Ethology **111,** 179—186 (2005)

Shoal Choice in Swordtails when Preferences Conflict

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Abstract

Individuals obtain a range of benefits from aggregating with others. Evidence suggests that group size and the phenotypic characteristics of potential group mates are both important attributes influencing the grouping decisions of prospective group members. Their interaction, however, remains poorly understood. Here we investigate, in a series of dichotomous choice experiments, what happens when a preference with respect to group size is pitted against a preference for assorting on the basis of body size in swordtail fish. When controlled for body size, we found that swordtails preferred to associate with a larger shoal. When controlled for group size, we found that swordtails preferred to associate with similar-sized fish. However, when offered the choice between a single size-matched shoaling partner and four dissimilar-sized shoal mates, we found that females associated randomly. Our results suggest that, depending on context, group size and body size may be equally important in guiding the aggregating decisions of swordtails. Future studies will likely offer valuable insights into shoaling behaviour by considering how, and under what circumstances, different grouping preferences might be prioritized.

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Introduction

Animal grouping decisions are based on the relative value of the costs and benefits associated with group membership. The attractiveness of a group to potential members may depend on a range of attributes. One of the most important is group size. Group size effects on antipredator responses are especially well documented (reviewed in Elgar 1989), and, in the context of group membership, larger groups are generally more attractive than smaller ones (Hager

& Helfman 1991; Lindström & Ranta 1993; Krause & Tegeder 1995; Krause et al. 1998). Grouping decisions, however, can also be influenced strongly by the phenotypic characteristics of existing group members. In shoaling fish, for example, individuals often assort with respect to characteristics such as body size (reviewed in Krause et al. 2000a), colour (McRobert & Bradner 1998), or species (Barber et al. 1998; Krause et al. 2000b). Grouping on the basis of such attributes is purported to decrease competition between group members and/or reduce predation risk by minimizing phenotypic oddity (Landeau & Terborgh 1986; Peuhkuri 1997; Ward et al. 2002).

What happens when preference for larger group size conflicts with that for assorting on the basis of phenotypic similarity? This question is biologically meaningful, as both group size and the phenotypic attributes of shoal mates can vary between groups (Krause et al. 1996). Few studies, however, have examined such tradeoffs explicitly (Ashley et al. 1993; Krause & Godin 1994; Bradner & McRobert 2001; Hoare et al. 2004). One possibility is that fish may prioritize their preferences. For example, if group size is more important than the phenotypic characteristics of potential shoal mates, fish may decide to join a large shoal comprising dissimilar-looking fish over a smaller group of similar-looking shoaling partners. Alternatively, fish could choose randomly if the attributes in conflict are equally important. Here, we use size variation in swordtail fish to evaluate how individual grouping decisions are affected when preference for joining a larger group has to be traded against that for assorting on the basis of body size.

Methods

Study Subjects and Holding Conditions

We collected female swordtails, *Xiphophorus birchmanni* × *X. malinche* (Rosenthal et al. 2003), along a 50-m stretch of the Río Calnali at the town of Calnali, Hidalgo, Mexico, using baited minnow traps. Female swordtails, unlike males, grow continuously before and after sexual maturity (Kallman 1989), and are reproductively active throughout the year (Morris & Ryan 1992). The two parental species of these natural hybrids do not differ in body size, and females of the two species are almost identical in appearance (Rosenthal et al. 2003). Variation in body size is likely because of both intrapopulation genetic variation and variation in female age (Kallman 1989). Like other swordtails, these fish live in mixed-sex shoals of two to hundreds of individuals, foraging on benthic microinvertebrates in shallow, rocky streams (Ryan & Rosenthal 2001; Rosenthal et al. 2003). We used only females in our experiments to control for sexual behaviours influencing association preferences. Mature females were identified by the presence of a gravid spot. In the study population, mature females ranged from 29 to 65 mm ($\bar{x} \pm$ SD 46 $\pm$ 8 mm, n = 106; Fig. 1). 'Large' females used in this experiment ranged from 54 to 59 mm ($\bar{x} \pm$ SD 56 $\pm$ 2 mm), 'small' females from 39 to 44 mm ($\bar{x} \pm$ SD 42 $\pm$ 2 mm). Females were returned to the adjacent

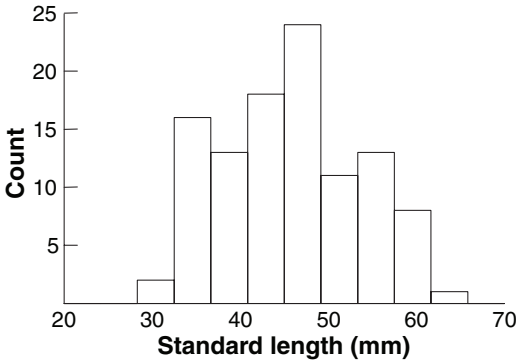

Fig. 1: Size distribution of sexually mature female swordtails

Rancho Ahuimol and held in 40 × 70 cm gray plastic tubs for 1–24 h prior to testing. Test subjects were housed separately from stimulus fish. All animals were released at the point of capture after testing.

Experimental Procedure

We conducted simultaneous-choice tests in 40 × 70 cm gray plastic tubs, filled to a height of approx. 10 cm containing two 10 × 30 cm clear plastic containers placed at opposite ends of the tubs. Experiments were conducted on a shaded patio to minimize differences in light intensity across and within test tanks. Stimulus females were placed in the clear containers and subject females were released within the test tank. Stimuli and subjects were allowed to acclimatize for 10 min before recording. To control for side biases, we alternated the side of presentation of each stimulus across subjects and to control for tank biases, we systematically varied the subjects (large vs. small) across tanks. Each subject fish was tested only once per experiment. Stimulus fish were rearranged after each trial so that each trial contained a unique stimulus combination. We continuously recorded association time for 5 min. Females were operationally defined as associating with a stimulus if their snouts were within 10 cm of the stimulus container. Recordings were made from an armchair positioned 2 m away from the test aquaria to minimize disturbance to the fish.

For expt 1 (shoal size preference), we presented subjects with four females of their own size class vs. one female of their own size class. For expt 2 (body size preference), subject females were presented with three 'large' females vs. three 'small' females. Fish were thus presented with the choice between individuals of the same size class (i.e. similar-sized shoal mates) vs. individuals of the other size class (i.e. dissimilar-sized shoal mates). For expt 3 (shoal size vs. body size), we presented subjects with one female from the same size class vs. four females from the other size class.

All statistical tests are two-tailed and were performed on arcsine square root transformed proportions of total response time for each trial.

Results

Experiment 1: Shoal Size

Large and small female subjects did not differ in their responses on the basis of shoal size (Mann–Whitney U-test: $U = 81$, $p = 0.58$, $n_{large} = 12$, $n_{small} = 12$). Overall females preferred to shoal with four females than associate with a single shoaling partner (paired t-test: $t = 4.68$, $p < 0.001$, $n = 24$; Fig. 2).

Experiment 2: Body Size

Large females spent significantly more time associating with similar-sized females than they did with small females (paired t-test: $t = 2.09$, $p < 0.05$, $n = 24$; Fig. 3a). Small females tended to prefer similar-sized shoal mates, although the results were not quite significant (paired t-test: $t = 1.77$, $p = 0.09$, $n = 24$; Fig. 3b). Overall, however, there was no statistically significant difference in the response of large and small subjects toward similar-sized vs. dissimilar-sized shoal mates (two-sample t-test: $t = 0.17$, $p = 0.87$). Specifically, we found that subjects associated preferentially with similar-sized shoal mates (paired t-test: $t = 2.76$, $p < 0.01$, $n = 48$).

Experiment 3: Body Size vs. Shoal Size

Females did not show a significant preference between four dissimilar-sized fish and one size-matched fish (paired t-test: $t = 0.33$, $p = 0.74$, $n = 48$; Fig. 4). There was no significant difference between large and small subjects in their response toward similar-sized vs. dissimilar-sized shoal mates (two-sample t-test: $t = 0.17$, $p = 0.87$).

Discussion

Group size and body size both appear to be important in guiding the shoaling preferences of swordtails. We found, in expt 1, that swordtails preferred to form a

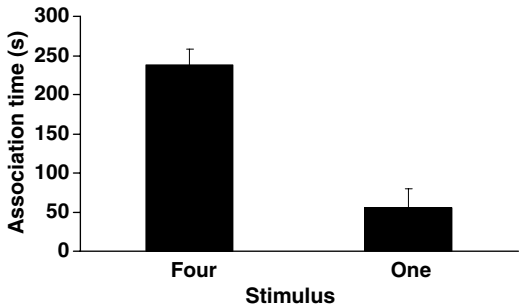

Fig. 2: Association time ($\bar{x} \pm SE$) of focal fish with four similar-sized fish vs. one similar-sized fish

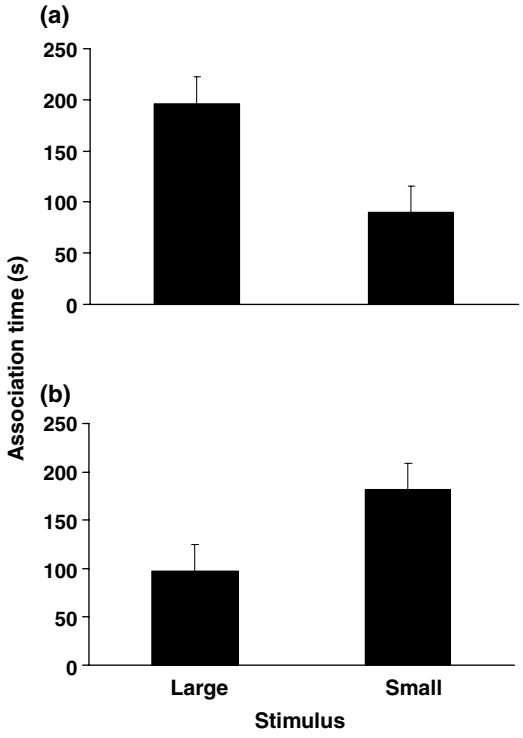

Fig. 3: Association time ($\bar{x} \pm SE$) of (a) large and (b) small focal fish with three large fish vs. three small fish

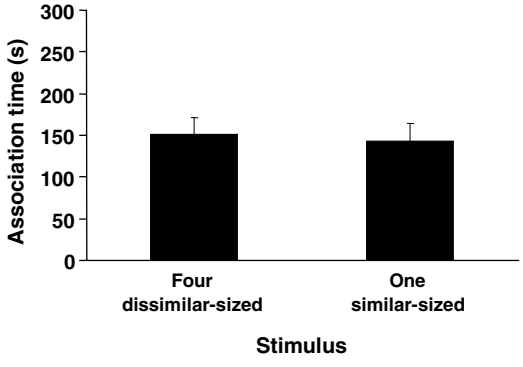

Fig. 4: Association time ($\bar{x} \pm SE$) of focal fish with four dissimilar-sized fish vs. one similar-sized fish

larger shoal by aggregating with four individuals, as opposed to associating with a single shoaling partner. Swordtails also exhibited a shoaling preference based on the body size of prospective shoal mates. Specifically, in expt 2, when we

controlled for group size, we found that females preferred to aggregate with fish that were of the same size as themselves. This second result provides a striking contrast to female mating preferences reported in several other species of swordtails, in which females of all sizes exhibit directional preference for larger males (*X. helleri*, Rosenthal & Evans 1998; *X. pygmaeus*, Ryan & Wagner 1987; *X. nigrensis*, Ryan et al. 1990). Our results suggest that associating with females in a shoaling context involves a fundamentally different set of decisions than associating with courting males.

More broadly, grouping preferences of the kind reported in our first two experiments are consistent with both laboratory and field studies across a range of taxa. Generally, such results are interpreted as being consonant with the benefits individuals can acquire from living in groups. Membership in larger groups, for instance, may benefit individuals through increased foraging efficiency, as in many birds and mammals (Elgar 1989). Aggregating as part of a larger group can also facilitate earlier detection of predators and/or dilute the individual risk of attack as demonstrated, for example, in colonial web-building spiders (Uetz et al. 2002) and several species of fish (Pitcher & Parrish 1993). Swordtails in our study population co-occur with visual predators including water snakes and fish-eating birds (B.B.M. Wong & G.G. Rosenthal, unpubl. data). In this regard, body size assortment could be especially important as an anti-predator strategy for sexually mature female swordtails because, unlike males, they show indeterminate growth resulting in a wide range of body sizes. Because individuals that differ in appearance from other members of a group are also more likely to be preyed upon selectively, by assorting into groups on the basis of phenotypic similarity, individuals may also be able to avoid the so-called 'oddity effect' (Landeau & Terborgh 1986).

What happens, however, when preference based on group size is pitted against preference for assorting on the basis of phenotypic similarity? In expt 3, when female swordtails were given the option of associating with either one size-matched individual or four dissimilar-sized fish, we found that focal subjects did not show a significant preference for one over the other. This suggests that, within the context of our experiment, group size was no more important than body size in guiding the aggregating behaviour of swordtails. Our result contrasts with those reported in banded killifish, *Fundulus diaphanus*, which prefer to associate with a small shoal of similar-sized fish over a large shoal of dissimilar-sized individuals (Krause & Godin 1994). However, in the absence of predation threat, killifish did not show a significant preference for large shoals even when the body size of prospective shoal mates were the same as the test subject.

Although we did not find any evidence that swordtails traded preference for group size against that for size assortment, it is important to keep in mind that shoaling preferences are likely to be context-dependent. In this regard, it is conceivable that situations may arise where the net benefits of one could be greater than the other. For example, membership of a larger group may be less desirable when foraging is a priority (Hoare et al. 2004). Although grouping can confer foraging benefits, competition between group members is an important

cost that often increases with group size (Elgar 1989). This competition could mediate the benefits of belonging to a larger group and potentially affect which preference takes precedence (Reebs & Saulnier 1997). Shoaling priorities may also be affected by a range of other factors including individual competitive ability (Metcalfe & Thompson 1995) and/or the local risk of predation (Ashley et al. 1993). Valuable insights will likely flow from greater attention being paid in the future to how, and under what circumstances, preferences important in guiding grouping decisions might be traded.

Acknowledgements

We thank S. Forbes, S. Reebs and two anonymous reviewers for their constructive comments on the manuscript, the Government of Mexico for permission to work in the Río Calnali, the Lara family for logistical support at Rancho Ahuimol, H. Fisher and C. O'Keefe for help with equipment, and the children of Calnali for assistance with collection. B.B.M.W. was supported by a Sir Keith Murdoch Fellowship.

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Received: June 2, 2004

Initial acceptance: September 2, 2004

Final acceptance: September 22, 2004 (S. Forbes)