Pectoral fins and paternal quality in sticklebacks

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Sexual selection through female mate choice exerts a strong selection pressure on males' sexual traits, particularly when direct benefits are involved. In species with male parental care, one would expect sexual selection to favour paternal quality, for instance through selection on morphological structures which promote quality. We experimentally studied the influence of pectoral fins on paternal quality in male three-spined sticklebacks (*Gasterosteus aculeatus* L.). After reductions of fin area to different degrees, similar-sized males had to perform a complete reproductive cycle in enclosures in the field. The collected data on fanning behaviour and egg development showed that a reduction in pectoral fin size affected paternal quality probably through an increased beat frequency of the pectorals. Thus, pectoral fins can potentially signal paternal quality to choosy females.

Keywords: stickleback; paternal quality; fanning; pectoral fin size; beat frequency; embryo development

1. INTRODUCTION

Choosy females exert a strong selection pressure on males in order to obtain either indirect benefits such as parasite resistance or direct benefits such as territory quality and broodcare or a combination of both (Kirkpatrick & Ryan 1991; Andersson 1994). It is often believed that the effects of direct benefits outweigh those of indirect benefits in the evolution of mate preferences (e.g. Kirkpatrick & Ryan 1991; Johnstone 1995; Ryan 1997; Kirkpatrick & Barton 1997). Species with exclusive male parental care, which is frequent among fishes with external fertilization (Gross & Sargent 1985), are well suited to the study of the benefits of mate choice, inclusive of indicators of parental quality.

The three-spined stickleback (*Gasterosteus aculeatus* L.) is a typical fish species with paternal care. During the parental phase, stickleback males protect their offspring by defending the nest and ventilate the eggs by regular beats of their pectoral fins. Fanning oxygenates the eggs and dilutes waste products. It can consume up to two-thirds of a male's time-budget (Van Iersel 1953). The fanning effort increases with the increasing oxygen demands of the eggs (e.g. with increasing egg number) which is achieved by adjusting the total fanning time and fanning bout length (Van Iersel 1953; Sevenster 1961). With increasing fanning effort, embryos develop faster (Van Iersel 1953). Because fanning is generated by movements of the pectoral fins, one might expect that fin morphology will affect the fanning efficiency. To our knowledge, there is no information so far about the influence of the pectoral fins on the various aspects of paternal care. In this study, we investigated the influence of fin size manipulations on embryo development and survival. Males of similar body size had to care for similar egg numbers after different experimental reductions of pectoral fin size. We expected a more pronounced decrease in paternal quality which was measured as embryo survival and/or development with greater reductions of fin area.

2. MATERIAL AND METHODS

(a) *Sticklebacks*

Approximately 600 fishes were caught shortly before the breeding season (early May 1995) from the Wohlensee population (near Bern, Switzerland, 46°57′ N, 7°28′ E) and stocked in 2001 tanks. Sixty males with developing breeding coloration and the most common standard body size (4.0–5.0 cm) were selected from the stock at the end of May and placed singly into 121 plastic aquaria with a layer of mud and nesting material (filamentous algae and mosses) which were separated by opaque grey partitions. The males were stimulated daily with a ripe female enclosed in a 11 container. The fishes were fed daily with frozen bloodworms. Females with extended bellies were regularly selected from the stock tanks and housed in groups of around 25 individuals in 551 aquaria. They were fed additionally with live *Tubifex*. After spawning, they were returned to other stock tanks. The stock tanks and male and female aquaria were supplied with cool (10–15 °C) running water from a well which kept the water temperature in the tanks well below 20 °C when the air temperature rose to 30 °C in summer. The tanks were lit 16 h a day.

(b) *Experimental design* (*general*)

In order to investigate the influence of the pectoral fin size of male sticklebacks on paternal quality independently from other correlated characters, we manipulated their fin sizes experimentally. Because enlargement of the pectoral fin size is impossible, we made reductions to different levels: two males of similar body size (maximum difference of 1mm) were operated on immediately after each other and one male's pectoral fin size was reduced to a larger extent than that of the other male (see § 2(e)). By doing so, we enlarged the variation in pectoral fin size experimentally, while keeping the reduction in pectoral fin size balanced throughout the season. Males had to care for four clutches of eggs under field conditions. The brood cycles of the males ran parallel throughout the season.

As a control group, we measured the fanning behaviour of ten additional males with intact pectoral fins from the same

stock population. These males were comparable to the experimental males in every respect except for the manipulation of their fin sizes. They were kept in enclosures located near those of the experimental males and they also had to care for four clutches of eggs under field conditions. Their brood cycles ran parallel to those of the experimental males. Because these males also served as controls in another experiment (M. Tognola and T. C. M. Bakker, unpublished data), fanning behaviour was quantified by direct observations from a distance (compare § 2(f)). We therefore have no data on the beat frequency of the control males' pectoral fins. The descriptions given below concern the experimental males.

(c) *Enclosures*

Twenty reproductively active males were transferred together with their nests from the male tanks to outdoor enclosures. The enclosures were situated in the shallow (water level 10–45 cm) littoral zone of the Wohlensee. Perforated (diameter 5 mm and centres 8 mm apart) aluminium plates with a height of 100 cm were fixed into a frame of 600 cm × 70 cm. Nine grey PVC plates (100 cm × 70 cm) divided the enclosure into eight compartments (75 cm × 70 cm), each with two walls of PVC and two of aluminium. These enclosures kept predators and large conspecifics out while allowing the exchange of water and drift food. The nests had to be built on the natural, oxygen-poor mud bottom. The nest sites were directed by the presence of two plants (*Myosotis scorpioides*) in one of the corners of the enclosures. During the experiments, the water temperature close to the enclosures was measured daily, around midday.

(d) *Clutches*

As soon as males had built a nest with a clearly visible entrance and courted to a ripe female enclosed in a transparent beaker with a perforated lid, we initiated spawnings. Each male spawned with four females within a short period of time (median 2.5 days and range two to six days). The number of eggs a female spawned was estimated from her loss of body mass. The mean egg mass ($\pm$s.d.) was 3.0 ± 0.2 mg ($n = 28$) (M. Tognola, unpublished data) for stickleback females of the 1995 Wohlensee population. Females were randomly assigned within males, but every last female was selected for her initial weight to minimize variation in the total egg number between males.

(e) *Experimental shortening of the pectoral fins*

For the first eight males, shortening of the pectoral fins was done before the males had received eggs. Because ripe females refused to spawn in empty nests of recently operated-on males on several occasions, we operated on the rest of the males after the last spawning. Within two males, a third person randomly determined which of the males would have the stronger reduction and released the males after the operation in their enclosures. The observer (R.K.) was thus naive as to the operational status of the males.

Prior to operation, the males were anaesthetized in 500 ml of a daily refreshed 0.1% solution of 2-phenoxy-ethanol. The male was then put gently into the round opening of a wooden block covered with soft foam rubber (figure 1). The operation was done under a ×6.4 magnification binocular microscope with a video tube. One of the pectorals was spread to a maximum and video recorded. Either *ca.* 2 mm or less than 1 mm of the outer edge of the fin was removed with a sterilized blade. The cut was parallel to the original edge and, therefore, did not change the shape of the fin. The operated-on fin was again video recorded
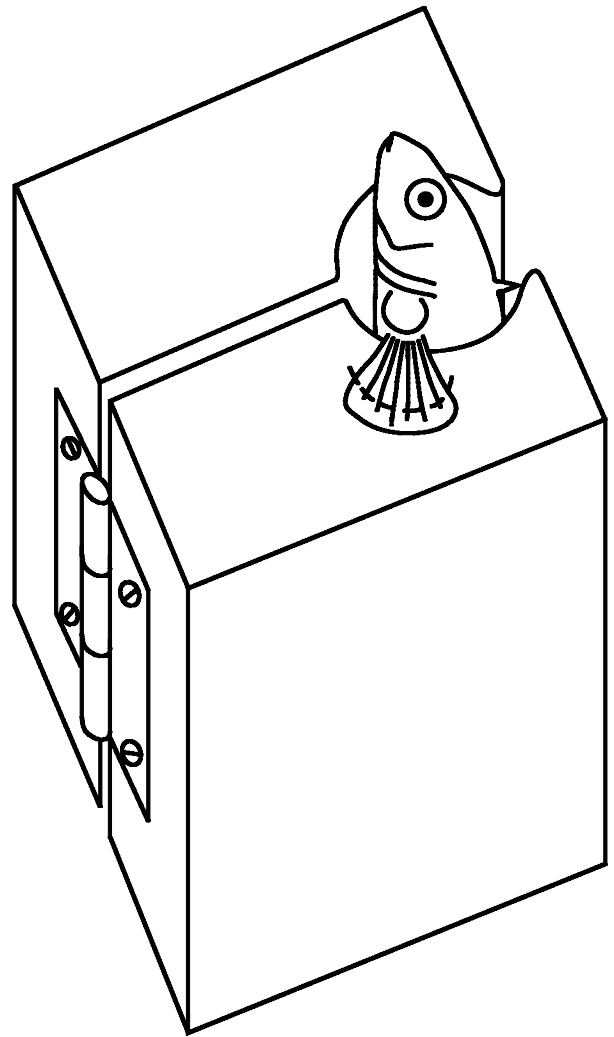

Figure 1. The apparatus used for the experimental reduction of pectoral fin size in male three-spined sticklebacks. The cut is indicated by the dotted line.

and the fish was turned around for the other pectoral fin's operation. At the end, we reanimated the fish in cold running tap water. After a recovery period of *ca.* 10 min, the male was put back into the enclosure where it resumed normal care activities within 1 h. In order to measure the pectoral fin area before and after operation, the fin's outlines were drawn from a video monitor, scanned and measured using NIH Image (v. 5.5). The fin area (mm^2) was calculated as follows: $(25.4 \sqrt{A}/(X \times F))^2/(X \times F))^2$, where A is the fin area in pixels (NIH Image 25.4 mm per inch), X is the scanning resolution (80 dpi) and F is the magnification factor (binocular microscope, video camera and monitor: ×14 in total).

Two males were left out of the analysis as the right pectoral fin of one male (largely reduced fins) became seriously mouldy, while another male (slightly reduced fins) had cannibalized his first two clutches shortly after spawning.

(f) *Observation of males during paternal care*

Male paternal care activities were observed on days 5 ($n = 7$ males) or 6 ($n = 11$ males) after fertilization of the first clutch via a video camera which was mounted above its nest. Observations were usually done before noon. An inverted clay flowerpot served as a collar around the objective and was dipped 2 cm under the water surface, thus preventing reflections of the water

surface. The vertical position of the camera was adjusted to the actual water level. Male parental behaviour was observed on a video monitor and recorded inside a boathouse, so that we could follow the males from a distance without disturbing them by our presence. Males usually resumed parental behaviour within 10 min after the installation of the video camera. The water temperature at the nest entrance was measured immediately after data collection.

The total fanning time and the number of fanning bouts were counted during a period of 30 min for each male starting after the male resumed parental behaviour. The fin beat frequency was measured from six to eight randomly chosen fanning bouts. We aimed at counting 100 beats per bout; however, many bouts were of shorter duration leading to an average of 81.81 beats per bout (range 67–100 and $n = 8$ males). During the slow-motion playback, the time needed for the number of fin beats counted was extracted from the frame counter of the video cassette recorder. After having scored the first eight males, it became clear that the beat frequency was highly repeatable within males (one-way ANOVA, $F_{7,52} = 41.87$, $p < 0.0001$ and $r_{I} = 0.85$). We therefore considered it sufficient to count three bouts for the following ten males. We estimated the amount of water a male can move with every fin beat by the product of the pectoral fin size after the operation and the beat frequency. This will be referred to as the fanning efficiency from now on.

(g) *Embryo survival and development*

Males were taken out of the enclosures shortly before hatching of the young, that is six to ten days after fertilization of the first clutch depending on the water temperature. Several male traits were quantified (see §2(h)) and the remaining eggs counted. Only eggs with live embryos were used in the analysis of embryo survival. Eggs from one nest were kept under standardized laboratory conditions until hatching (zero to four days), that is in a 500 ml vessel at 15 °C in aerated water from a well. The water was daily refreshed and newly dead eggs were removed. The vessels were checked three times a day until the first young had hatched. The developmental time was calculated as the difference between the time and date that the first young hatched and the date of its fertilization.

(h) *Male characteristics*

We took slides of the anterior half of the ventral side and one lateral side at introduction of the males into the enclosures. The intensity of the male red breeding coloration was quantified by densitometer analysis (for the methodological details see Bakker & Mundwiler (1994)). After the experiment the number of *Pomphorhynchus laevis* in the intestine was assessed by dissection of the males.

The probabilities of the statistical tests are two-tailed. When the direction of change could be predicted *a priori*, we used directed testing according to Rice & Gaines (1994).

3. RESULTS

The control ($n = 10$) and experimental males ($n = 18$) were not significantly different with respect to body size, intact pectoral fin area and the number of eggs they had to care for (*t*-tests, all $p > 0.23$). The fin reductions did not change the unsigned differences between the left and right pectoral fins within males significantly (paired *t*-tests, absolute asymmetry $p > 0.60$ and relative asymmetry $p > 0.49$). No significant differences between the

control and experimental males were evident in their fanning behaviour (percentage of time spent fanning, $t = 1.22$, d.f. $= 26$ and $p > 0.23$, and number of fanning bouts per minute $t = 0.13$, d.f. $= 26$ and $p > 0.89$). Thus, the fin manipulations did not seem to result in abnormal parental care. Similar results were obtained when we treated the large- and small-reduction groups of experimental males separately (ANOVAs with d.f. $= 2, 25$; all $p > 0.34$).

Because the fanning effort is known to be influenced by the oxygen demand of the developing embryos in a linear fashion (e.g. Van Iersel 1953; Östlund & Ahnesjö 1998), the fanning data were standardized for the developmental stage of the embryos and the water temperature by taking the residuals from linear regressions. The developmental stage of the embryos for each nest at the time of scoring fanning was estimated by dividing the day of observation by the total duration of the individual parental phase.

There was no significant correlation between the pectoral fin sizes before and after operation ($r = 0.46$, $n = 18$ and $p > 0.053$), the trend being due to two extreme males, that is the male with the smallest intact fins which were greatly reduced and the male with the biggest intact fins which were slightly reduced (without the two extremes $r = 0.24$ and $p > 0.36$). The pectoral fin size after operation did not correlate significantly with the redness index and parasite load with *P. laevis* ($r = 0.07$ and $p > 0.77$, and $r = 0.17$ and $p > 0.50$, respectively). There existed a significant correlation between reduced fin size and body size ($r = 0.52$ and $p = 0.03$) but this was caused by the two smallest males being in the large-reduction group (without the extremes $r = 0.40$, $n = 16$ and $p > 0.12$). The mean (s.d.) male body size was 47.0 $\pm$ 1.24 mm. The pectoral fin size was reduced by 9.1–50.3% (median 29.1%). The beat frequency of the pectoral fins during fanning was 361 $\pm$ 34.1 beats min^{-1} with a range of 293–424 beats min^{-1}. There existed a significant negative correlation between the fin size and standardized beat frequency (figure 2*a*) ($r = -0.64$, $n = 18$ and $p < 0.01$) suggesting that males (actively or passively) compensate for a reduced pectoral fin size. However, the fanning efficiency, which was approximated by the product of the fin area and beat frequency, still correlated with the pectoral fin size (figure 2*b*) ($r = 0.91$, $n = 18$ and $p < 0.0001$). Males could thus only partly compensate for a pectoral fin size reduction. The alternative, that males with reduced fins allocate a higher portion of their daily time-budget to fanning activity, could not be detected (figure 2*c*) ($r = 0.14$, $n = 18$ and $p > 0.57$). The offspring of males with a higher beat frequency had an extended developmental time to hatching (figure 2*d*) ($r = 0.53$, $n = 14$ and $p_{\text{directed}} < 0.032$). As was expected under variable and changing field conditions, the relationship between the pectoral fin size and developmental time was not significant ($r = -0.03$, $n = 18$ and $p > 0.90$).

The expected relationship between reduced paternal quality (measured as the beat frequency) and increased embryo mortality (measured as the percentage of eggs lost) in the same 14 males was not significant ($r = -0.19$ and $p > 0.52$). The negative relationship was more suggestive, although not significant, when we included all 18 males ($r = -0.34$ and $p > 0.16$). Contrary to expectation,
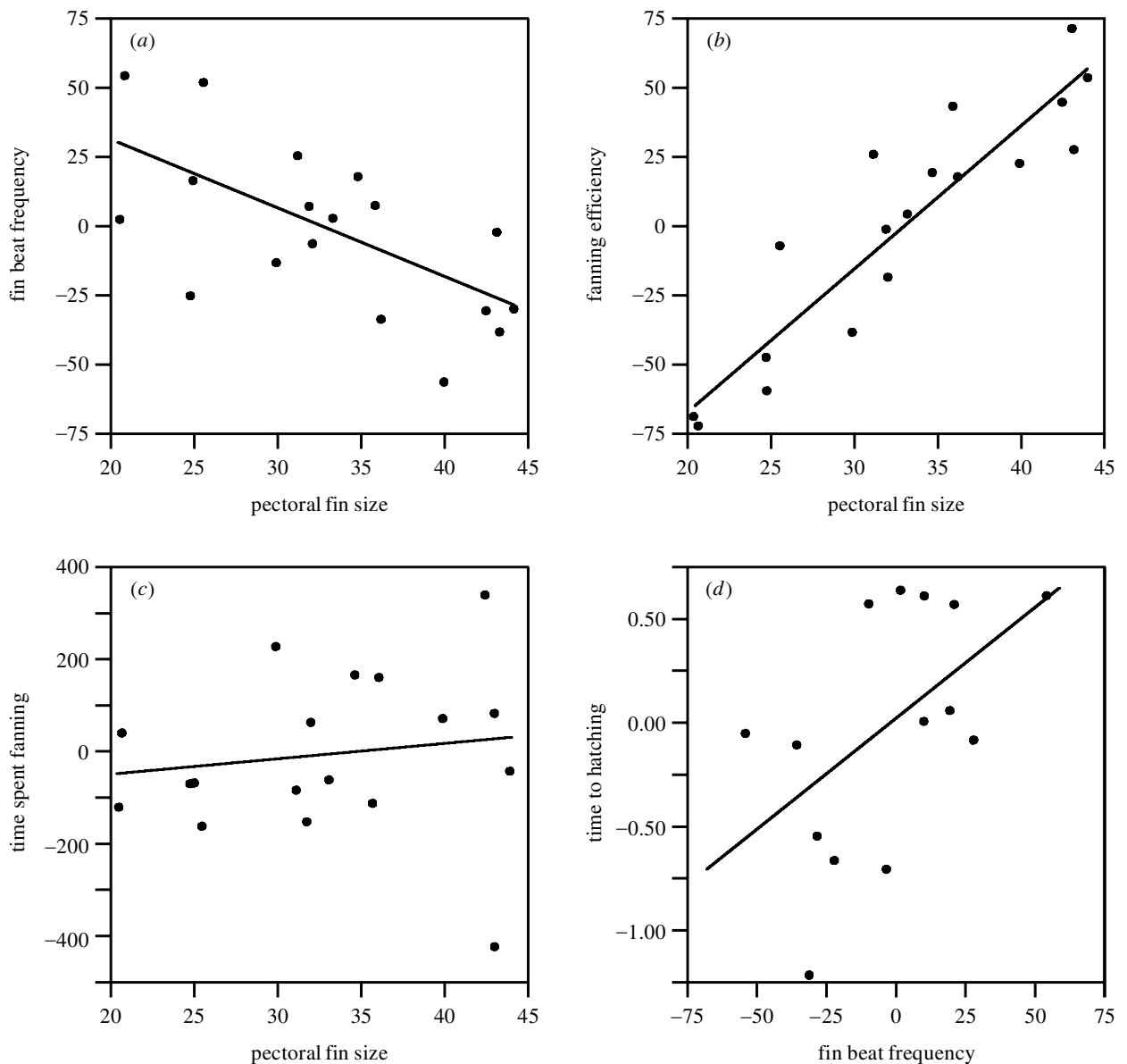
Figure 2. Relationships between the pectoral fin size and (*a*) the standardized fin beat frequency, (*b*) standardized total amount of water moved per fin beat, and (*c*) standardized time spent fanning for 18 males. (*d*) Relationship between the standardized developmental time of offspring until hatching and standardized fin beat frequency. The time to hatching was standardized for the mean water temperature through embryo development per nest and was available for 14 males.

the developmental rate and mortality rate of the embryos were not positively associated ($r = 0.06$, $n = 14$ and $p > 0.83$).

Although we performed the experiments pairwise in order to balance the extent of the fin reductions as much as possible throughout the breeding season, a direct paired comparison of parental quality is hampered by variation in the exact fin reductions between males and pairs and changes in the effects of the fin size reductions on paternal quality during the breeding season. Although males differed significantly within pairs as to pectoral fin size (paired *t*-test, $p < 0.001$) and beat frequency of the pectorals ($p = 0.03$), this does not necessarily result in within-pair differences in paternal quality. This effect can be demonstrated when we rank the seven male pairs for which data on the developmental rate of their offspring were available, according to the date of the first clutch

(range, 18 June–24 July). The pair ranking tended to correlate with the mean water temperature through embryo development ($r = 0.72$, $n = 7$ and $p < 0.07$). The pair ranking did not correlate significantly with the within-pair differences in pectoral fin size ($r = 0.36$, $n = 7$ and $p > 0.42$) but did correlate significantly with the within-pair differences in the standardized developmental time of their offspring until hatching ($r = 0.76$, $n = 7$ and $p < 0.05$). The embryos of males with the more strongly reduced fins developed more slowly in the later breeding pairs only. This result, together with the positive correlation between the within-pair difference in egg development (additionally standardized for within-pair differences in egg number) and the percentage fin reduction of males from the large-reduction group ($r = 0.77$, $n = 7$ and $p < 0.05$), suggest that the males with the smaller fins were driven to the limit of their paternal care ability. The

latter correlation was not significant when males of the small-reduction group were taken as the independent variable ($r = 0.31$, $n = 7$ and $p > 0.50$).

4. DISCUSSION

We showed that an experimental reduction in the pectoral fin size in sticklebacks led to a reduction in paternal quality. Reduction of the pectoral fin size enhanced the fin beat frequency during ventilation of the embryos in the nest. However, the increased beat frequency could not compensate fully for the reduced paternal quality leading to an extended developmental time of the offspring. This result suggests that females may benefit directly from choosing males on the basis of the movements or size of their pectoral fins. Our results further suggest that females cannot judge paternal quality on a single trait in isolation but have to judge fin movements or size in connection with the demands of paternal care (which are deduced from variables such as water temperature and the number of eggs already present in the nest) (Perrin 1995).

The size of the pectoral fins in three-spined sticklebacks is sexually dimorphic (Brønseth & Folstad 1997; Bakker & Mundwiler 1999): males have relatively larger pectoral fins than females during the breeding season. Larger fins may have evolved through the functional demands of paternal care (ventilation and territorial defence) and sexual selection through female choice (Ryan & Keddy-Hector 1992). Our study suggests that pectoral fin size or correlated movement is an honest indicator of paternal quality. In our study population, infestation with the common acanthocephalan *P. laevis* was negatively associated with relative pectoral fin size (Bakker & Mundwiler 1999). This means that pectoral fin size could be an indicator of genetic quality as well. Thus, pectoral fin size may signal direct and indirect benefits towards a potential mating partner simultaneously (cf. Moore 1994).

It is unknown in sticklebacks and other fish species whether females use pectoral fin size or movement for choice decisions. In general, in fish with paternal care body size is an important criterion of mate choice (Kraak *et al.* (1999) and references therein). Pectoral fin size shows a positive allometry with body size (Bakker & Mundwiler 1999) and, thus, larger males have larger fins. For fishes using their pectoral fins for fanning, larger males could simply be better fathers because they have larger fins. Large males have a selective advantage through female choice for paternal quality in addition to male–male competition (but see Forsgren 1997; Qvarnström & Forsgren 1998). It is still possible that females assess pectoral fin size independently of body size, e.g. during the male's courtship dance (Brønseth & Folstad 1997) or movements of the pectorals.

Fin size was negatively related to beat frequency in our manipulated fishes. Further, within the group with the more strongly reduced pectorals and within the group with the slightly reduced fins this relationship was similar (*y*-intercepts ANCOVA, $F = 3.34$, d.f. = 1, 15 and $p = 0.96$). This result suggests that a similar relationship may exist for intact fins. Such a relationship may be dictated by the physics of moving fins in a medium of water or may represent the energetically least costly solution.

Embryo survival in the nest is affected by both the male's ability and willingness to provide brood care. Strategic decisions may lead to a lower investment into current reproduction in favour of better chances for a second brood cycle. One reason for embryo losses is cannibalism, which means that males consume part of their own clutch (e.g. FitzGerald 1992). We had expected parallel changes in egg mortality and development based on earlier findings with unmanipulated males under the same conditions but with larger clutches (T. C. M. Bakker and L. Bobbio, unpublished data). It seems that the more severe the fin size reduction, the greater the male's willingness to care for the present offspring, possibly because of different expectations of future reproduction.

Our experiments were performed pairwise throughout the breeding season: the breeding cycle of a male with strongly reduced fins ran parallel to that of another male with slightly reduced fins. Nonetheless, a paired comparison was hampered by the within-pair variation in fin size differences and the change in paternal demands during the breeding season. Due to higher water temperatures, at the end of the season the demands of paternal care are higher for a given fin size and a given number of eggs in the nest. Our results suggested that the paternal quality of males with strongly reduced fins was not sufficient at the end of the breeding season. Under standardized laboratory conditions, a direct paired comparison could have been made but it is questionable whether differences in paternal quality would have been detected when males had to care for only four clutches of eggs under optimal laboratory conditions. Under field conditions, four clutches were sufficient to detect an effect of fin size manipulation whereas the average number of eggs in nests in the field can be much higher (e.g. Kraak *et al.* 1999).

It is unknown for three-spined sticklebacks whether males can actively regulate their fanning performance by adjusting their fin beat frequency independently of the water temperature. Such a regulation was suggested for some species, e.g. *Cottus gobio* (Morris 1954), *Spinachia spinachia* (Östlund & Ahnesjö 1998) and *Pomatoschistus microps* (Jones & Reynolds 1999) but not for others, e.g. *Lepomis macrochirus* (Coleman & Fischer 1991). It is thus possible that the increase in beat frequency is physically coupled to the reduction in fin size as is suggested by the data in Barlow (1964) for *Badis badis*.

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