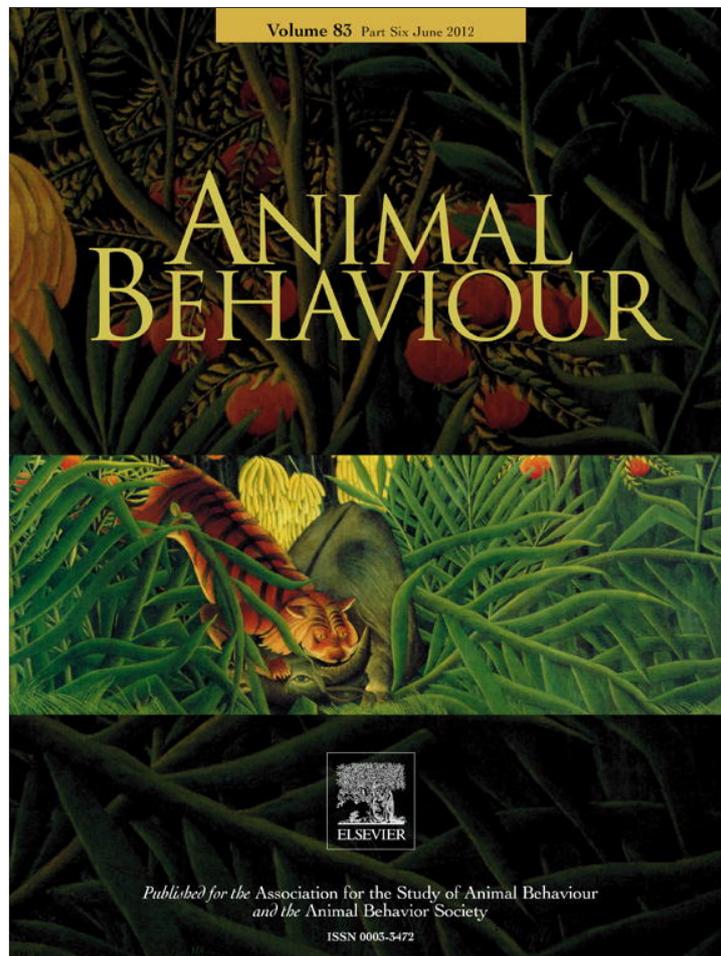


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# Animal Behaviour

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## Individual sociability and choosiness between shoal types

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In social species, individual and group fitness and social dynamics in groups often depend on group size and on the group's social composition (e.g. the mix of personality types within groups). In turn, the size and social composition of groups is an emergent outcome of the grouping tendencies of individuals. While grouping behaviour has often been studied at a species level, within-species variation in grouping tendency has rarely been studied. We examined the role of personality type in shoaling preferences in a social fish, the western mosquitofish, *Gambusia affinis*. After scoring individuals for their social personality types (sociability), we gave individuals the choice to associate with shoals that differed in size and in the average sociability of individuals in the shoal. Shoal preferences depended on both the individual's sociability and on shoal size and composition in sociability types, and on the interaction between the individual's sociability and shoal size and composition. On average, fish preferred large to small shoals and groups made up of social individuals to groups made of asocial individuals at least when shoal size was small. Individual sociability types were linked to the time individuals spent far from any shoal and to consistent differences in choosiness about social contexts. Asocial individuals shoaled less and swam more between shoals than social ones, but preferred large shoals during the short time that they shoaled. These results can help explain patterns of group size and composition and individual and population-level personality-dependent dispersal.

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In many taxa, individuals form more or less cohesive groups (swarms, herds, flocks, shoals or schools; Pulliam & Caraco 1984; Krause & Ruxton 2002). Individuals benefit from living in social groups through social information that aids in food localization, reduced predation risk (confusion/dilution/vigilance effects) or higher success in finding mates (Godin et al. 1988; Pitcher & Parrish 1993; Krause & Ruxton 2002). However, social groups also impose costs on individuals including stronger competition (e.g. for food, mates), increased disease transmission and predator attraction (Cote & Poulin 1995; Krause & Godin 1995). Group size can thus have major impacts on individual fitness and group dynamics. Importantly, group size is not a random property, but is instead an emergent outcome of the grouping tendencies of individuals in the population. Larger groups form if individuals generally exhibit stronger grouping tendencies. A key individual trait that can influence grouping tendencies is the individual's personality type (aka behavioural types), where some individuals are consistently more bold, aggressive or sociable than others (Dall et al. 2004; Sih

et al. 2004; Bell 2006; Reale et al. 2007, 2010; Sih & Bell 2008). For example, by definition, more sociable individuals should be more likely to join groups than asocial ones. Or, because being in a social group can reduce predation risk, more cautious individuals might exhibit a stronger preference for being in a group (Budaev 1997; Ward et al. 2004; Leblond & Reeb 2006).

Beyond group size, another key group property is the mix of personality types in the group, which can also influence the behaviour and fitness of each individual in the group (e.g. Magnhagen & Bunnefeld 2009). For example, the aggressiveness and sociability of group members can change the cohesion of a group and in turn its efficiency as protection against predators. Similar patterns can be expected for the average activity, boldness or exploratory behaviour of a group. Furthermore, the benefits of group size or of the group's social composition can depend on the personality of the focal individual. For example, interactions between the individual's personality, the group's mix of personality types and group size can change the balance between food localization and competition within a group, a major driver of social grouping.

Given that the benefits of being in a group depend on group size, the group's mix of personalities and the personality type of each individual, a key issue that has rarely been studied is to understand how an individual's personality type affects its group size

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preference or its preference for groups with a particular mix of personality types (e.g. Saltz 2011).

We studied the role of personality type in shoaling preferences in a social fish, the western mosquitofish, *Gambusia affinis*. In many fish species, individuals shoal for at least part of their life (Pitcher & Parrish 1993). Shoaling fish often prefer to group with larger shoals made of similar, healthy or familiar individuals (Pitcher & Parrish 1993; Hoare et al. 2000; Krause et al. 2000a, b; Ward et al. 2002; Lee-Jenkins & Godin 2010). Individual personality types differ, however, in their shoaling tendencies. Bold fish are expected to shoal less or to adopt positions at the exterior or at the front of shoals where predation risk is higher (Budaev 1997; Ward et al. 2004; Leblond & Reeb 2006). Bold individuals that are more risk prone in order to forage more have higher foraging rates (Biro & Stamps 2008) and are thought to adopt a producer strategy in a social group (Kurvers et al. 2010). In three-spined sticklebacks, *Gasterosteus aculeatus*, bold individuals indeed exhibit a weaker tendency (relative to shy ones) to shoal, and are more likely to adopt a producer strategy (while shy individuals are scroungers), and thus are more likely to lead shoal movements where shy individuals follow bold ones (Ward et al. 2004). The mix of personality types in a shoal also influences outcomes, including the distribution and intensity of social interactions (Pike et al. 2008), the foraging success of all shoal members (Dyer et al. 2009) and even dispersal from the group (Cote et al. 2011). While the above-cited studies showed individual variation in shoaling tendency and the role of personality types in this variation, it is less well known how shoal composition in personality types affects individual shoal preferences in interaction with the individual's own personality type (Harcourt et al. 2009).

In western mosquitofish, we have repeatedly found strong and consistent individual differences in shoaling tendency (Cote et al. 2010b, 2011). In this species, we term an individual's shoaling tendency its sociability (individual variation in attraction to others; Budaev 1997; Cote & Clobert 2007; Reale et al. 2007; Rodriguez-Prieto et al. 2010). In contrast to some other species, mosquitofish that are bolder in a novel environment tend to shoal more and not less (higher sociability). Moreover, individual dispersal behaviour is negatively related to individual and population sociability levels (Cote et al. 2010b, 2011). We studied how individual choosiness for shoals of different size and composition in sociability types depends on individual sociability type. Two well-established ideas that we tested are that, on average, individuals in highly social species generally prefer to join larger shoals, and that in particular more sociable individuals prefer to join larger shoals. More novel hypotheses that we tested are that shoal choice also depends on the mix of personality types in the shoal, and, furthermore, that shoal choice might depend on an interaction between the individual's personality and the group's size or composition.

Finally, we examined the intuitively reasonable, yet rarely quantified possibility that individuals are consistent not just in their social preferences, but also in the strength of their choosiness (Sih & Bell 2008); that is, some individuals are consistently choosier than others about their social groups. The notion that individuals with different personalities might differ in their social group choices leads to the possibility of individual social specialization, which has been mentioned in several review articles (Bergmüller & Taborsky 2010; Krause et al. 2010; Reale et al. 2010), but rarely quantified (Bergmüller et al. 2010).

We first measured individual sociability level (attraction to a large shoal), a behaviour that has been shown to be consistent over time. Using some of these fish, we created small and large shoals made of only social or only asocial individuals. Then, using the remaining fish, we looked at the relationship between individual preferences for these different shoal types and the focal

individual's own sociability type. We predicted that (1) for higher safety, fish should generally prefer larger shoals over smaller shoals, and shoals made of social individuals over those made of asocial fish, (2) asocial fish should consistently shoal less regardless of the shoal's size or mean personality type and (3) asocial fish should be consistently less choosy than more sociable fish about shoal size or social composition.

## METHODS

Six hundred mosquitofish (ca. one-third males, two-thirds females) were transported from the Sacramento-Yolo Mosquito and Vector Control District to the Center for Aquatic Biology and Aquaculture (CABA), University of California, Davis, U.S.A. in March 2010. At the Sacramento-Yolo Mosquito and Vector Control District, we captured fish with fish nets from a large rearing pool and brought them to CABA in coolers provided with bubblers. Fish were held in groups of 60 in 80-litre glass aquaria with recirculating pumps and filters on a natural photoperiod (for late April, 14:10 h light:dark) at 22 °C and fed TetraMin flakes ad libitum. Mosquitofish were acclimated to these conditions for >1 month prior to behavioural observations, which were carried out in April 2010.

To give focal fish a choice between 'stimulus shoals' that differed in their group properties, we first created 16 stimulus shoals of two different sizes composed of fish of two different sociability types (see below). Then, over a 1-week period, we assayed 80 fish (block 1) for their sociability (using six other shoals, see below) and then for their shoal preferences. The following week, we repeated these assays with 80 additional fish (block 2). Only females were used for this experiment to remove variation from sexual interactions.

### Measuring Sociability

Following methods from our previous studies (Cote et al. 2010b, 2011), we assayed individual sociability by taking individuals out of their home tanks and placing them individually in 5.7-litre plastic tubs, with 2.5 litres of well-water, and a 12 cm piece of 5 cm diameter PVC pipe that served as a refuge. This takes focal individuals away from their familiar groups where their attraction to the group may depend on a history of social interactions (which differs for different individuals) and instead places each individual in a standardized situation. One day later, we recorded the amount of time spent near a shoal of conspecifics in a standardized assay (Ward et al. 2004; Cote et al. 2010b, 2011). The experimental arena was an aquarium (25 × 50 cm and 30 cm high filled to a depth of 13.6 cm with 17 litres of well-water) divided into three compartments (two small and one large centre compartment) using two transparent glass partitions 12.5 cm away from each side wall. One compartment held a stimulus shoal, while the other was left empty. The partitions allowed visual but not physical or olfactory interaction between the shoal and the focal individual. We used six predetermined stimulus shoals each comprising 14 randomly chosen mosquitofish (seven females, seven males). Although we did not assay or control for the personality types of the individuals in these shoals, using a relatively large shoal size ensured that shoals were all similar in average personality type. One of six predetermined stimulus shoals was introduced to one of the small compartments of each of six aquaria 1 h before experiments began while the other small compartment was left empty as a control. After 1 h, the focal fish was introduced into the centre of the larger compartment and allowed to acclimate for 10 min. Previous work showed that after 10 min of acclimation, fish no longer showed signs of stress (e.g. constant swimming along the sides of the tank) associated with being moved, and that behaviour was stable over the next 10 min (e.g. sociability scores for the 5 min after

acclimation and for the following 5 min were strongly correlated;  $P < 0.0001$ ).

Black curtains surrounded the aquaria and a video camera connected to a monitor allowed us to observe fish without disturbing them. The position of the focal fish was recorded every 12 s for 10 min. We chose to do that instead of recording behaviour continuously because it allowed us to observe several fish at the same time in a way that is highly repeatable between methods ( $r^2 = 0.96$ ,  $N = 8$ ), and between two observers ( $r^2 = 0.96$ ,  $N = 28$ ). The large compartment was divided with vertical and horizontal marks every 3 cm; sociability = % time spent shoaling and was defined as the number of observations in which the focal fish was within the 3 cm closest to the stimulus shoal divided by the total number of observations. When the assay was complete, individuals were weighed and returned to their individual home tub.

#### *Creation of Shoal Types*

We created four types of stimulus shoals (four replicates of each) varying in shoal size and the sociability of individuals composing the shoal: large shoal with asocial individuals (LA); large shoal with social individuals (LS); small shoal with asocial individuals (SA); and small size with social individuals (SS). We first assayed sociability for 240 fish and used the more social and more asocial ones (as opposed to fish of intermediate sociability) to create our stimulus shoals. On each of 3 consecutive days (days 1–3), 80 adult females were held overnight in individual plastic tubs as described above. Sociability scores (% time shoaling) were obtained and then fish were distributed in 16 11.4-litre plastic tubs, with 10 litres of well-water and a piece of PVC pipe that served as a refuge. Although the distribution of sociability scores is not trimodal (because this species is strongly social, the distribution is skewed towards higher values of % time spent shoaling), to create shoals that differed in average sociability, we classified individuals into three categories: social, asocial and intermediate, each representing about one-third of the total. Social individuals spent more than 75% of their time next to the shoals, intermediate individuals between 50 and 75% and asocial individuals less than 50%. Social and asocial individuals were then released in the 16 tubs randomly. Large and small shoals were made of 10 and four individuals, respectively. Because we kept shoal compartments constant in size, we could not distinguish effects of shoal size from shoal density. The density in the holding tanks was about 1.33 fish/litre, which was intermediate between the density for small shoals (0.94 fish/litre) and the density for large shoals (2.35 fish/litre). Focal individuals thus presumably perceived small and large shoals as low and high densities in comparison to their holding conditions.

Mean body mass did not depend on shoal type (shoal size:  $F_{1,12} = 0.32$ ,  $P = 0.59$ ; social type:  $F_{1,12} = 0.5$ ,  $P = 0.49$ ; interaction shoal size \* social type:  $F_{1,12} = 0.02$ ,  $P = 0.90$ ); mean sociability score varied, of course, with shoal sociability type but not with shoal size (social type:  $F_{1,12} = 224.29$ ,  $P < 0.0001$ ; shoal size:  $F_{1,12} = 0.00$ ,  $P = 0.97$ ; interaction shoal size \* social type:  $F_{1,12} = 0.05$ ,  $P = 0.83$ ).

#### *Individual Preference for Shoal Types*

Two days after creating shoals (day 5), we placed, at night, 80 females (block 1) into plastic tubs as described above and on day 6 we assayed their sociability. When the assay was complete, individuals were weighed and returned to their individual home tub. Then, over 4 days (one test per day), each individual went through four different choice tests between two different types of shoals. Shoal choice tests were made in the same aquarium in which the focal individual had been assayed for sociability. These aquaria

were divided lengthwise into three compartments (two small and one large centre compartment, see above). In each aquarium, two stimulus shoals were released in the two small compartments and had 1 h of acclimation before shoal choice tests started. The shoals were kept in the aquarium for the day. The two shoals of an aquarium were always of different types, creating four different shoal choice treatments: LA versus LS, SA versus SS, LA versus SA, LS versus SS. The 16 shoals were randomly allocated to these shoal choice treatments with each shoal used twice in both choice treatments that apply for that shoal type. Overall, we created 64 pairs of shoals with four different pairs used every day for 10 fish. Using so many pairs of shoals, as opposed to using one or two pairs of shoals minimizes the effects of shoal characteristics other than size and sociability type on focal fish choice. However, because each shoal was only used twice per treatment, we did not include pair identity as a factor in statistical models. Shoal placement on the right versus left side compartments was randomized.

Focal individuals had only one shoal choice test per day. The order of shoal choice tests over the 4 days was randomly chosen for each focal individual but balanced so that all individuals were tested with all four choice treatments. After 10 min of acclimation, we recorded the focal individual's position every 12 s for 10 min. The large compartment was divided with vertical marks into eight areas each 3 cm wide, numbered 1–8. Fish were considered to be close to a shoal if they were in either zone 1 or 8 (i.e. within 3 cm of a shoal). If a fish was in either of the two middle zones (4 and 5), it was in a neutral region. Time spent in zones 2, 3, 6 or 7 was on one side of the tank, but not close to a shoal; these observations were not included in the analysis because it was not clear whether the fish was exhibiting a clear preference. After the assay, focal fish were returned to their individual holding tubs until the next day for the next shoal choice test. Another block of 80 individuals was assayed 3 days after the last day of shoal choice for the first block.

#### *Statistics*

Nine focal fish died in the course of or the day after the end of the experiment. Fish death was apparently not caused by the experiment (death rates for fish included and fish not included in the experiment were similar). We removed them from all analyses leaving a sample size of 151 fish.

#### *Time spent in neutral compartments*

We first analysed how individual sociability score affected the probability of being in the neutral area during the four shoal choice tests. We assumed that being in the neutral area indicates a lack of preference and/or of motivation to shoal. The probability of being in the neutral area was analysed using a repeated measures mixed generalized linear model (GLIMMIX procedure in SAS 9.2) with a logit link and a binomial error distribution. The number of times a fish was observed in the neutral area was the response term (i.e. events) and the total number of observations (i.e. 50 observations) was the binomial denominator (i.e. trials or number of draws). Because there were four shoal choice tests, we had four repeated measures per individual. The model included individual sociability score, body mass, trial day and block. Trial day was included to test for changes caused by increased familiarity with the test conditions. As we had two blocks in our experiment, we added a random factor 'block' in the model. We used type III *F* tests for fixed effects. The Laplace approximation method was used for approximating likelihood. We also analysed the repeatability of time individuals spent in the neutral area over the four shoal choice tests. We calculated intraclass correlation coefficients from linear mixed models with % time spent in the neutral area (after a square-root

transformation to approach normal distribution) as the dependent variable and fish identity as a random factor. Repeatability analyses are further described in the section Repeatability of choosiness below.

#### *Effect of shoal social type*

We analysed whether fish tended to shoal preferentially with large shoals and how this preference depended on the social personality type of the focal fish and of individuals in the shoal. For these questions, we used two of the four shoal choice tests, LA versus SA and LS versus SS, which addressed whether fish preferred large shoals over small shoals when shoals were made of asocial individuals versus social ones.

First, we obtained the % shoaling time spent close to the large shoal by dividing the number of times the fish was close to the large shoal by the number of observations in which the fish was close to either of the two shoals. We excluded the other observations, as fish were not making a clear choice. Note that fish were much more often close to a shoal than in the neutral area (see *Results*). We analysed whether the % time spent close to a large shoal was different from 50% in LA versus SA and in LS versus SS assays using a Student's *t* test ( $H_0 = 0.5$ ).

Second, we examined how individual sociability and shoal sociability influenced individual preferences for large shoals by using a repeated measurement model with two repeated measures per individual (from the two shoal choice tests) using a mixed generalized linear model (GLIMMIX procedure in SAS) with a logit link and a binomial error distribution. The number of times a fish was observed close to the large shoal was the response term (i.e. events) and the number of observations in which the fish was close to one of the two shoals was the binomial denominator (i.e. trials). The model is basically the same one as for the % time spent in the neutral area, except that we added a factor describing the shoal social type and an interaction between sociability of the focal individual and the shoal social type.

#### *Effect of Shoal Size*

To examine whether fish tended to shoal preferentially with social shoals as opposed to asocial shoals, and how this preference depended on the sociability of the focal fish or shoal size, we used the two other shoal choice tests: LA versus LS and SA versus SS. We basically did the same kind of analysis as above, except that (1) in the first analysis, the dependent variable was the % shoaling time spent close to the social shoal, and (2) in the second analysis, the number of times a fish was observed close to the social shoal was the response term (i.e. events), the number of observations in which the fish was close to one of the two shoals was the binomial denominator (i.e. trials) and the additional factor in the second analysis was the shoal size.

#### *Repeatability of choosiness*

Finally, we looked at repeatability of choosiness using data from the four shoal choice tests together. To assess choosiness, we calculated the absolute value of [(number of times the fish was close to one shoal arbitrarily chosen/number of observations in which the fish was close to one of the two shoals) – 0.5]. If fish were not choosy, we expected them to spend 50% of their 'shoaling time' close to each shoal; shoal choosiness is then zero. If fish stayed the entire 'shoaling time' close to one shoal, shoal choosiness is 0.5.

Repeatability was assessed by intraclass correlation coefficients (ICC, Lessells & Boag 1987; Nakagawa & Schielzeth 2010). To obtain variance components, we used linear mixed models with fish 'choosiness' as the dependent variable and fish identity as a random

factor. Repeatability is a measure of change in trait expression of individuals across time (within-individual variance), relative to the change in the study population (Lessells & Boag 1987; Bell et al. 2009; Nakagawa & Schielzeth 2010). We calculated ICC and 95% confidence intervals, CI, using the macro ICC9 in SAS 9.2. The Wald Z test was used to assess the statistical significance of the fish identity effect. We use a square-root transformation to approach a normal distribution.

#### *Ethical Note*

This research was approved by the Institutional Animal Care and Use Committee of the University of California Davis (Protocol no. 15247). The Sacramento-Yolo Mosquito and Vector Control District raises mosquitofish at its facility and provides them to District residents. We justify our sample sizes as follows. We first created six shoals of 14 fish randomly chosen to identify sociability types. Using 14 fish allowed us to homogenize shoal composition in personality type. Then, we gave each focal fish a choice between two stimulus shoals composed of 10 or four asocial or social fish. Fish with intermediate sociability levels (i.e. 1/3) cannot be clearly attributed to a social category. We thus excluded them when creating stimulus shoals. For sociability and preferences assays, we had to create several shoals of each type. Otherwise, we could not have separated the effect of shoal social type and size from the effect of a given shoal. Finally, we performed preference assays on 160 focal fish. This number allowed us to get enough fish of each social level to have statistical power. Overall, we used 412 fish. The remaining fish were used for another experiment. At the end of the experiment, fish were euthanized by an overdose of MS-222 with a lethal concentration (1000 mg/litre, <http://www.merckvetmanual.com/mvm/index.jsp?cfile=htm/bc/170404.htm>). Fish were kept in the solution for 10 min until all signs of opercular movements had ceased.

## RESULTS

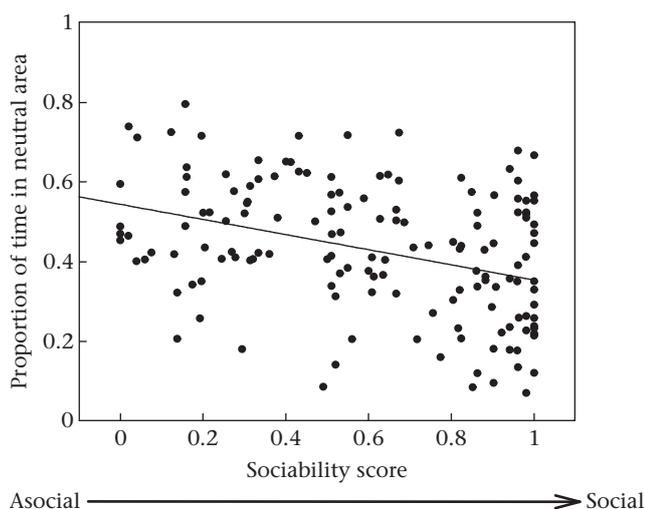
### *Time Spent in Neutral Area*

The probability that a fish was in the neutral area was on average  $\pm$  SE  $0.24 \pm 0.01$  (range 0–0.85). For data pooled across all four choice treatments, this probability depended on individual sociability scores (estimate:  $-1.00 \pm 0.22$ ,  $F_{1,453} = 21.02$ ,  $P < 0.0001$ ). Less sociable animals spent more time in the neutral area. Heavier females also spent more time in the neutral area (estimate:  $3.07 \pm 1.07$ ,  $F_{1,452} = 8.19$ ,  $P = 0.004$ ); but there was no effect of trial day (estimate:  $0.005 \pm 0.01$ ,  $F_{1,452} = 0.18$ ,  $P = 0.67$ ). Individual differences in time spent in the neutral area was repeatable over the four shoal choice tests ( $r = 0.47$ , 95% CI: 0.39–0.55,  $Z = 6.72$ ,  $P < 0.001$ ). The relationship between sociability and time spent in the neutral area was also significant when we used each individual's mean time spent in the neutral area over the four tests (estimates:  $-0.18 \pm 0.04$  SE,  $F_{1,149} = 22.31$ ,  $P = 0.002$ ; Fig. 1).

### *Time Spent Close to Large Shoals*

We use the terms 'probability of being near the large shoal' and 'preference for the large shoal' to indicate the probability that when a focal fish was close to either shoal, it was close to the large one. Similarly 'probability of being near the social shoal' or 'preference for the social shoal' is the probability that when a focal fish was close to either shoal, it was close to the social one (and see following section).

When both shoals were made of asocial individuals, the probability that a fish was close to the large shoal was on average  $\pm$  SE  $0.63 \pm 0.02$  (two-tailed *t* test versus 0.5:  $t_{151} = 5.26$ ,  $P < 0.0001$ ;

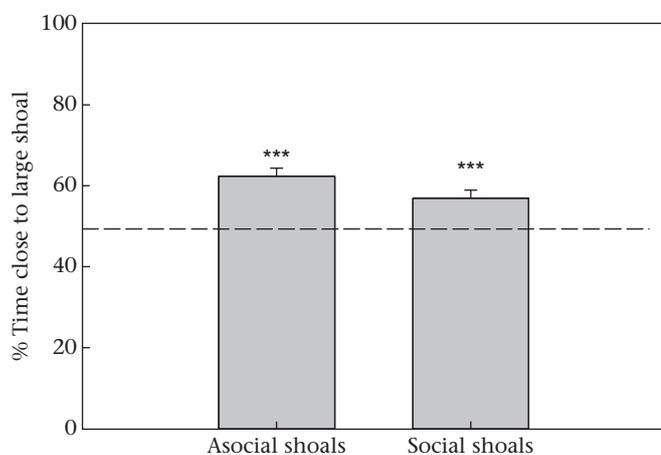


**Figure 1.** Proportion of time spent in the neutral area (square-root transformed, averaged for each individual over four tests) depending on individual sociability scores.

Fig. 2). When both shoals were made of social individuals, the probability that a fish was close to the large shoal was on average  $\pm$  SE  $0.57 \pm 0.02$  (two-tailed  $t$  test versus 0.5:  $t_{151} = 2.92$ ,  $P = 0.004$ ; Fig. 2). Overall, fish were significantly more likely to be observed close to large than small shoals (Table 1). Preference for the large shoal exhibited a significant shoal sociability \* individual sociability interaction (Table 1). Preference for the large shoal (over the small shoal) was stronger when the focal individual was less sociable, and this relationship was stronger when shoals were made of social individuals (social shoals, estimate:  $-0.55 \pm 0.09$ ,  $F_{1,146} = 40.92$ ,  $P < 0.0001$ ; asocial shoals, estimate:  $-0.35 \pm 0.09$ ,  $F_{1,146} = 13.54$ ,  $P = 0.003$ ). This does not mean that asocial individuals spent more time next to large shoals than social individuals. Asocial fish generally spent less time near any shoal (and more time in the neutral area) than social fish, but when they were close to a shoal, they tended to be close to the larger one. Preference for the larger shoal was not significantly related to body mass, but increased with trial day (Table 1).

*Time Spent Close to Social Shoals*

When both shoals were large, the probability of being next to the social one was on average  $\pm$  SE  $0.51 \pm 0.02$  (two-tailed  $t$  test



**Figure 2.** Mean  $\pm$  SE % shoaling time spent close to the large shoal depending on the shoal's sociability type. \*\*\* $P < 0.001$ .

**Table 1**

Individual preference for large versus small shoals depending on the focal individual's sociability score, shoal sociability treatment, body mass and trial day

	Estimates $\pm$ SE	F	P
Intercept	0.17 $\pm$ 0.29	–	–
Individual sociability	–0.53 $\pm$ 0.30	$F_{7,147}=2.02$	0.16
Shoal sociability treatment (A)	0.18 $\pm$ 0.09	$F_{7,147}=3.79$	0.05
Interaction (A)	0.35 $\pm$ 0.14	$F_{7,147}=6.73$	0.01
Body mass	–1.56 $\pm$ 1.43	$F_{1,147}=1.19$	0.28
Trial day	0.19 $\pm$ 0.02	$F_{1,147}=85.31$	<0.0001

Random effects: block and intercept. Estimates are given for social shoals (A).

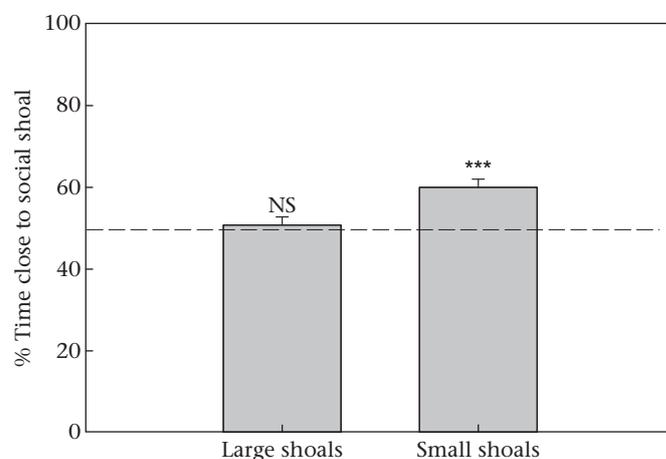
versus 0.5:  $t_{151} = 0.34$ ,  $P = 0.74$ ; Fig. 3); that is, they did not prefer the social shoal. In contrast, when both shoals were small, the probability of being next to the social shoal was on average  $\pm$  SE  $0.60 \pm 0.02$  (two-tailed  $t$  test versus 0.5:  $t_{151} = 4.06$ ,  $P < 0.0001$ ; Fig. 3). Fish preference for social shoals was greater when shoal size was small (Table 2). Preference for more social shoals was not significantly related to individual sociability scores and body mass, but increased significantly with trial day (Table 2).

*Repeatability of Choosiness*

Fish choosiness was repeatable but to a lower extent than time spent in the neutral area ( $r = 0.15$ , 95% CI: 0.08–0.24,  $Z = 3.33$ ,  $P = 0.0004$ ). Because individual sociability is repeatable (Cote et al. 2010b, 2011) and is linked to choosiness in social situations (see above), we also added individual sociability scores to test how choosiness was explained by individual sociability. Individual choosiness was positively related to individual sociability scores (estimates:  $0.08 \pm 0.03$  SE,  $F_{1,452} = 9.99$ ,  $P = 0.002$ ). This relationship was also significant when we used the mean individual choosiness over the four tests (estimates:  $0.08 \pm 0.03$  SE,  $F_{1,149} = 9.99$ ,  $P = 0.002$ ; Fig. 4).

**DISCUSSION**

A major tenet of animal behaviour is that benefits and costs of being in a group depend on group size (see earlier references). A second major idea in animal behaviour and of game theory, in particular, is that individual fitness and social group dynamics depend on the mix of behavioural types in the group (see earlier references). Whereas many studies on effects of group size or composition set these group properties experimentally, in reality,



**Figure 3.** Mean  $\pm$  SE % shoaling time spent close to the social shoal depending on shoal size. \*\*\* $P < 0.001$ .

**Table 2**  
Individual preference for social versus asocial shoal depending on the focal individual's sociability score, shoal size treatment, body mass and trial day

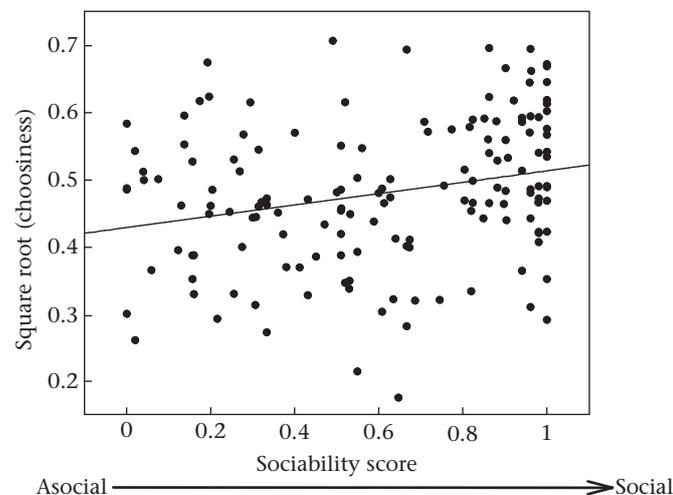
	Estimates±SE	F	P
Intercept	0.06±0.34	–	–
Individual sociability	0.57±0.35	$F_{7,147}=2.62$	0.10
Shoal size treatment (L)	−0.46±0.09	$F_{7,147}=24.70$	<0.0001
Interaction (L)	−0.02±0.13	$F_{7,147}=0.02$	0.89
Body mass	−0.54±1.72	$F_{7,147}=0.10$	0.75
Trial day	0.04±0.02	$F_{1,147}=3.81$	0.05

Random effects: block and intercept. Estimates are given for large shoals (L).

they emerge from the aggregate of individual choices about group joining or leaving (i.e. from individual grouping tendencies). Here, we added to the existing literature on individual grouping tendencies in several important ways. First, while many previous studies have looked at individual preferences relative to tendency to associate with groups of different size, we also examined individual preferences for associating with groups of different average personality type. In addition, we provided a rare case of a study examining how preferences for groups of different size and average personality depend on the focal individual's own personality. Personality-based group choice preferences violate the simplifying assumption of random interactions in ways that can have important impacts on social dynamics and evolution. Finally, our study is one of a few to quantify individual differences in not just preferences in different social contexts, but also choosiness across several situations. Below, we discuss interpretations and implications of our main results.

#### Explaining Shoal Preferences

When fish spent time close to one of the two shoals, they showed a clear preference for larger over smaller shoals. Shoal size is well known to influence benefits and costs of being in a group (e.g. Hoare et al. 2004). Large shoals detect predators sooner (Magurran et al. 1985; Godin et al. 1988) and individuals in large shoals can allocate more time to foraging (Godin & Smith 1988). However, shoal size is also positively related to food competition and parasite transmission (Pulliam & Caraco 1984; Cote & Poulin 1995). As a consequence, when alarm cues are present (risk is



**Figure 4.** Individual choosiness depending on individual sociability scores. The square roots of the average [(number of times the fish was close to one shoal arbitrarily chosen/number of observations where the fish was close to one of the two shoals) – 0.5] for the four shoal tests are shown.

high) fish form larger groups, while when food cues are present fish form smaller groups (Hoare et al. 2004).

Beyond corroborating past studies showing that individuals tend to prefer larger shoals, we found that the preference for large shoals was significantly lower when shoals were made of social individuals. A plausible explanation is that to yield benefits of shoaling, a shoal made of social individuals does not need to be as large as a shoal made of asocial individuals. This might in turn decrease the motivation to shoal with a large group to acquire shoal size-dependent benefits. Indeed, our fish also displayed a preference for shoals of social fish over shoals of asocial fish. Asocial individuals spent more time far from others (see above). We thus suggest that for a given group size, groups of social fish are more cohesive (smaller nearest-neighbour distance or higher synchronization of movements) than groups of asocial fish. Fish often increase shoal cohesion in response to predators or alarm cues in order to increase survival during encounters with a predator (Magurran & Pitcher 1987; Mathis & Smith 1993). Fish might therefore exhibit a preference for shoals of higher cohesiveness because it affords higher protection. An alternative explanation is that levels of aggression were probably lower in shoals made of social individuals and in larger, higher density shoals. Our overall suggestion is that group choice based on the group's personality might be mediated by how the group's personality affects social cohesion or aggression in the group. Further studies are needed to test these ideas.

We further found that individual preferences for shoal size depended on both the individual's personality and an interaction between the focal individual's personality and the average personality of the shoals. Asocial individuals preferred large shoals over small shoals more than social individuals did, and this effect was even stronger when the two stimulus shoals were made of social individuals. This does not mean that asocial individuals spent more time (than social individuals) close to large shoals overall, as asocial individuals spent much more time in the neutral area, but when asocial individuals decided to stay close to a shoal, they stayed preferentially next to large as opposed to small shoals. This result is at first unexpected because we were expecting asocial individuals to prefer small shoals and social individuals to prefer large shoals (Cote & Clobert 2007). A plausible explanation is that asocial individuals generally gain less (than social individuals) from being in a group. In that case, asocial individuals might not gain significant group benefits unless they are in a large group. They thus generally spend little time near groups (and instead, spend more time in the neutral area), but when shoaling, show a clear preference for larger over smaller groups. In contrast, social individuals might gain benefits from being in either a small or large group; thus while they prefer larger groups the preference is not strong. Another explanation might be that asocial fish may need stronger stimuli to arouse social attraction. Only large shoals would provide such stimuli.

Shoaling tendencies can also depend on an individual's bold/shy personality type. Previous studies on shoaling tendency showed that bolder fish tend to shoal less or take a position at the exterior/front of the shoal relative to cautious individuals (Budaev 1997; Ward et al. 2004; Leblond & Reeb 2006). In some studies, the tendency to shoal is used as a metric of risk-taking behaviour (Ward et al. 2004; Wilson et al. 2010). Our results might thus also be explained in part by a relationship between sociability and risk-taking behavioural types. However, our previous studies repeatedly showed a weak positive rather than a negative relationship between sociability and boldness in a novel environment; that is social fish that tend to shoal more tend to be bolder (which by itself should tend to make them shoal less), not more cautious. More generally, we suggest that it might be common for group choice to

depend on an interaction between the focal individual's personality and the size or social composition of alternative groups.

Finally, we found that the preference for large shoals and for social shoals increased over successive trial days. It appears that after more experience, individuals refined their preferences resulting in more pronounced preferences for large and social shoals.

#### *Implications of Shoal Preferences*

That animals exhibit social group preferences that depend on their own and on the group's personality violates the random mixing assumption made by many simple evolutionary models. The most fundamental implication of our results is thus that they quantify complex, group size-dependent, personality-dependent preferences that should generate particular nonrandom mixes of personality types. If density is high enough to form large shoals, then the fact that our fish generally preferred larger shoals (with asocial individuals generally avoiding shoals, but preferring larger shoals when they were made up of social individuals) should result in relatively large shoals that include a mix of primarily social individuals with some asocial ones. In contrast, if density is too low to form large shoals, social individuals should still join small shoals, but asocial individuals might avoid groups altogether, resulting in small groups of primarily social individuals. Small shoals, however, might be unstable since social individuals still show a tendency to prefer larger groups if they are available.

If animals can successfully join social groups that have properties that fit their preferences, then this represents a form of social niche construction where animals shape their social environment, in this case by choosing their environment (Saltz 2011). Social niche construction can have important effects on social behavioural evolution (Bergmüller & Taborsky 2010). For example, if social individuals do well at higher density with other social individuals, while asocial individuals do well alone and thus avoid groups, then both types should be able to find their preferred social situations. This then allows them both to develop and to evolve further social niche specializations that are adapted to their preferred social conditions. If, however, group choices conflict for different types, then individual attempts to enact social niche construction by group choice may be thwarted by the simultaneous choices made by other individuals; that is, in social games, 'you can't always get what you want'. For example, in a hawk–dove game, hawks may seek to join doves, but may be unable to do so if doves avoid hawks. The general point is that further studies like ours documenting individual differences in grouping tendencies and factors that affect them are critical for evaluating the potential role of social niche construction in social evolution.

Quantifying social group preferences can also help explain personality-dependent patterns of dispersal in our study species (Cote et al. 2010a, b, 2011). That asocial individuals showed a higher tendency not to be near a shoal fits our earlier observation that asocial individuals generally disperse more than social individuals. We also earlier found that social fish dispersed more than otherwise when their population included more asocial fish. In those populations, shoals might be smaller and less tight. In that situation, social individuals might tend to shoal less and thus disperse more to find populations with larger, more cohesive shoals. Recent studies suggest that personality-dependent and group context-dependent dispersal can have major impacts on many issues in spatial ecology (e.g. ecological invasions; Fogarty et al. 2011; Sih et al. 2012) and evolution (Cote et al. 2011). Further studies are thus needed to understand better how shoal behaviour and cohesion depend on shoal size and social composition, and how cohesion relates to patterns of dispersal.

#### *Individual Differences in Choosiness*

Individual differences in choosiness can be seen as a component of a behavioural syndrome (Sih & Bell 2008) where some individuals are consistently choosier than others across time or across multiple contexts. Although choice and choosiness are key aspects of behavioural ecology (diet choice, mate choice, habitat choice, social group choice), surprisingly few studies have examined individual consistency in choosiness (Bell et al. 2009), and even fewer have looked at how individual differences in choosiness (i.e. a choosiness syndrome) might be related to other personality traits (Sih & Bell 2008).

Here, we found that mosquitofish indeed exhibited consistent individual differences in choosiness as measured either by time spent in the neutral area or by the strength of preference for one shoal over another. The degree of choosiness about social situations seems likely to have fitness implications; however, to emphasize, being more choosy is not necessarily better than being less choosy. Instead, these can represent alternative strategies that can each do well in some circumstances. A key here is a speed–accuracy trade-off (Trimmer et al. 2008; Chittka et al. 2009). Being choosy requires collecting, processing and evaluating information to make a decision. The process of choosing a proper social group can take time and energy, and can expose animals to risk (e.g. predation risk). Thus even if animals benefit from choosing the right social situation, if being choosy is costly, it can favour less choosiness. In addition, the optimal degree of choosiness is likely to differ depending on the costs and benefits of being choosy in different situations. Being consistently more or less choosy can bias individuals of either type to exhibit inappropriate levels of choosiness in some circumstances. Documenting consistent individual differences in choosiness thus opens up fascinating, important questions that deserve more study.

Beyond simply finding that individuals differ in choosiness, we found that choosiness (in particular, when fish stayed close to one of the two shoals) was also positively linked to individual sociability. Regardless of shoal type, more asocial fish exhibited lower preferences for one of the two stimulus shoals when they got closer to a shoal than more social fish. This result is independent of shoal size or shoal social type. Our choosiness metric does not separate whether social fish chose a specific shoal depending on its characteristics or only stayed close to the first shoal they saw (i.e. shoal fidelity). However, most fish continued to move between shoals even after the 10 min of acclimation. Moreover, by analysing the first versus the last 5 min of observations separately, we obtained a choosiness metric that was related to sociability scores only for the last 5 min (first 5 min: estimates:  $0.02 \pm 0.03$  SE,  $F_{1,452} = 0.80$ ,  $P = 0.37$ ; second 5 min: estimates:  $0.07 \pm 0.02$  SE,  $F_{1,452} = 2.63$ ,  $P = 0.009$ ). This suggests that during the first 5 min, social individuals moved between shoals as much as asocial fish, whereas during the second 5 min, asocial fish kept moving while social fish often settled next to a specific shoal.

The relationship between sociability and social group choosiness has a plausible adaptive explanation. In mosquitofish, asocial individuals might often be producers that do not rely on social information during their daily activities and, furthermore, seek to avoid scroungers; that is they might base their behavioural decisions on private information about environmental conditions rather than on social information. Social groups are not important to them; thus they are not choosy about social group properties. In contrast, social individuals might be choosier about their social group, because the properties of the social group have a large effect on their fitness. Alternatively, social individuals might simply be more sensitive (than asocial individuals) to variation in social group properties, and thus choosier. An interesting next step would be to test whether individual differences in choosiness between social groups is related to individual differences in degree of flexibility,

which is a key factor affecting ability to respond well to environmental change, in general.

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