

Experience influences shoal member preference in a species pair of sticklebacks

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Recognition of suitable group members can be learned through experience or can be genetically based. To determine when learning may be important in social recognition, we compared the social recognition of juveniles and adults of 2 sympatric species of three-spined sticklebacks (*Gasterosteus* spp.). We altered the social environment of both species, rearing individuals with varying numbers of conspecifics and heterospecifics. We measured the effect of this social experience with heterospecifics on shoaling tendency and shoal member preferences. We also explored age effects by comparing juveniles and adults. Experience modified both the degree of sociality and the choice of social partners. We found that juveniles of both species had a stronger tendency to shoal than adults and that experience with heterospecifics influenced social tendency for juvenile benthics but not limnetics. Use of body size cues in selecting social partners by juveniles was also altered by experience. Only juveniles raised with conspecifics preferred conspecifics that were similar in size. Experience had a large effect for adults who preferred to associate with the species they had been raised with. Differences between juveniles and adults were more pronounced than differences between species. Our results suggest that individuals learn their species identity from the social environment and that this affects social preference. Learned social preferences may also have implications for the maintenance of reproductive isolation between these species. *Key words*: group formation, learning, shoaling behavior, social recognition, speciation, three-spined stickleback. [*Behav Ecol* 19:667–676 (2008)]

Individuals may benefit from selectively forming groups. These benefits can lead to preferences for certain types of group members. If predation is reduced when groups are composed of similar individuals, individuals may prefer group members that are the same color (Engeszer et al. 2004; Modarressie et al. 2006), the same size (Ranta et al. 1994), or the same species (Krause and Ruxton 2002). Grouping with conspecifics may also be beneficial if conspecifics transfer information to each other about food (Templeton and Giraldeau 1996; Reeb and Gallant 1997) or predators (Treherne and Foster 1981; Mathis et al. 1996). If groups of familiar individuals have reduced aggression (Utne-Palm and Hart 2000), increased cohesion (Chivers et al. 1995), or enhanced social learning (Swaney et al. 2001), individuals may prefer familiar group members. Individuals may also prefer to form groups with kin if grouping provides inclusive fitness benefits (Waldman 1984; FitzGerald and Morrisette 1992; Brown GE and Brown JA 1996; Frommen, Mehlis, et al. 2007).

In order to select group members, individuals need to be able to recognize those that possess suitable phenotypes. Recognition involves the production of a cue or a signal by one individual and the evaluation of that cue or signal by another individual (Sherman et al. 1997). Recognition can be based on cues, such as body size, and evolved signals, such as vocalizations (Sherman et al. 1997; Maynard Smith and Harper 2003). Because our focus is primarily on the role of learning rather than the basis for recognition, we will use the term “recognition cues” to refer to both recognition cues and signals. We acknowledge that both cues and signals may be involved but do not attempt to distinguish between them in this work. Individuals evaluate cues by comparing the cue to a template, which is an internal representation of the phenotype

associated with suitable individuals (Beecher 1982). What an individual does if the phenotype matches the template is determined by decision rules (Reeve 1989; Liebert and Starks 2004). Whereas some species recognize group members using genetically determined templates (Grosberg and Quinn 1986; Keller and Ross 1998; Queller et al. 2003), others use learned templates (Sherman et al. 1997; Hauber and Sherman 2001; Tang-Martinez 2001; Mateo 2004). However, for many species, we do not know if templates are genetically based or learned.

An individual can learn a template from its own phenotype or from the phenotypes of individuals it has interacted with (Holmes and Sherman 1982). The template is likely to be based on a phenotype that is reliably present and easy to learn (Sherman et al. 1997). Many social animals have parents, siblings, or other conspecifics reliably present in the social environment, and templates can be based on the phenotypes of these individuals.

Evidence is accumulating that learning plays a role in individual, group member, and kin recognition for many social species. The ability to recognize kin can be learned from the early social environment in mammals (Holmes and Sherman 1982; Holmes 1994; Heth et al. 1998), birds (Hatchwell et al. 2001), amphibians (Waldman 1981), fish (Winberg and Olsen 1992; Griffiths and Magurran 1999; Griffiths 2003; Hain and Neff 2006; Frommen, Lutz, and Bakker 2007), and some insects (Schausberger 2007). Social insects learn to recognize the distinct odor of their colony from nest mates and reject individuals that do not possess the correct cuticular hydrocarbon blend (Shellman and Gamboa 1982; Pfennig et al. 1983; Gamboa et al. 1996; Breed et al. 1998; Lahav et al. 1999; Lorenzi et al. 1999). Social insects can also learn to recognize familiar non-nest mate individuals (Errard et al. 2006; Leonhardt et al. 2007; Nowbahari 2007). Preferences for familiar group members (not necessarily kin) might be based on learning individually distinctive phenotypes in many species (Griffiths and Magurran 1997a, 1997b; Dale et al. 2001; Tibbetts 2002; Ward and Hart 2003; D’Ettorre and Heinze 2005). Alternatively, these preferences may be based on learning familiar phenotypes, such as familiar habitat odor cues (Ward et al. 2005, 2007), familiar color cues (McCann and Carlson 1982;

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Engeszer et al. 2004; Spence and Smith 2007), or familiar species cues (Warburton and Lees 1996). Whether recognition of kin, group members, and familiar individuals is based on shared or distinct mechanisms is a matter of debate (Tang-Martinez 2001).

Moreover, we still do not know how often social recognition is learned rather than genetically based. We also cannot predict when learning is likely to be involved in recognition. Social recognition may change over ontogeny as predation risk, diet, and habitat change (Butler et al. 1999; Despland and Hamzeh 2004; Gramapurohit et al. 2006). Thus, the role of learning in social recognition could also change across life stages. The early social environment may have a disproportionate effect on the recognition of kin and conspecifics later in life because some species imprint on parental (Immelmann 1969, 1972; Kruijt et al. 1983) or sibling phenotypes (Schutz 1965). In ants, nest mate recognition is based on learning early in life: during the larval stage (Isingrini et al. 1985; Carlin et al. 1987) or the first few days as an adult (Feneron and Jaisson 1995). Social recognition may also differ between species that differ in levels of social behavior. Selective pressures for increased sociality might change the strength of preferences for group members. It may also alter the phenotypes that suitable group members should possess. However, we do not know if changes in sociality would alter the role learning plays in social recognition.

We studied the recognition of species of group members in 2 species of three-spined stickleback fish (benthics and limnetics, *Gasterosteus* spp.). We wanted to determine if sticklebacks learned species identity of social partners from the environment or if recognition of species was genetically based. We also asked if social recognition was influenced by differences in either age or social behavior. Both species live in Paxton Lake, British Columbia, but limnetics inhabit the pelagic zone of the lake and benthics inhabit the littoral zone. Although these species have not been formally described, they are genetically distinct species (McPhail 1984, 1992; Taylor and McPhail 1999, 2000; Gow et al. 2006) maintained by sexual isolation (Ridgway and McPhail 1984; Nagel and Schluter 1998; Rundle et al. 2000; Boughman 2001) and ecological selection against hybrids (Schluter 1995; Hatfield and Schluter 1999; Rundle 2002; Gow et al. 2007). Limnetics are social and prefer to associate with a shoal of conspecifics over a single fish, but benthics do not (Larson 1976; Vamosi 2002). Adult benthics are often solitary and can be aggressive toward other individuals (Larson 1976). We do not know if these differences in social behavior are due to genetic differentiation between the species or differences in social experience. Nor do we know when these adult differences in shoaling behavior arise, as there have been no studies on juvenile shoaling behavior.

Sticklebacks have opportunities to learn recognition cues from social interactions throughout their lives. Males of both species provide care for eggs until hatching and guard the fry for several days afterward (Tulley and Huntingford 1987; Rowland 1994). We do not know how long fry remain in groups with kin, but we observe very large shoals of older juveniles in the wild (Kozak GM, personal observation). Thus, juveniles have the opportunity to learn phenotypic cues either from their siblings or from later social partners. This continues into adulthood, as limnetics continue to shoal, but benthics move into the littoral zone and become less social.

In order to test whether experience influences the degree of sociality and the choice of shoal members in this pair of species, we manipulated the social environment and asked if this affected social preferences. The social experience ranged from being reared with very few conspecifics (and many heterospecifics) to being reared only with conspecifics. We then measured the tendency to shoal and the choice of shoal members. Kin recognition could influence social preferences,

but we wanted to focus on general recognition mechanisms so we ruled out kin recognition by only allowing individuals to choose between fish that were both unfamiliar and unrelated. We predicted that levels of social behavior might differ with experience, age, or species. These social tendencies could, in turn, influence the strength of shoal member preferences. If social experience influenced the choice of shoal members, then preferences should be for those phenotypes experienced in the rearing environment. If learning played no role, there should be no differences between individuals that were raised in different social environments. We also investigated at what age and in which species social recognition was learned in this sympatric pair of sticklebacks.

MATERIALS AND METHODS

Rearing treatments

In order to obtain offspring of both species, we collected adult benthic and limnetic three-spined sticklebacks (*Gasterosteus* spp.) from Paxton Lake, British Columbia, in April 2005 using minnow traps. The Paxton pair is 1 of 4 independently evolved stickleback species pairs in the Strait of Georgia region (McPhail 1994). We transported these fish to the University of Wisconsin–Madison, where we performed *in vitro* fertilization. We euthanized a male with an overdose of MS222, dissected the testes, and released sperm over a clutch of eggs stripped from a gravid female. We waited 15 min for fertilization to occur before separating eggs from the clutch using forceps. We performed 15 benthic crosses (15 benthic males and 15 benthic females) and 19 limnetic crosses (17 limnetic males and 19 limnetic females). Eggs from a single family could be split among multiple treatments. We selected benthic parents with reduced or absent pelvic spines to aid in distinguishing between the species (all limnetics have pelvic spines; McPhail 1992).

We transferred fertilized eggs to a plastic cup divided into 2 compartments by black plastic window screen (mesh size: 2×2 mm). We put benthic eggs on one side of the eggcup and limnetic eggs on the other side. The window screen allowed olfactory cues to pass between the eggs. The cup was placed in a 109-l tank (75 cm long \times 31 cm wide \times 48 cm high) over an airstone. We allocated eggs of each species to eggcups to create a range of experience with conspecifics and heterospecifics. Experience with conspecifics ranged from few conspecifics present in the tank (minority treatment), equal numbers of conspecifics and heterospecifics (equal), many conspecifics (majority), and only conspecifics (naive). Eggcups received an average of 35 eggs (minority 2–5 of 35 eggs, equal 15–20 of 35 eggs, majority 30–33 of 35 eggs, and naive 35 eggs). Eggs for each species in each treatment were derived from 1 to 2 families. When the fish hatched, fry fell to the bottom of the 109-l tank. Individuals remained in this home tank, visually and chemically isolated from other tanks, throughout the experiment. Difficulties in obtaining exact numbers of eggs, along with hatching failure, resulted in a range of ratios for each treatment. After hatching, we counted the number of benthic and limnetic fry in the tank and calculated the ratio of conspecifics to the total number of fish of each species: minority = 0.04–0.24, equal = 0.43–0.57, majority = 0.76–0.96, and naive = 1. We use these ratios as our measure of experience with heterospecifics. Benthic and limnetic fry could be distinguished by color, shape, and the presence of pelvic spines. Densities in the tanks were adjusted before 9 weeks of age to between 20 and 45 fish while maintaining the ratio of conspecifics to heterospecifics. Total number of fish in the tank did not influence time spent with a shoal (linear regression: juvenile $F_{1,38} = 0.76$, $P = 0.39$; adult $F_{1,43} = 1.01$, $P = 0.32$) or time

spent with conspecifics (linear regression: juvenile $F_{1,30} = 0.29$, $P = 0.60$; adult $F_{1,47} = 0.70$, $P = 0.41$). All individuals in the tank were allowed to freely interact, and we did not observe any qualitative increases in aggression between hetero-specific individuals.

We created additional families that were used as stimulus fish. Multiple families were housed in 109-l tanks separated by species. We always used stimulus fish that were unrelated and unfamiliar to the focal fish. In this way, we avoided the possibility of kin or individual recognition.

We reared the fish at 18 °C and fed them a mixture of brine shrimp (*Artemia* spp.) and bloodworms (*Chironomus* spp.). We kept the fish on a 14:10 light:dark cycle until they were 12 weeks old. To simulate seasonal light changes, we reduced light duration by 30 min per week to 10:14 light:dark and maintained this from 15 to 40 weeks of age. Then we increased light duration by 30 min per week to 14:10 light:dark by 48 weeks of age. We conducted social preference testing for juveniles when fish were 15 weeks old and for adults when fish were 41 weeks old. Stickleback fish are reproductively mature at approximately 48 weeks of age. Increased day length does stimulate reproduction in sticklebacks, but very few fish displayed reproductive traits (males with nuptial color or gravid females) at the time of adult testing. Reproductive adults were not used as focal or stimulus fish in social preference tests. We observed little aggression in home tanks prior to social preference tests.

Social preference testing

We conducted 2 preference tests to measure the tendency to shoal (shoaling tendency test) and the species individuals preferred to shoal with (species preference test). Social preferences are commonly used as a measure of recognition (Engeszer et al. 2004; Ward et al. 2005; Spence and Smith 2007). Juvenile and adult fish were tested for both shoaling tendency and species preference. All conspecific individuals in a tank had the same rearing experience and were presented with the same stimulus fish, so we used averages of responses for each species in each tank. We tested 5–12 conspecific individuals per tank as juveniles and 2–8 conspecific individuals per tank as adults (the number tested depended on the number of fish present in the tank). We had 33 tanks in total: 11 benthic minority/limnetic majority tanks, 11 limnetic minority/benthic majority tanks, 2 limnetic and benthic equal tanks, 4 naive benthic tanks, and 5 naive limnetic tanks.

Our standard setup for our social preference tests was a tank divided into 3 compartments: 2 stimulus compartments (left and right) and a focal compartment. Window screen mounted on plexiglass frames separated the compartments, allowing both visual and chemical cues to pass between the focal and the stimulus fish. In juvenile tests, each stimulus compartment was 15 cm long \times 50 cm wide \times 58 cm high and the focal compartment was 25 cm long \times 50 cm wide \times 58 cm high. To accommodate larger adults, each stimulus compartment was 20 cm long \times 50 cm wide \times 58 cm high and the focal compartment was 44 cm long \times 50 cm wide \times 58 cm high. For both tests, we marked shoaling preference zones on a transparency taped to the front of the tank. The shoaling preference zone was the area of the focal compartment within 2 body lengths of each stimulus compartment (6 cm for juveniles and 12 cm for adults). This measure is comparable with natural shoaling distances of 2–4 body lengths (Pitcher and Parrish 1993).

For both tests, we placed a focal individual from a rearing treatment into the central compartment. In the stimulus compartments, we placed stimulus fish that were unrelated and unfamiliar to the focal fish and unrelated to any fish that the focal fish had experienced in its rearing environment. All fish had been fed in their home tanks at least 1 h prior to testing.

In the testing tank, we allowed the focal fish to acclimate for 5 min. If a focal fish had not moved at the end of the acclimation period, the trial was aborted. If the fish had moved, we recorded when the focal fish entered and exited each preference zone for the next 5 min. All observations were made from behind a blind. After the trial, we removed the focal individual and measured its body length. All juvenile focal fish were measured with a plastic ruler, and all adults were measured with calipers. Benthics and limnetics from wild populations differ in adult body size (McPhail 1992), and we wished to determine if they differed in size in our laboratory population, both as juveniles and as adults. We also hypothesized that body size differences between an individual and the shoal might affect the tendency to associate with the shoal because this occurs in other three-spined stickleback populations (Peuhkuri et al. 1997). Variation in size amongst focal fish and between species prevented us from controlling for body size differences between individuals and stimulus shoals. Instead, we controlled the effect of size statistically by using size difference as a covariate in our analyses.

Shoaling tendency test

In the shoaling tendency test, individuals chose between associating with a shoal of 10 fish and a single fish. We selected 11 stimulus fish of 1 species that were similar in size from a tank that contained fish unrelated and unfamiliar to the test fish. We placed this group of 11 stimulus fish in 1 randomly chosen stimulus compartment (left or right). The stimulus fish were allowed 20 min to acclimate to the testing tank. We then moved one of the fish from the group to the other stimulus compartment and gave the fish 10 min to acclimate. After every trial, we moved the single stimulus fish back to the group of 10 and we selected another fish to be the single stimulus fish in order to minimize effects of identity of the single fish. The rearranged groups were allowed to acclimate for 10 min before another trial was run. We tested the shoaling behavior of each species from each rearing treatment twice, once with conspecific and once with heterospecific stimulus fish. We conducted these tests on different days and in random order. For juvenile trials (benthic $n = 19$; limnetic $n = 19$), we only measured the length of the focal fish. For all adult trials, we additionally measured the length of all stimulus individuals (benthics $n = 21$ tanks; limnetic $n = 23$ tanks). We calculated body size difference as the absolute value of the difference in length between the focal individual and the average of the stimulus shoal fish.

Species preference test

In the species preference test, we placed a group of 10 similarly sized benthic fish in 1 stimulus compartment. In the other, we placed a group of 10 similarly sized limnetic fish. Both stimulus shoals were unrelated and unfamiliar to the test fish. Because limnetics and benthics differ in body size (McPhail 1992), we could not match benthic and limnetic groups for size. Species shoals were assigned to left or right compartments randomly. The shoals were allowed 30 min to acclimate to the tank. For juvenile trials (benthic $n = 16$ tanks; limnetic $n = 16$ tanks), we measured the length of 5 individuals in each stimulus shoal. For the adult trials (benthic $n = 25$ tanks; limnetic $n = 29$ tanks), we measured the length of all stimulus individuals. We calculated body size difference as the absolute value of the difference in length between the focal individuals and the average of the conspecific stimulus fish.

Statistical analysis

We conducted our statistical analyses using SAS (version 9.1). For all statistical tests, we analyzed juveniles and adults separately. The data were normally distributed and showed no

heteroscadacity. The interpretation of preference tests depends entirely on the null hypothesis defined (Underwood and Clarke 2005, 2006). For shoaling and species preference, we calculated our measure of preference based on the null hypothesis that a fish with no preference would spend equal time in each preference zone by chance. In our experiment, focal fish could have chosen to remain in the neutral zone in the middle of the tank, so they were not forced to be in either preference zone at any given time. Our measure of preference (time spent in preference zone A – time spent in preference zone B) did not include time spent outside of the preference zones. Thus, we defined preference as a significant difference between the time spent in each preference zone.

Our measure of shoaling tendency was the difference in time spent in the preference zone near the group of 10 fish and near the single fish. A fish that preferred to associate with shoal should spend more time near the group of 10 fish. Thus, we determined if fish preferred either the group of 10 fish or the single fish by testing if the difference between the time spent with each was different from zero using a *t*-test. We also compared the time spent with the shoal between individuals as juveniles and adults using a paired *t*-test. To determine what factors influenced the amount of time spent shoaling for juveniles, we used an analysis of covariance (ANCOVA) including species, experience (ratio of conspecifics to total number of fish in the tank), and their interaction. Insufficient data on body size of the stimulus shoals prevented us from including it as a factor in the juvenile analyses. For adults, we included species, experience, body size difference (from the shoal), and the interactions between these factors. We removed non-significant interactions to simplify our model.

For species preference analyses, we calculated the difference in time in the preference zone near the conspecific shoal and near the heterospecific shoal. Again, we predicted that if the focal fish had no preference (either was not attracted to any shoal or was attracted to both shoals equally), it would spend equal amounts of time in each preference zone. Thus, the difference in time spent with the conspecific shoal and the heterospecific shoal gave us a measure of preference for a conspecific group. We used ANCOVA to determine which factors influenced the difference in time spent with the conspecific shoal and time spent with the heterospecific shoal. Once again, our model included species, experience, body size (difference from the conspecific shoal), and the interactions between these factors, and we removed nonsignificant interactions.

In our species preference analyses, there was a significant interaction between 2 continuous variables: experience and body size. In order to visualize this interaction, we pooled the species and treated our analysis as a multiple regression of time with the shoal on body size and experience, $Y = \beta_0 + \beta_1(\text{body size}) + \beta_2(\text{experience}) + \beta_3(\text{body size} \times \text{experience})$. Using a method from Aiken and West (1991, p. 12), we restructured the regression equation so that $Y = (\beta_0 + \beta_2 \times \text{experience}) + (\beta_1 + \beta_3 \times \text{experience})(\text{body size})$. By inputting a numerical value of experience, we generated simple regression equations on body size, $Y = \beta_0 + \beta_1(\text{body size})$. The experience values used were the mean experience value for minority individuals (juvenile mean = 0.14; adult mean = 0.13) and the mean value for majority individuals (juvenile mean = 0.86; adult mean = 0.87). We calculated the regression lines for body size at these values and performed simple slope analysis to test if the slopes at different levels of experience differed from zero (Aiken and West 1991). Equal and naive treatments were left out of this visualization for simplicity. Thus, we were able to compare how body size affected shoaling in individuals with very different levels of experience.

We also analyzed the data using experience as a categorical factor (minority, equal, majority, and naive) instead of as

a continuous one, but this gave us similar results and those analyses are not included.

Because body size differs between benthics and limnetics in the wild (McPhail 1992), we examined the body sizes of our focal fish. We calculated average body size per species per tank and compared benthics and limnetics using a *t*-test.

RESULTS

Size differences between the species

Juvenile benthics and limnetics did not differ in size (benthic mean = 32.57 ± 17.2 mm, limnetic mean = 33.6 ± 23.18 mm, $t_{50} = -0.82$, $P = 0.42$). Adult benthics were larger than adult limnetics (benthic mean = 51.77 ± 22.93 mm, limnetic mean = 45.5 ± 17.64 mm, $t_{48} = 5.07$, $P < 0.001$).

Shoaling tendency

Both benthics and limnetics spent more time with a shoal than a single conspecific as juveniles (Figure 1a; benthic $t_{19} = 3.62$, $P = 0.002$; limnetic $t_{19} = 3.26$, $P = 0.004$), but not as adults (benthic $t_{21} = -0.12$, $P = 0.91$; limnetic $t_{22} = 1.71$, $P = 0.10$). However, the decrease in shoaling between juveniles and adults was not statistically significant (pairwise difference: benthic $t_{18} = 1.82$, $P = 0.09$; limnetic $t_{18} = 0.20$, $P = 0.84$). Benthics and limnetics did not differ in shoaling tendency at either age (juvenile $t_{38} = 0.11$, $P = 0.92$; adult $t_{44} = 1.23$, $P = 0.23$).

In juveniles, experience influenced the time spent with a conspecific shoal only in benthics (Figure 2; ANCOVA: species $F_{1,36} = 3.67$, $P = 0.06$; ratio $F_{1,36} = 3.54$, $P = 0.07$; species \times ratio $F_{1,36} = 5.61$, $P = 0.02$). Species, experience, and body size did not explain any variation in shoaling tendency for adults.

Juvenile limnetics and adult benthics spent more time with a shoal than a single heterospecific (Figure 1b; juvenile benthic $t_{19} = 1.47$, $P = 0.16$; adult benthic $t_{21} = 2.36$, $P = 0.028$; juvenile limnetic $t_{19} = 2.91$, $P = 0.009$; adult limnetic $t_{22} = 1.64$, $P = 0.12$). However, there was no significant difference between juveniles and adults (pairwise difference: benthic $t_{17} = -0.005$, $P = 1.0$; limnetic $t_{18} = 0.12$, $P = 0.91$). We could not identify any specific traits that influenced the amount of time spent with heterospecific shoals.

Species preference

Experience influenced species preference in benthics and limnetics both as juveniles and as adults. Adults spent more time shoaling with the species they had experienced in their social environment (Table 1, Figure 3). In juveniles, experience altered the effect of body size on shoaling with conspecifics (Table 1, Figure 4a,b). Majority juveniles spent more time with conspecifics as the body size difference decreased. In contrast, minority juveniles spent equal amounts of time with similarly and differently sized conspecifics. Body size did not have a significant effect on species preference in adults (Table 1, Figure 4c,d). There was no detectable difference in preference between the species for juveniles (Table 1, benthic mean = -30.54 ± 20.18 ; limnetic mean = -5.08 ± 20.18) or adults (benthic mean = -45.54 ± 21.46 ; limnetic mean = -4.37 ± 19.92), although benthics showed a stronger effect than limnetics.

DISCUSSION

Learned social recognition

Our manipulation of social experience led to differences in social preference in benthic and limnetic sticklebacks. Our results

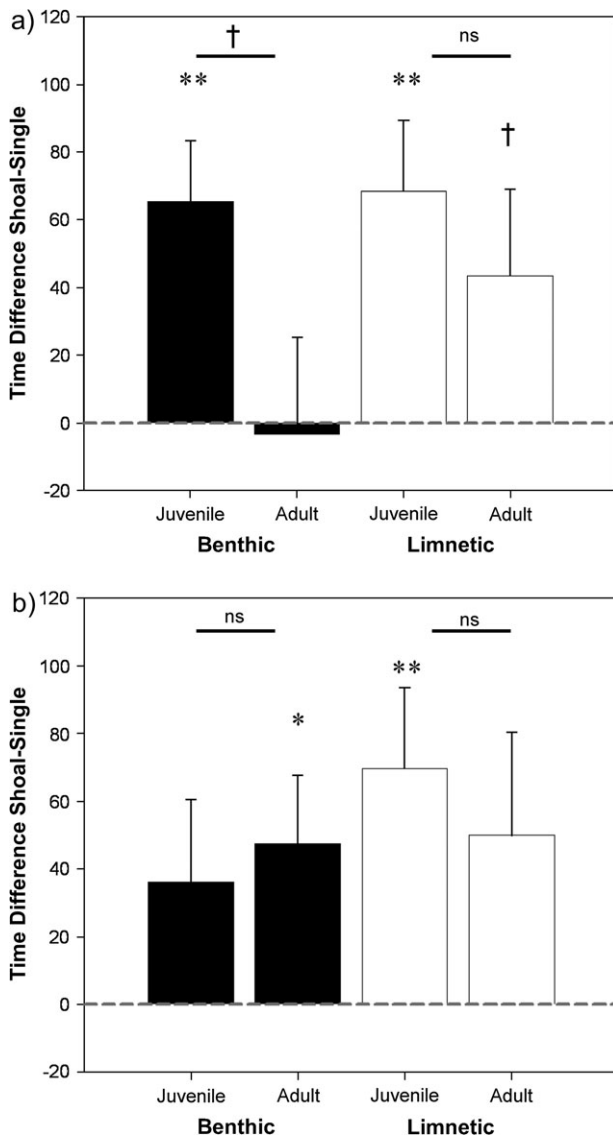


Figure 1
Time spent shoaling in juveniles and adults. Mean difference + 1 standard error (s) juveniles and adults spent with a shoal over a single fish in the shoaling tendency test. The dashed line is equal time spent with the shoal and single fish. (a) Conspecific stimulus fish and (b) heterospecific stimulus fish. * $P < 0.05$, ** $P < 0.01$, and † ≤ 0.10 .

suggest that the recognition template is learned through experience in both juveniles and adults. In juveniles, experience influenced the choice of groups based on body size. In adults, individuals raised with heterospecifics associated with groups of heterospecifics instead of conspecifics. These results suggest that individuals matched the phenotypes of unfamiliar stimulus fish against phenotypes learned through social interactions. Juveniles focused primarily on size, and adults focused on species identity.

Social recognition cues change through ontogeny

Our results suggest that learning is important to social recognition at multiple ages. Although we cannot identify the precise time at which learned recognition occurs, our results suggest that this learning influences social preference throughout life. What changes with age is not the extent of learned

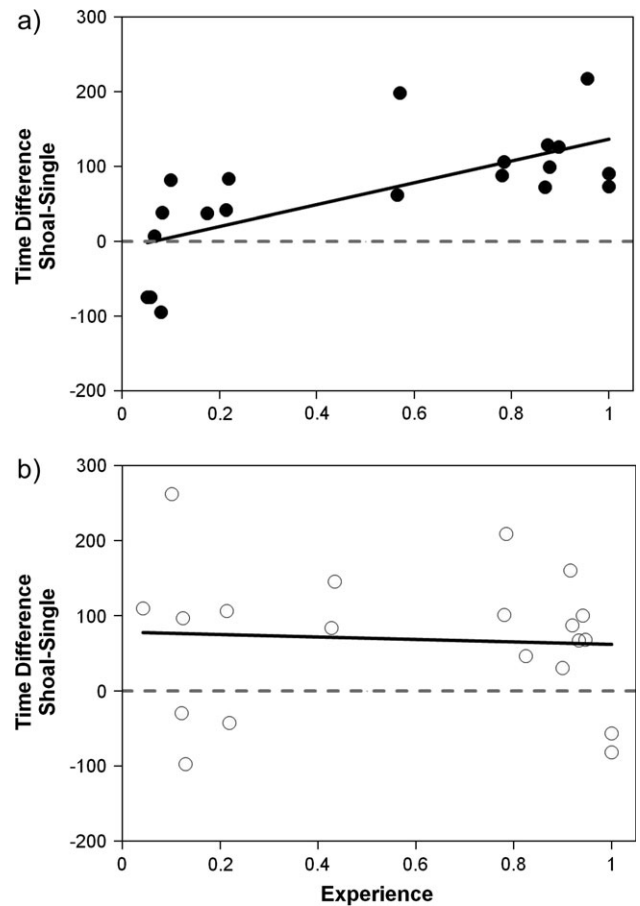


Figure 2
Experience and shoaling tendency in juveniles. Difference in time spent with a shoal over a single fish in relation to experience (proportion of individuals in the tank that are conspecifics). The solid line shows the predicted value, and dashed line indicates time expected if fish were associating randomly. (a) Juvenile benthics ($\beta = 145.29 \pm 68.50$) and (b) juvenile limnetics ($\beta = -16.71 \pm 68.50$).

recognition, but the precise morphological cues used to choose groups.

Juvenile benthics and limnetics use relative body size of potential group members to select groups that are similar in size to themselves. Majority juveniles shoaled with conspecifics, unless the fish in the shoal were substantially larger than the focal fish. Minority juveniles did not seem to use body size to choose shoals. It is likely that minority juveniles were different in size from the fish in their social environment and perhaps this altered their use of size when choosing groups. For example, preference for familiar phenotypes might have conflicted with preference for similar size social partners. Choosing groups based on size could be related to benefits of shoaling with individuals of similar size, which may include reduced predation and competition (Ranta and Lindström 1990; Ranta et al. 1994) and increased group cohesion (Watkins et al. 1992). Preferences for shoals of similarly sized individuals have been found in three-spined sticklebacks (*Gasterosteus aculeatus*) from the Baltic Sea (Ranta et al. 1992; Peuhkuri et al. 1997) and many other social fish species (Ranta et al. 1994; Krause and Ruxton 2002).

Relative body size did not influence social preference for adults. It appears that adults are relying instead on other species-specific cues learned through the social environment. Although we do not yet know which traits are used to identify

Table 1
Factors influencing social preference in juveniles and adults

Source of variation	df	Mean square	<i>F</i>	β	<i>P</i>
Juveniles					
Species	1	4835.48	0.77	-25.45 ± 29.03	0.38
Experience	1	24570.52	3.91	36.69 ± 69.16	0.06
Body size	1	13820.56	2.20	24.14 ± 16.28	0.15
Experience \times body size	1	42041.50	6.69	-77.49 ± 29.97	0.02
Error	27	6288.56			
Adults					
Species	1	22570.88	1.97	-41.18 ± 29.34	0.17
Experience	1	75101.51	6.55	182.10 ± 71.14	0.01
Body size	1	2320.49	0.20	3.93 ± 8.74	0.65
Experience \times body size	1	21667.27	1.89	-22.02 ± 16.02	0.18
Error	49	11463.34			

The results of ANCOVA models for the difference in time (s) spent with conspecific and heterospecific shoal. df, degrees of freedom.

species, body shape is a likely candidate because it differs reliably between species (McPhail 1984). Additionally, shape differences are more pronounced in adults (McPhail 1984), which could make it easier for adults to learn and use shape to choose groups. Therefore, the traits used in social recognition may differ with age because of differences in reliability of body size and species-specific cues. In many taxa, juveniles and adults differ in appearance: in color, plumage, or degree of sexual dimorphism. Learning throughout life may provide a simple way to track these differences and use the most informative cues at each age (Sherman et al. 1997).

Degree of sociality

In addition to changes in the basis for social recognition, shoaling tendencies also differed over ontogeny. Juveniles of both species showed strong shoaling tendencies, whereas adults did not. We have observed very large groups of juveniles (up to 500 individuals) of both species in the wild, including some mixed species shoals (Kozak GM, personal observation). This suggests that juveniles benefit from shoaling, but more work is needed to identify these benefits. It could be that shoaling reduces predation or improves foraging and growth more effectively in juveniles than in adults.

Despite these ontogenetic changes, we found no difference in the overall level of shoaling between the species as juveniles. There were slight but nonsignificant differences in shoaling between adults of the 2 species. These differences were in the same direction as a previous study with wild-caught fish, which found a significant shoaling tendency in adult limnetics but not in adult benthics (Vamosi 2002). The reduced differences between benthics and limnetics in our study suggest that these species do not differ in sociality as dramatically as previously thought. Raising the species in a common laboratory environment produces similar social patterns. Fish raised in the laboratory may be missing a critical part of the environment, such as predation or social foraging, that strengthens shoaling tendencies in adult limnetics and weakens them in adult benthics.

We predicted that the contribution of learning to social recognition might change with age or with sociality. We found no difference between species in the degree of sociality and little difference in how learning influenced social preference. We did find differences between ages in the degree of sociality and also in the cues used in social recognition. However, learned recognition is important to both species at both ages.

These results are largely consistent with our predictions, although prior work led us to expect larger differences in sociality between limnetics and benthics. Future studies on social recognition in other species that show more extreme differences in sociality will give us a better idea of how sociality might

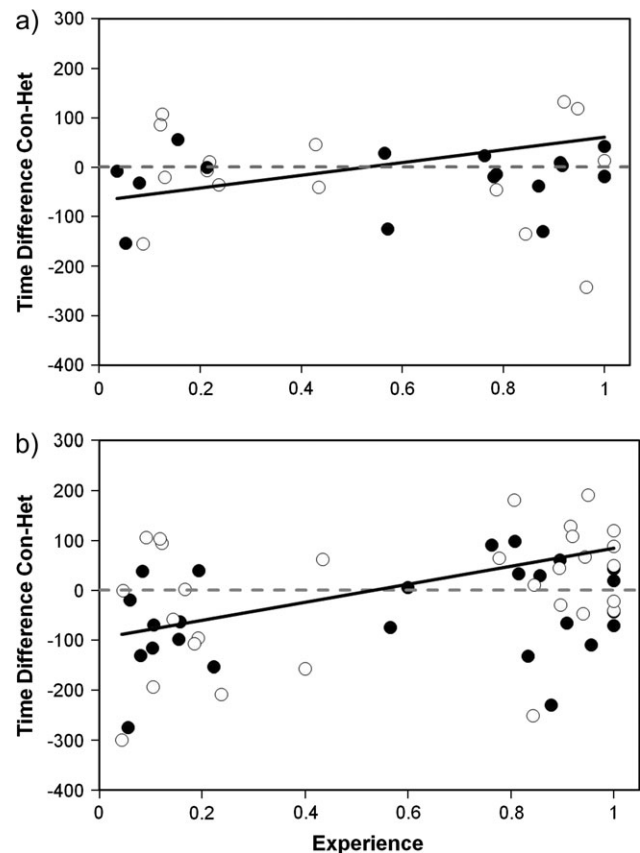
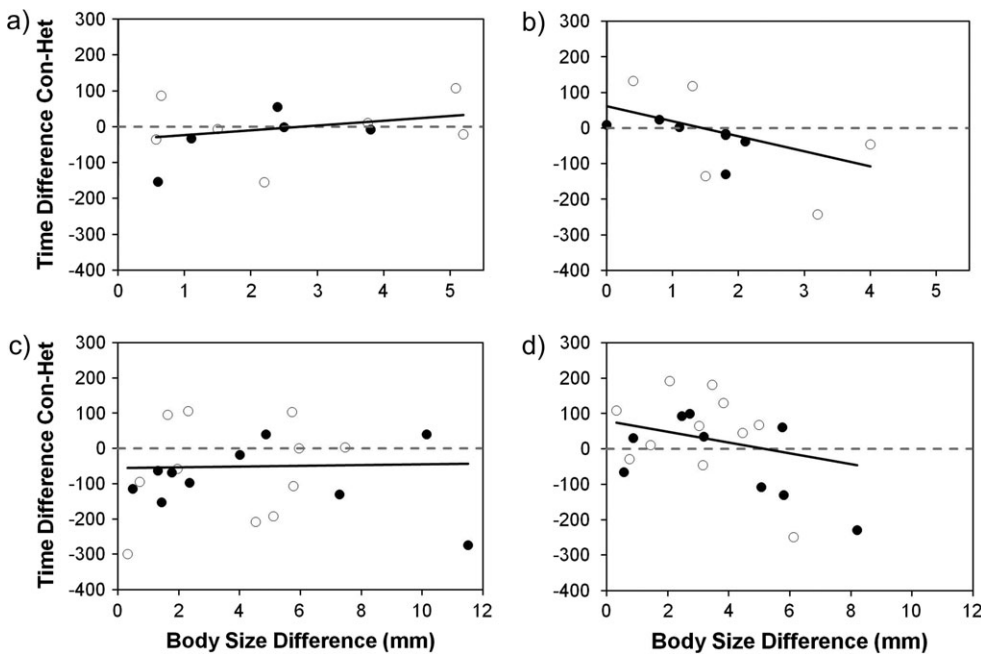


Figure 3
 Experience and time spent with the conspecific shoal. Difference in time spent with conspecific shoal and heterospecific shoal in relation to experience for benthics (solid circles) and limnetics (open circles). The solid line shows the predicted values calculated from the ANCOVA analyses (with species pooled). The dashed line denotes equal time with each shoal. (a) Juveniles and (b) adults.

**Figure 4**

Body size, experience, and time spent with conspecifics. Difference in time spent with conspecific and heterospecific shoal in relation to body size (millimeters) for minority fish (left) and majority fish (right). Benthics are solid circles, and limnetics are open circles. The solid line shows the predicted value (species pooled). The dashed line denotes time expected if fish were associating randomly. (a) Minority juveniles ($\beta = 18.90 \pm 14.72$, $t_{31} = 1.28$, $P = 0.21$), (b) majority juveniles ($\beta = -68.57 \pm 30.76$, $t_{31} = -2.23$, $P = 0.03$), (c) minority adults ($\beta = 0.22 \pm 7.40$, $t_{53} = 0.03$, $P = 0.98$), and (d) majority adults ($\beta = -15.66 \pm 9.75$, $t_{53} = -1.61$, $P = 0.11$).

influence the extent to which recognition is learned. Furthermore, studies that limit the opportunity for learning to certain ages will help us quantify the effect of age more precisely.

Effect of experience on sociality

The 2 species did differ in how experience influenced juvenile shoaling. Juvenile benthics needed experience with conspecifics to develop levels of shoaling equivalent to limnetics. Experience with conspecifics had no effect on juvenile limnetic shoaling. Limnetics showed high shoaling tendencies in all contexts, suggesting they might have an innate tendency to shoal. Perhaps, this is because limnetics consistently benefit from shoaling through improved foraging and reduced predation. Finding patches of zooplankton might be enhanced by group foraging because the number of individuals in a group reduce the variance in time between finding food patches (Horwood and Cushing 1977; Ruxton et al. 1995). Both species forage on zooplankton as juveniles, but only limnetics forage on zooplankton as adults. Thus, benthics may only benefit from group foraging at one life stage, and their shoaling behavior might consequently be more influenced by conditions. Switching between group and solitary foraging in response to resource distribution is widespread in animals and also occurs in fish (Ryer and Olla 1995; Johnson et al. 2002).

Predation levels also may affect how experience influences shoaling. Fish from high predation habitats do not need experience with predators (Magurran 1990) but do seem to need experience with conspecifics to develop the levels of shoaling observed in the wild (Paxton 1996). Predators differ in benthic and limnetic habitats (Reimchen 1980; Vamosi 2002), and these differences could contribute to differences in sociality. Future work is needed to determine if predation or resource distribution alter the levels of social behavior displayed by benthics and limnetics both as juveniles and as adults.

Consequences of learning from the social environment

Social interactions provide the opportunity to gain different types of information about suitable group members, such as

color, species, relatedness, group identity, and individual identity. The importance of social interactions as sources of information suggests that altering the nature of these interactions could strongly affect which individuals are preferred as group members. Most research focuses on a single type of recognition and often on a single modality, so we do not yet know how individuals acquire different types of information from the social environment and use it to make recognition decisions. This is likely to be an important direction to pursue. Research on species recognition during mate choice suggests that mating decisions require integrating information about species, attractiveness, and quality of potential mates (Phelps et al. 2006). Does social recognition require integration of kinship, familiarity, and similarity to an individual's own phenotype? We hope future studies will address these issues on how simple social preferences measured in the laboratory lead to group formation in nature.

Implications for speciation

The extent to which recognition in one context can be generalized to other contexts remains unknown. However, species recognition in social contexts is likely to lead individuals to preferentially associate with conspecifics. Therefore, a social preference for conspecifics might lead individuals to interact, forage, and mate with conspecifics. Species recognition is often important to preventing hybridization during mating. Therefore, learned species recognition may contribute to the maintenance of reproductive isolation between species if there is a connection between species recognition in social contexts and in mating contexts. In support of this, individuals that sexually imprint on heterospecifics also recognize heterospecifics as rivals in territorial encounters (Hansen and Slagsvold 2003). We are currently investigating the possibility that learned recognition influences sexual isolation in benthic and limnetic sticklebacks.

If species recognition in social contexts is learned, then changes in recognition can occur rapidly. Learned species recognition may promote rapid speciation because it can forgo the need for genetic change (Irwin and Price 1999). Speciation in sticklebacks has been rapid. Benthics and limnetics have evolved from marine sticklebacks within the past

10 000–15 000 years (McPhail 1984, 1993; Taylor and McPhail 1999, 2000). Our results show that species recognition is learned, so there is a distinct possibility that it has played a role in this rapid speciation. In another rapidly diverged pair of species from the Lake Victoria cichlid species flock, mate recognition by females is learned from the maternal phenotype (Verzijden and ten Cate 2007). More work is needed to determine if there is a general connection between learned recognition and speciation.

Our detailed study of social recognition in benthic and limnetic sticklebacks has provided several key insights. Social recognition and species identity appear to be learned in both benthic and limnetic sticklebacks. The degree of sociality is influenced more by experience in benthics, but overall, recognition is similar despite previously reported differences in social behavior. Juveniles are more social, and the degree of sociality is more influenced by experience than adults. Therefore, examination of recognition at one stage cannot always be generalized to another. Our results suggest that individuals learn their species identity from the social environment, and this influences their choice of social partners. It may also affect mate selection and thus may have implications for sexual selection and speciation.

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