matched-pairs signed-ranks test, $n = 42$, $z = 3.11$, $P < 0.002$) and dead males ($n = 20$, $z = 3.93$, $P < 0.0001$). In live males, the number of live parasites was not significantly correlated to the number of dead worms ($r_s = 0.04$, $n = 59$, $P > 0.78$) nor in D1 females ($r_s = 0.31$, $n = 15$, $P > 0.24$), but the numbers of live and dead worms were significantly positively correlated in D2 males ($r_s = 0.57$, $n = 22$, $P < 0.01$).

Males and females had similar parasite loads, as determined in D1 and D2 fish: the prevalence of infection was similar for the sexes in both samples (χ^2 test with continuity correction, $P > 0.70$ and $P > 0.91$, respectively), as was the intensity of infection in infected individuals (Mann-Whitney *U*-test, $P > 0.60$ and $P > 0.20$, respectively).

The relationship of pectoral fin size and condition

Table 2 Multiple regression of standardized pectoral fin length on components of condition, i.e. mass of stomach contents, body mass (minus liver mass) after starvation, liver mass and body size, in caring males at the 1993 Hasli site (group L3). The variables were $\log_{10}(x)$, or in the case of stomach contents, $\log_{10}(1 + x)$ transformed. Model: $n = 28$, $r^2 = 0.38$, $F = 3.57$, d.f. = 4,23, $P = 0.02$

Variable	Standard regression coefficient	<i>t</i>	<i>P</i> -value
Stomach contents	0.58	3.50	<0.01
Body mass	0.78	1.90	0.07
Liver mass	-0.32	1.32	>0.19
Body size	-0.57	1.62	>0.11

with infection status was analysed using reproductively active males at the Hasli site in 1993 (group L3). Whether a male harboured *P. laevis* or not was revealed by its standardized pectoral fin size: infected males had significantly smaller fins than uninfected males (*t*-test, $t = 2.22$, d.f. = 27, $P < 0.04$). This relationship was confirmed in the larger data set of reproductively active males in 1993 ($t = 2.82$, d.f. = 46, $P < 0.01$). Infected males also had a lower body condition during the egg-collection phase ($t = 2.52$, d.f. = 29, $P < 0.02$), but not at the end of the paternal phase ($P > 0.21$). Neither standard pectoral fin size nor condition at the beginning nor at the end of the breeding cycle were indicative of the number of parasites (i.e. the total, live or dead) in infected males (all $P > 0.24$).

Discussion

The current findings confirmed Brønseth & Folstad's (1997) finding of a sexual dimorphism in the relative pectoral fin size of sticklebacks during the reproductive season. Because the present authors compared the relative pectoral fin sizes of the sexes in several field samples and in parasite-free, laboratory-reared fish of well-defined reproductive status, they circumvented several shortcomings of Brønseth & Folstad's (1997) study, namely small sample size, the ill-defined male reproductive status caused by the sampling method, and confounding effects of parasite mass and sexual differences in parasite prevalence and/or intensity (see below).

Relatively large pectoral fins are probably beneficial to caring males (see 'Introduction'). Like Brønseth & Folstad (1997), the present authors found that males with relatively large pectoral fins had a greater condition factor at the end of the care period, and

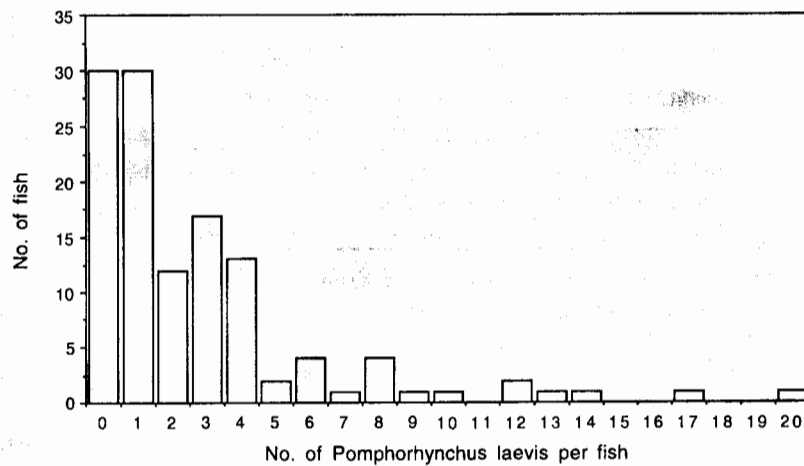


Fig. 2 Frequency distribution of the number of (live and dead) *Pomphorhynchus laevis* in 121 reproductively active males in the Wohlensee population between 1991 and 1994.

furthermore, had relatively more food in their stomachs, suggesting increased foraging efficiency. Because the present authors measured body mass after starvation, they could not determine which prey items made up the stomach contents. The possibility that males with relatively large pectoral fins consumed more of their own eggs cannot be excluded. However, this seems unlikely because the standardized pectoral fin size also correlated with condition during the egg-collection phase ($P = 0.05$). Relatively large pectoral fins may also make fanning more efficient. The experimental reduction of pectoral fin size resulted in an increased beat frequency of the fins during fanning, but at the cost of developmental rate of the embryos (R. Künzler & T. C. M. Bakker, unpublished data).

The extra pectoral fin growth of male sticklebacks may be androgen dependent, as is often the case in secondary sexual extensions of fins (e.g. Yamamoto, 1969; Kirpichnikov, 1981; Basolo, 1991). Males which were parasitized by *P. laevis* had relatively smaller pectoral fins than uninfected males. Infection will trigger the immune system in which androgens play a regulatory function (Folstad & Karter, 1992; Wedekind & Folstad, 1994). The subsequent reallocation of energy to immune function and reduction in androgen synthesis may be responsible for reduced fin growth in infected males. Relative pectoral fin size was not further reduced by the level of infestation. Infestation *per se* may be the main determinant of the immune response, not the intensity of infection. Similarly, Kennedy *et al.* (1987) and McMinn (1990)

found that sigmoid display rate in male guppies, *Poecilia reticulata* Peters, was reduced by the presence of the nematode parasite *Cammalanus cotti*, but not further reduced by multiple infection. Sigmoid display rate is a predictor of female mate choice in guppies and is affected by tail fin size (Bischoff, Gould & Rubenstein, 1985). Thus far, the present authors' data on the relationship between pectoral fin size and parasites are correlational, and have to be extended by experiments in order to reveal causality. For instance, the possibility that males with relatively small pectoral fins were more susceptible to parasites because they had a lower physical condition cannot be excluded.

In contrast to the present findings is the larger pectoral fin size of male sticklebacks which were infected by the cestode *Schistocephalus solidus* (Brønseth & Folstad, 1997). However, the mass of *S. solidus* can be greater than that of its stickleback host (e.g. Milinski, 1990), thereby severely changing body form and mass of its host. Thus, the greater fin size of infected males may simply be a reaction to cope with the increased body mass and volume. Brønseth & Folstad (1997) also established positive correlations between parasite intensity of infected hosts and pectoral fin size for the most common parasite species except for small (possibly juvenile) specimens of *Diphyllbothrium* species. The interpretation of the above authors was that males with large fins experienced increased parasite exposure and/or were more susceptible to parasites. In the present study, relative pectoral fin size was not significantly

correlated with parasite intensity. A complication of Brønseth & Folstad's (1997) study is that prevalences were so high that all males were at least infected by two parasite species. Therefore, the associations between male traits and particular parasites are unavoidably confounded by other parasite species. Moreover, the positive association between relative pectoral fin size and parasites may have had a non-conservative influence on the sexual dimorphism in fin size, as established by Brønseth & Folstad (1997). Because the above authors only sampled nine females for comparison, parasite prevalences and/or intensities may easily differ by chance alone between the sexes. Further sex differences in parasite susceptibility may exist (Poulin, 1996; Schalk & Forbes, 1997; Wedekind & Jakobsen, 1998). Unfortunately, Brønseth & Folstad (1997) gave no data on parasites in female sticklebacks.

Do the opposite correlations between pectoral fin size and infection status in the present study and that of Brønseth & Folstad (1997) suggest that pectoral fin size is an ambiguous signal, and therefore, not likely to be used as a criterion in mate choice? The present authors question this. Firstly, there may be population differences: Folstad *et al.* (1994) also established a positive correlation between the intensity of red breeding colouration and infection status in Norwegian sticklebacks, whereas Swiss sticklebacks showed a reverse relationship after experimental infection with a different parasite (Milinski & Bakker, 1990). Secondly, different parasites may have different effects on secondary sexual traits (e.g. Wedekind, 1992). Thirdly, the information about male quality which is transmitted by relative pectoral fin size may only be properly evaluated in connection with the expression of other sexual traits like breeding colouration.

The pectoral fins are rather inconspicuous to the human eye because these organs are transparent; only the fin rays (usually 10 per fin) are highlighted to some extent by four rows of melanophores along the entire length of each ray. It seems unlikely that females can directly assess pectoral fin size, but the present authors have not confirmed this, nor have they assessed its conspicuousness under ultraviolet radiation (Bennett, Cuthill & Norris, 1994). Females may use other male traits as indicators of pectoral fin size. Relative pectoral fin size may be indirectly assessed from particular locomotion patterns. Pectoral

fins are used for steering and braking (Geerlink, 1989), so movement patterns which involve changes in direction and speed may reveal pectoral fin size. The zigzag courtship dance of sticklebacks is well-known, and consists of a series of jumps in an imaginary plane between the nest and the female in such a way that the male is moving in a zigzag-like manner towards the female. It is likely that the pectoral fins play a role in the courtship jumps, as was also suggested by Brønseth & Folstad (1997), so that females may be able to get information on relative pectoral fin size by characteristics of the zigzag dance. Courtship display correlates with reproductive success in several fish species with male parental care (Gronell, 1989; Knapp & Kovach, 1991; Knapp & Warner, 1991; Karino, 1995). In the bicolor damselfish, *Stegastes partitus* Poey, courtship rate is an honest indicator of male parental quality (Knapp & Kovach, 1991).

The other way that female three-spined sticklebacks may indirectly get information about relative pectoral fin size and paternal care ability is by observing males during fanning activity. Part of the courtship sequence in sticklebacks is one or more nest visits by the male; the female stays at a certain distance from the nest while the male performs some nest activities including fanning. Fanning during courtship is called displacement fanning because it is also performed before there are eggs in the nest (e.g. Sevenster, 1961). Rohwer (1978) interpreted displacement fanning as female deception because females prefer to spawn in a nest which already contain eggs (e.g. Goldschmidt, Bakker & Feuth-de Bruijn, 1993). An alternative functional interpretation would be that displacement fanning is an honest signal of male parental care ability. The other species of the stickleback family also include displacement fanning (or displacement sucking in the case of *Apeltes quadracus* (Mitchill); *Spinachia spinachia* (L.); Rowland, 1974) in their courtship except for (McLennan, 1993).

Although there are conflicting reports about the damaging effects of *P. laevis* in fish (e.g. Chubb, 1965; Hine & Kennedy, 1974), it is likely that the parasite reduces the fitness of its host in small fish species like the stickleback. The present authors found that the intensity of infection in sticklebacks found dead in the field was greater than that in sticklebacks which were reproductively active at the same time. Furthermore, infected males had a poorer body condition. Additionally, the parasitization status correlated with

relative pectoral fin size in reproductively active males, and thereby, may decrease reproductive success by reducing male attractiveness and paternal care ability.

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