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# Schooling and learning: early social environment predicts social learning ability in the guppy, *Poecilia reticulata*

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Social behaviour is extremely widespread in the animal kingdom and has a heritable component in many species. However, the degree to which social behaviour is phenotypically plastic and influenced by conditions individuals experience during early ontogeny is less well understood. Using the guppy as a model species, we examined the importance of early social environment upon the development of a number of social behaviours. We reared guppies at relatively low and high conspecific densities to investigate how early experience impacted shoaling behaviour and social learning ability in this species. Guppies reared at low densities had a significantly higher shoaling tendency than guppies reared at higher densities. Furthermore, individuals reared at low densities located a food resource more often and quicker than individuals reared at high densities in a foraging maze trial with trained demonstrators. After 8 consecutive days of maze trials we removed the demonstrators to investigate social learning skills. Guppies reared at low densities located food faster alone than guppies reared at high densities, implying that they were more adept at socially learning foraging information. This intriguing relationship between early social environment and the development of shoaling behaviour and social learning skills may have considerable implications for captive breeding programs in conservation and aquaculture.

Social behaviour has been documented in a huge number of species representing a broad range of animal taxa. Such widespread adoption of sociality suggests that it confers significant benefits to group members. These benefits range from protection against predation to locating food or mates and reducing the energetic costs of movement (Krause & Ruxton 2002). Furthermore, individuals in groups that lack information about the local environment can learn from other more knowledgeable individuals from within the social unit, a process known as social learning (Suboski & Templeton 1989). Social learning refers to any learning that derives from information produced by others (Giraldeau 1997), enabling individuals to acquire information rapidly and inexpensively. Boyd & Richerson (1985) postulated an evolutionary trade-off between reliable but expensive self-acquired information and less reliable but inexpensive socially acquired information (the 'costly information hypothesis'). Social learning has been documented in a variety of taxa (colonial insects: Langridge et al. 2004; noncolonial insects: Coolen et al. 2005; fish: Vilhunen et al. 2005; birds: Johanessen et al. 2006; mammals: Cook & Mineka 1989) and in a number of different contexts (foraging: Laland & Williams 1997; mate choice: Dugatkin 1992; antipredator behaviour: Vilhunen et al. 2005). Social learning processes are thought to be relatively simple in most cases (Galef 1988). For example, an individual exploiting a new food patch may inadvertently draw the attention of others to its location, a process known as 'local enhancement' (Thorpe 1956). Galef (1988) proposed that local enhancement is explicable simply in terms of social attraction, the tendency of individuals of social species to approach conspecifics, an idea supported experimentally in the laboratory (Laland & Williams 1997) as well as in the field

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(Reader et al. 2003). This suggests that individuals with a stronger tendency to associate with others may be more adept at social learning.

An individual's tendency to associate with conspecifics has a strong heritable component in many species (Huntingford & Wright 1993). For example, population differences in shoaling tendency in guppies thought to be driven by differences in predation pressure persist in future generations of laboratory-reared fish, despite the absence of predators (Seghers 1973). Yet, whereas a variety of studies have investigated the genetic basis of animal social behaviour, surprisingly little is known about the role of ontogeny in its development. A growing body of evidence suggests that early experience is profoundly important in the development of an animal's phenotype and that many adaptive behaviours show a high degree of phenotypic plasticity. Recently, behavioural ecologists have begun to investigate the plasticity of social behaviour as a function of an individual's rearing environment. Examples include the importance of early social environment in the development of mate-choice behaviour in zebra finches (Adkins-Regan & Krakauer 2000), agonistic behaviour in rhesus macaques (Newman et al. 2005) and territoriality in brown trout (Sundström et al. 2003). However, little attention has been paid to the importance of early social environment in the development of grouping behaviour (but see Paxton 1996) and, indeed, the impact that changes in an individual's tendency to group with conspecifics may have upon associated behaviours such as social foraging and learning.

We investigated the influence of early social environment upon an individual's grouping tendency and acquisition of social learning skills, rearing Trinidadian guppies in relatively high- and low-density treatments. Guppies are ideal candidates for answering questions of this nature as they have been previously shown to socially learn foraging information (Laland & Williams 1997) and display a high degree of plasticity in behaviour as a function of rearing environment (Chapman et al. 2008). We tested two competing hypotheses: first, that individuals reared at high densities will be more adept at responding to the social cues of conspecifics, and hence will be better social learners, and second, that individuals reared at high density will exhibit a reduced tendency to associate with conspecifics, as they may suffer greater costs from informational parasitism and/or intraspecific competition by remaining with the group. This reduction in shoaling tendency will disrupt the flow of information from one individual to another, leading to individuals reared at high densities being less adept at social learning.

## METHODS

### Rearing Conditions

All fish used in this experiment were the descendents of wild-caught guppies caught from the Tacarigua River in the Northern mountain range of Trinidad in 2005 (Trinidad national grid reference: PS 787 804; coordinates: N10°40.736′W061°19.168′). We assigned juveniles of $\leq 10$ mm in size (mean $\pm$ SD $= 8.22 \pm 0.11$) to one of two different density rearing conditions for a period of 70 days. In the low-density treatment, we reared juveniles at a density of one to four fish per tank. In the high-density treatment, we reared juveniles at a density of $7-12$ fish per tank. Within-treatment variation in density was in part due to mortality (see Results for details). Each tank was 24 by 15 by 15 cm and contained a foam filter and gravel substrate. Water depth was maintained at 9 cm. We fed the fry daily with ZM100 advanced fry feed using a 2-mm$^2$ spatula per fish per day for 49 days. After this we fed the juveniles freeze-dried bloodworm (*Chironomus* spp.: two per individual per day) for the remainder of the rearing period (21 days). We reared 14 replicates of each treatment between October 2006 and March 2007. Replicates had staggered start dates, with two replicates of each of the two treatments beginning at a given time to control for any effect of start date.

### Experimental Assays

Sixty days after its allocation to a rearing treatment, we assayed a single focal individual from each treatment for shoaling tendency. A second assay, investigating social foraging, began on day 62 and lasted for 8 consecutive days. On the 9th consecutive day (day 70 from the beginning of the experiment), we placed the focal fish in the maze alone to assess the degree of social learning achieved. To minimize disturbance in all trials the sides of the tank were opaque; we observed focal individuals with the use of a mirror angled at 45° above the tank.

### Shoaling Tendency

To investigate shoaling behaviour, we allowed focal fish to swim freely in a tank containing two choice chambers: one contained three unfamiliar juvenile guppies (stimulus body length mean $\pm$ SD $= 1.39 \pm 0.07$ cm; focal (low density) $1.2 \pm 0.1$ cm; focal (high density) $1.19 \pm 0.16$ cm) and the other was unoccupied. The choice arena was a rectangular tank of dimensions $32 \times 20 \times 20$ cm, with 7 cm water depth and gravel substrate. We placed a transparent perforated cylindrical plastic choice chamber (diameter 8 cm) 2 cm from each end of the tank such that 12 cm separated the two choice chambers. A 'shoaling zone' of two body lengths ($\sim 3$ cm) surrounded each chamber, and a neutral zone was located in the centre of the tank ($\sim 6$ cm at the narrowest point).

At the beginning of each trial we introduced a focal fish into the neutral zone. Following a 5-min acclimatization period, we monitored the focal individual's behaviour for a further 5 min. When the focal fish was within two body lengths of a choice chamber we considered it to be shoaling with the individuals within that chamber. We recorded the time spent in each shoaling zone, and we calculated overall shoaling tendency as the proportion of time spent associating with the occupied chamber of the total time associating with either chamber. In this way we controlled for the possibility that guppies may be attracted to the choice chamber itself rather than the fish

within it. We assayed a single focal juvenile from each of the 14 replicates of the two density treatments. We alternated the occupancy of the choice chambers between trials and the order in which individuals from the two treatments were tested. We changed the stimulus fish after a focal fish from each treatment had been assayed. Once tested, focal fish were returned to their original rearing tanks.

## Social Foraging Task

### Maze setup

The maze consisted of a plastic tank of dimensions 46 by 35 by 30 cm divided into three compartments (Fig. 1). Water depth was kept constant at 16 cm. The largest compartment (referred to as the refuge zone) contained two plastic aquarium plants of equal size and was shaded from overhead light. From the refuge zone, fish could enter either one of the two smaller chambers through a 6 by 6 cm square hole. The two smaller chambers were not shaded and contained only a circular feeding ring (diameter 6 cm), which was attached to the wall of the exterior corner at surface level. The left-hand chamber was the feeding chamber; in all of the foraging trials the feeding ring in this chamber contained a pinch of freeze-dried bloodworm. The right-hand chamber's feeding ring was always empty. From the refuge compartment, fish did not have a direct line of sight to the food. Holes were colour coded either red or yellow using a border of masking tape to provide a landmark to naïve individuals. The feeding chamber hole's colour was alternated between replicates to control for any variation attributable to the colour preference of guppies.
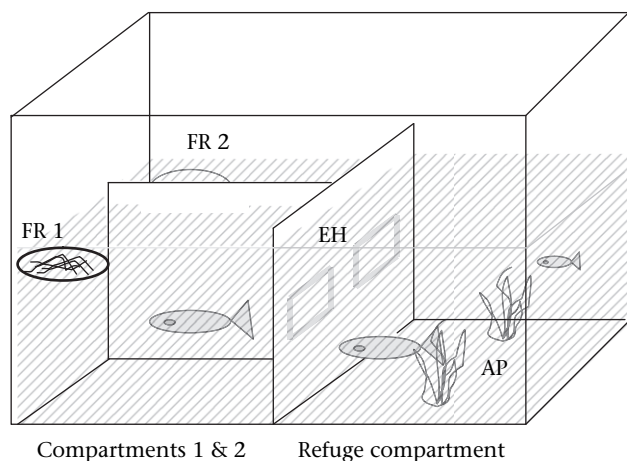


**Figure 1.** Foraging maze set-up (not to scale). Guppies are introduced into the refuge compartment, which contains two aquarium plants (AP) and is in shadow. At this point the entry holes (EH) to compartments 1 and 2 are blocked with Perspex sheets. Once all fish are within the refuge compartments, the Perspex is removed and individuals can swim through either of the two colour-coded entrance holes to compartment 1 or 2. Compartments 1 and 2 each contain a feeding ring (FR 1 and FR 2, respectively) at surface level. Bloodworm can be located in FR 1 (the lower compartment) but not in FR 2.

### Demonstrator husbandry and training

Eleven days prior to the beginning of the foraging trials, we randomly assigned 20 adult female guppies from the source population to the 'red' or 'yellow' demonstrator tank, with 10 fish in each. Holding tanks were $50 \times 20 \times 20$ cm; contained gravel substrate, an aquarium plant and a foam filter; and had opaque sides to minimize the effects of any external disturbance. Training lasted 10 days, with training occurring once daily. On the first 5 days, we placed all 10 demonstrators within the foraging maze for 15 min, with freeze-dried bloodworm located in the fixed surface ring in either the red or the yellow compartment (depending upon training group assignment). For the second half of the training, we introduced the fish into the maze in groups of three or four, to acclimatize the demonstrators to the group size they would experience over the period of the actual foraging assay.

### Experimental protocol

On day 1 of the 8-day foraging trial we haphazardly selected two demonstrators from the demonstrator stock tank and placed them in the refuge zone of the maze. The entrances from the refuge zone to the two smaller chambers were blocked with sheets of white Perspex at this point. We haphazardly selected a focal fish from the low-density treatment and introduced it to the refuge zone. We removed the Perspex blocking the entrances to the two smaller chambers, and the trial began when the three fish resumed movement. We recorded the time taken for both the focal fish and the first demonstrator to feed. Trials lasted for 15 min. Focal fish that fed before the demonstrator were given a score of 0, and focal fish that did not feed were given a score of 15 min (900 s). Once the trial was over, we placed the focal fish within a transparent, perforated bottle (250 ml) and returned it to its original tank. This was to enable identification of the focal fish for the remaining trials, while allowing those fish to retain visual and olfactory experience of their rearing treatment between assays. We placed used demonstrator fish in a second holding tank, where they remained until the following day's trial. After this, we replenished the bloodworm and placed two different demonstrators in the maze task, along with a focal fish from the high-density rearing treatment. The trial began again. We changed water after every two trials and alternated the treatment trial order (within and between days). We introduced any demonstrators that did not partake in the trial with observers into the maze for 15 min following the end of the day's social foraging trials. This process was repeated once daily over 8 consecutive days for each of the 28 focal fish, allowing us to calculate the number of days (of 8) that focal fish successfully completed the task. On the 9th day, we introduced the focal fish into the maze alone to gauge the effectiveness of the previous 8 days' training in a 'solo' trial. Following the same procedure detailed above, we recorded the time taken by the focal fish to enter a compartment, the time taken to enter the correct compartment, and the time taken to feed.

## Statistical Analysis

All data were checked for deviations from normality and homogeneity of variance. Where appropriate, we log-transformed the data to achieve parametric assumptions. When transformations failed to achieve parametric assumptions, we used nonparametric tests. We used linear models to investigate the log time taken for a demonstrator to feed, the log time taken to enter a compartment, and the log time taken to feed in the solo trial. We performed a repeated-measures analysis using a generalized linear mixed-effects model with a quasi-Poisson error distribution and individual ID as a random factor and day and treatment as fixed factors to investigate the time taken to enter a feeding compartment after a demonstrator in the social foraging trial. Furthermore, we used a linear mixed-effects model with individual ID as a random factor and day and treatment as fixed factors to investigate the time taken to feed after a demonstrator in this trial. We fitted generalized linear models with binomial and quasibinomial error distributions to the frequency the focal fish fed and the shoaling tendency data, respectively, with details of specific fixed effects below. We did not include start date and designated goal zone in the statistical analysis of the social foraging and learning trials, as we controlled for these experimentally. In the case of nonsignificant results, we provide the exact $P$ value unless $P > 0.2$. We carried out all statistical analysis using R (freeware available at www.r-project.org/) or SPSS 11.0. We dropped nonsignificant interactions from the analysis.

# RESULTS

## Low-Density Treatment

To justify the inclusion of both fish reared alone and fish reared at densities of 3 and 4 in a single 'low-density' class, we tested for differences in social foraging and social learning between them by adding fish reared in isolation as an additional treatment to the models. We found no evidence of differences between densities of 1 and densities of 3 and 4 (time to locate food after a demonstrator: $t = -1.62$, $df = 2$, $P = 0.12$; time to complete learning task: $t = -0.67$, $df = 2$, $P > 0.2$). However, we acknowledge that the statistical power of these tests is quite low due to the small sample sizes when the low-density treatment is divided into 1 versus 3 and 4 ($N = 7$).

## Mortality and Body Length

Relative mortality did not differ between treatments (Mann−Whitney $U$: $Z = -1.517$, $N = 28$, $P = 0.15$): overall in the low-density treatment mortality was 10.5%, and it was 18.5% in the high-density treatment. There were no differences in initial body length of fry assigned to the high- and low-density treatments (Mann−Whitney $U$: $Z = -0.516$, $N = 162$, $P > 0.2$) or the final body length after 70 days (Mann−Whitney $U$: $Z = -0.662$, $N = 130$, $P > 0.2$).

## Shoaling Tendency

We found a significant effect of treatment, with fish reared at low densities exhibiting a higher shoaling tendency (GLM: $t_1 = -1.98$, $P < 0.05$; Fig. 2). Body length had no impact upon shoaling behaviour (GLM: $t_1 = 1.08$, $P > 0.2$).

## Social Foraging Maze Trial

Demonstrators did not differ in the time taken to feed between treatments but showed improvement over time (LM: treatment: $F_{1,221} = 1.52$, $P > 0.2$; day: $F_{1,221} = 6.38$, $P < 0.05$). Individuals reared at low density were quicker to follow demonstrators out of the refuge compartment (GLMM: treatment: $t_{26} = 2.718$, $P < 0.05$), and individuals improved over time (GLMM: day: $t_{195} = -4.214$, $P < 0.001$). Our analysis of the time the focal fish took to feed after a demonstrator uncovered significant effects of both treatment and day. Fish reared at low densities fed significantly faster than fish reared at high densities (REML: treatment: $F_{1,26} = 17.68$, $P < 0.001$; Fig. 3). Furthermore, the time taken to feed decreased as a function of time (REML: $F_{1,195} = 7.93$, $P = 0.005$; Fig. 3). Fish reared at low density successfully completed the maze trial (i.e. fed) significantly more frequently than fish reared at high density (GLM: $z_1 = 3.95$, $P < 0.001$). We also uncovered an effect of body length, with smaller fish feeding more often than larger fish (GLM: $z_1 = -2.13$, $P < 0.05$).

## Solo Maze Trial

We found no treatment or body length effect upon the time taken to enter a feeding compartment in the solo maze trial (LM: treatment: $F_{1,25} = 3.65$, $P = 0.12$; body length: $F_{1,25} = 0.13$, $P > 0.2$). However, fish reared at low
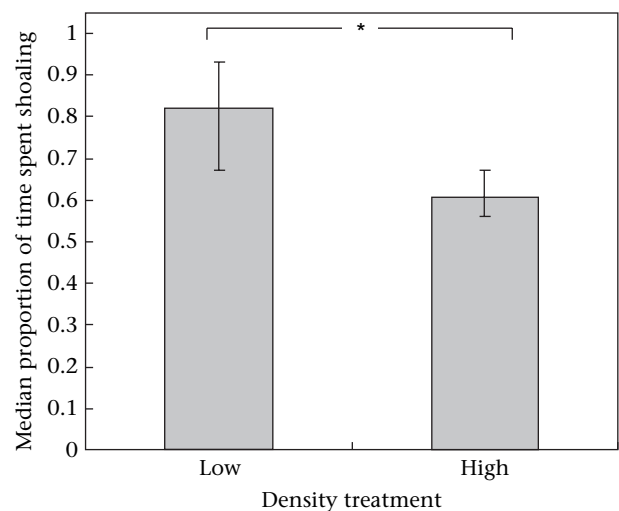
**Figure 2.** Median proportion of time (with IQR) focal fish spent shoaling (in seconds) with stimulus fish in a shoal-choice trial, of the total time the focal fish spent associating with either choice chamber. *$P < 0.05$.
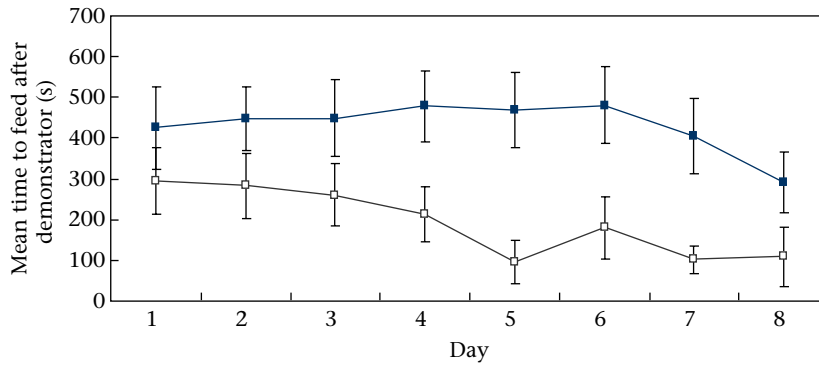
**Figure 3.** Mean time (±SE) taken to feed after a demonstrator (in seconds) in a foraging maze trial. ■: Fish reared at high density. □: Fish reared at low density. Fish from low-density backgrounds fed significantly faster than fish from high-density backgrounds ($P < 0.001$).

density began feeding sooner than fish reared at high density (LM: $F_{1,25} = 6.67$, $P = 0.016$; Fig. 4).

## DISCUSSION

Our results highlight the importance of early social environment in the development of shoaling and social foraging behaviour in the Trinidadian guppy. First, guppies reared at low densities have a significantly stronger shoaling tendency than guppies reared at high densities. Previously, shoaling behaviour was shown to have a strong heritable component in guppies (Seghers 1973; Breden et al. 1987) and in other species (e.g. sticklebacks: Hunting-ford & Wright 1993; zebrafish: Wright et al. 2003). Here we show that shoaling behaviour is highly plastic as a function of early social environment, within a given population. We propose that guppies reared at high densities experience a greater intensity of competition and more aggression than guppies reared at low densities, in the absence of predator cues, increasing the cost of group formation and resulting in a weaker shoaling tendency. Evidence from a variety of studies suggests that a positive relationship

exists between population density and levels of individual aggression (Ruzzante 1994; Blanchet et al. 2006).

Second, guppies reared at low densities were better at exploiting information from conspecifics than individuals reared at high densities. Individuals from low-density tanks fed significantly sooner following a trained demonstrator, and they fed on more days than individuals reared at high densities. Using social cues to locate food is likely to be beneficial in species such as the guppy that forage upon unpredictable and ephemeral food resources in the wild. Exploratory behaviour can also be costly, as group leaders potentially face greater predation risk (Krause et al. 1998), especially in the case of ambush predators, which tend to attack individuals at the front of a group (Bumann et al. 1997). Hence, in addition to the clear foraging benefits of being a more effective exploiter of social information, there may be additional costs to asocial foraging.

However, it is clear that being adept at benefiting from social facilitation in this way (what Coussi-Korbel & Fra-gaszy (1995) call 'isomorphic coordination') is not the same as being adept at socially learning foraging information. Thus, despite fish from both rearing treatments improving at locating food at the same rate in the social facilitation trials (as shown by the nonsignificant interaction between treatment and day), this has no bearing upon the impact of rearing treatment upon social learning ability. Only after individuals are tested alone following a period of 'training' can we make claims about differences in social learning. Our results suggest that not only were low-density guppies better at using the social information produced by others, they were also better at socially learning the location of food as demonstrated in the final solo maze trial. We propose that the mechanism by which juveniles reared at low densities were better social learners is their stronger shoaling tendency: individuals that associated more strongly with conspecifics were better at locating food with trained demonstrators over a number of trials, which translated into learning the information more effectively. Fish reared at low densities were quicker to follow demonstrators into a feeding compartment than fish reared at high densities, further supporting this hypothesis. Experimental evidence from Laland & Williams (1997) first implicated grouping tendency as facilitating social learning. Our results suggest not only that is this
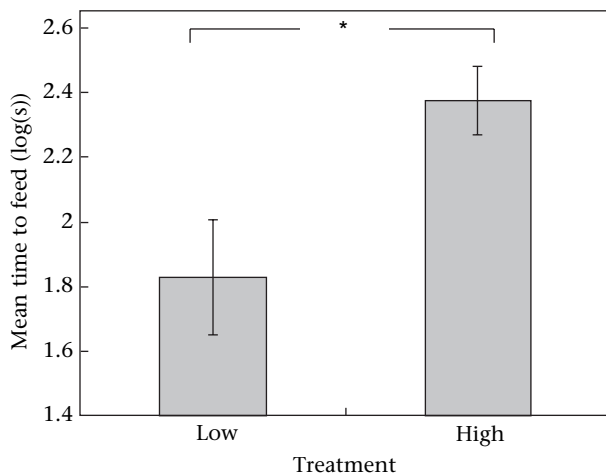


**Figure 4.** Mean time (±SE) focal fish took to feed (log seconds) in a foraging maze trial without demonstrators after 8 consecutive days of training. *$P < 0.05$.

the case, but also that there is a positive relationship between grouping tendency and social learning ability.

We recognize that an alternative (but less parsimonious) hypothesis to explain our data is that fish learned the route asocially, regardless of the presence of the demonstrators. The question of the importance of early experience in the development of asocial learning ability is an interesting one and deserves further attention. However, in our experiments the asocial learning hypothesis has no explanatory power when examining the differences evident between density treatments, nor does it account for the fact that the majority of times focal fish fed following a demonstrator.

We have documented an intriguing relationship between early social experience and shoaling and foraging behaviour and an individual's ability to socially learn foraging information. Although we are as yet unable to make any statement regarding the generality of this pattern, our findings may have implications for aquaculture and captive breeding programs. Hundreds of species of fish are reared in hatcheries to be released into the wild every year (Welcomme & Bartley 1998; in Brown & Laland 2001), yet postrelease mortality is often extremely high (Olla et al. 1998). For example, every year approximately 5 billion salmon reared in hatcheries are released into the wild, with only a 5% survival rate to adulthood (McNeil 1991). A number of factors are thought to play a role in this increased mortality, including the loss of 'wild genes' from captive populations, the transmission of pathogens and parasites, and life-history shifts caused by domestication (Petersson et al. 1996). An additional factor for the failure of many restocking programs is that captive-reared animals lack the appropriate skills necessary to survive and prosper in the wild, for example, in avoiding predation or locating food (Short et al. 1992; Stoinski et al. 2003). A great deal of recent work has focused upon how postrelease survival may be improved via 'life skills training' while still in captivity (Griffin et al. 2000; Brown & Laland 2001). Our results suggest that by lowering the density in the hatchery environment, individuals may become more adept at socially learning locally appropriate skills from their wild counterparts following release. We speculate that this could potentially improve their survival in the wild and that an interesting future focus would be to test these hypotheses upon species relevant to fisheries management and conservation biology. Our work supports recent work by Braithwaite & Salvanes (2005), which suggests that quite simple modifications to current hatchery environments may have a significant impact on the efficacy of captive breeding programs.

Individuals that experience a low-density environment in their early ontogeny may suffer costs in addition to the benefits we have reported here, for example, in the form of a reduction in competitive ability. Further experimental work could shed light on the importance of these costs. Evidence supporting the importance of early experience in the development of adaptive behaviours is growing (Braithwaite & Salvanes 2005; Chapman et al. 2008), and many questions in this field remain unanswered.

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