## Original Article

# Social information use and social learning in non-grouping fishes

## Mike M. Webster and Kevin N. Laland

School of Biology, Harold Mitchell Building, University of St Andrews, St Andrews, Fife KY16 9TH, UK

Although it is natural to expect that group-living animals will utilize social learning, the expectation for non-grouping species is less clear. Only a few studies have explored the relationship between sociality and social learning. Here we presented 4 non-grouping fish species, fifteenspine sticklebacks (*Spinachia spinachia*), bullhead sculpins (*Cottus gobio*), stone loach (*Barbatula barbatula*) and juvenile European flounders (*Platichthys flesus*) with social information provided by groups of a shoal-forming heterospecific, the threespine stickleback (*Gasterosteus aculeatus*). Using a binary choice procedure we allowed individual test subjects to select between simulated prey patches. Although the test subjects could not sample the patches directly they were able to use information generated by the heterospecific demonstrators to select the "richer" of the 2 patches. For comparison we also recorded social information use in 2 shoaling species, threespine, and ninespine sticklebacks (*Pungitius pungitius*). We saw evidence of social information use and social learning in all 6 species, with no differences seen between social and non-grouping species. We argue that social learning is not likely to be restricted to group-living species, since many solitary species too are regularly exposed to social stimuli from both conspecifics and heterospecifics, and can benefit from using social information. We suggest that researchers have much to learn about the sensory, perceptive, and cognitive mechanisms underlying social learning, and the extent to which these vary (if at all) between grouping and non-grouping species.

*Key words:* **copying, learning, producer-scrounger, social information, social learning.**

## INTRODUCTION

Although access to social information is one of the many advantages of living in groups, there is little compelling evidence that social information use or social learning are adaptions specifically associated with sociality (Lefebvre and Giraldeau 1996). On the one hand, Templeton et al. (1999) compared social learning between 2 corvid species, finding that the more social of the 2 was better at social than asocial or individual learning, whereas the other performed similarly in both types of learning. In contrast, in a meta-analysis of social learning in more than 100 primate species, no relationship was found between social learning performance and social group size after phylogeny was controlled for (Reader 1999; Reader and Lefebvre 2001). Other studies have documented social learning in non-grouping species, where such behavior—if closely linked to group-living—might not be expected to occur. Fiorito and Scotto (1992) reported social learning in the octopus (*Octopus vulgaris*) (but see comments by Biederman and Davey 1993). Wilkinson et al. (2010) found that red-footed tortoises (*Geochelone carbonaria*) could socially learn to navigate around an obstacle, whereas Kis et al. (2015) demonstrated that bearded dragons (*Pogona vitticeps*)

could learn to open a trapdoor after seeing a conspecific do so, with individuals being more likely to open it to the same side that their demonstrator did.

There are at least 2 reasons why social learning ability might not be closely tied to group living. The first is that all animals, whether solitary or gregarious, are likely to be exposed to social information some of the time, and potentially quite frequently. Cues may come from mates, offspring or broodmates, depending upon the social and mating system of the species concerned, or from conspecifics in neighboring territories or at patchily distributed resources, where non-group-living animals occasionally aggregate. Heterospecifics may also be an important, and arguably overlooked, source of social information, particularly if they exploit the same resources or are subject to the same threats as non-group-living observers (Sullivan 1984; Coolen et al. 2003; Ward et al. 2005; Seppänen et al. 2007; Webster et al. 2008; Avarguès-Weber et al. 2013; Goodale et al. 2014; Ward and Webster 2016). Second, social learning may reflect learning performance more generally, with social cues being but one class of cue among many that are available in the environment (Heyes 2012).

In this study we were particularly interested in quantifying social information use and social learning by non-grouping fishes exposed to social cues from heterospecifics, predicting that they would prove capable of both. To test this idea we compared social

Address correspondence to M.M. Webster. E-mail: mike.m.webster@gmail.com

information use and social learning in 4 non-grouping species of fish from 4 different families: fifteenspine sticklebacks (*Spinachia spinachia*, Gasterosteidae), bullhead sculpins (*Cottus gobio*, Cottidae), stone loach (*Barbatula barbatula*, Balitoridae) and juvenile European flounders (*Platichthys flesus*, Pleuronectidae). All of the populations of these species used in this study live in locations where the facultatively social threespine (*Gasterosteus aculeatus*, Gasterosteidae), the heterospecific demonstrator used in this study, is common. All of these species are predators of invertebrates, with bullheads, stone loaches and flounders being benthic predators and fifteenspines feeding epibenthically and within the water column. Threespines are generalist foragers, feeding from the substrate, vegetation and water column. They therefore represent an ecologically valid source of social information about the distribution of prey resources to all of these species. Moreover, threespines have previously been shown to be effective demonstrators in social learning tasks using heterospecific observers (Coolen et al. 2003). In addition to testing these 4 non-grouping species, for comparison we also tested the threespines themselves and another facultatively social species, the ninespine stickleback (*Pungitius pungitius*, Gasterosteidae). We performed a battery of binary choice tests in which individuals of each species were presented with groups of demonstrators that were either feeding or not feeding or feeding at a higher versus a lower rate. Fish were tested while these were visible (social information use) or after they had been removed from sight (social learning). We also performed trials in which differently sized groups of demonstrators were presented, either feeding or not feeding, in order to test for shoaling behavior. We predicted that the 4 non-grouping species would perform equally as well as the 2 shoaling species in the social information use and social learning treatments but that only the 2 social species would show a preference for joining larger shoals in the shoaling conditions.

## METHODS
### Overview

We used a laboratory binary choice procedure to investigate how fish use socially transmitted information to assess and learn about the relative quality of 2 simulated prey patches. A test subject, hereafter the observer, was placed within a holding unit in a central test tank. At either end of the test tank was a smaller tank containing a number of threespine stickleback demonstrators. In some trials these were presented with a prey-like stimulus that was not visible to the observer. The demonstrators attacked the stimulus, providing the observers with social information and effectively simulating a social foraging scenario (see pilot experiment in Supplementary Material). The observers were allowed to watch the demonstrators before being released and allowed to approach them. We used the amount of time that the observer spent close to each demonstrator group as a measure of its attraction, taking a bias towards one demonstrator group over the other as being indicative of social information use. This approach is based upon that of Coolen et al. (2003), and has been used extensively by our group in similar experiments investigating social learning (Laland et al. 2011).

### Study animals

We used 6 fish species, threespine, ninespine, and fifteenspine sticklebacks, bullhead sculpins, stone loaches and juvenile European flounders. Bullheads, stone loaches, and flounders are non-shoaling, benthic-living species that live in and among the substrate.

Flounders are diadromous and enter freshwater rivers as juveniles, whereas the other 2 species live permanently in freshwater. Fifteenspines are found in coastal marine and brackish environments. In both bullheads and fifteenspine sticklebacks the males provide parental care. In contrast, threespines and ninespines are facultatively social, occurring singly or in groups of up to several hundred. Both are found in freshwater and brackish environments and threespines are also found in coastal marine areas. In both of these species the males also provide parental care. Threespines co-occur with all of the species used in this study, and were used as demonstrators to provide social cues in all of the experiments described below.

These experiments were conducted in 2 bouts between 2008 and 2012. Bullheads ($n = 17$, 40–55 mm in length), stone loaches ($n = 18$, 40–65 mm) and threespine and ninespine sticklebacks ($n = $ ca. 100 and 18 respectively, 35–45 mm) were collected from Melton Brook, Leicestershire, UK in August 2008 and transported to our laboratory at the University of St Andrews. We also collected ca. 200 threespine sticklebacks at this time from the Kinnessburn stream in St Andrews, UK. The threespines and ninespines were held in single species (and population in the case of threespines) groups of 18–25 in 90 L aquaria, whereas the bullheads and stone loaches were held in single species groups of 5–6 in 90 L aquaria. In September 2012 we collected 25 juvenile flounders (35–50 mm) from the freshwater lower reaches of the Kinnessburn stream and 22 fifteenspine sticklebacks (45–85 mm) from rockpools on the shore of St Andrews bay, both in St Andrews, UK. These were held in single species groups of 8–9 and 7–8, respectively, also in 90 L aquaria. All aquaria were visually and chemically isolated from one another. Each aquarium contained course sand, plastic plants and an internal filter. The temperature of the lab was held at 8 °C and the light:dark regime at 12:12. The fifteenspine sticklebacks were held in seawater, whereas the other species were held in freshwater. The fish were fed a diet of frozen bloodworms and mysids once per day. They were held in the lab for 6–8 weeks before being tested. The bullheads, stone loaches, threespines and ninespines were tested in September-December 2008, and the flounders and fifteenspines were tested between November 2012 and February 2013, using the procedures described below. After testing the threespines and ninespines were retained in the laboratory for use in further experiments, whereas the other fish were released at their point of capture.

### Design and procedure

The experimental apparatus consisted of a single large glass tank (45 × 30 × 30 cm, water depth 12 cm) and 2 smaller Perspex tanks (27 × 15 × 12 cm, water depth 12 cm). The smaller aquaria contained the demonstrator groups and were set 0.5 cm from either end of the larger one, which held the observer. Each of the 3 tanks contained a 1 cm deep layer of coarse sand. The observer arena contained seawater when the fifteenspines were tested and was filled with freshwater for all of the other species. The threespine demonstrators were always held in freshwater. Within the observer arena, yellow plastic bars, 1 cm wide and 1 cm deep, secured to the base of the tank and rising to the surface of the sand divided the tank into 3 zones. These were set 8 cm from either end of the observer arena. The 2 areas between the ends of the tank and the bar were designated the prey patch goal zones.

Within each of the demonstrator tanks we placed a feeder unit. The feeder unit consisted of a 4 × 4 cm base, 30-cm-tall tower. The feeder units were placed in the corner of the demonstrator

chamber furthest from the observer arena. The front wall of the feeder unit, facing the demonstrators, was transparent so that the demonstrators could see the prey stimulus. The inside rear wall was white, as was the base, to maximize the visibility of the prey stimulus. The side walls were opaque blue, so that the observer in the centre of the tank could not see the prey stimulus. The prey stimulus consisted of a point of red of light delivered by a laser pointer mounted 45 cm above the feeder unit. This was switched on periodically as described below, simulating a prey delivery. Sticklebacks readily attack red objects (Smith et al. 2004) and we have previously shown that observers are attracted to others that are directing attacks towards prey and prey-like stimuli, even if they are not actually able to capture these (Webster and Laland 2012). The demonstrators struck at and attacked the point of light, performing characteristic feeding-like behavior (see Supplementary Material). The observers were able to see this behavior but could not see the red laser point, and could therefore only base their patch choices upon visual cues received during the demonstration phase. We used the red laser pointer rather than actual prey because it allowed us to control the duration of the prey stimulus period precisely and because it prevented the demonstrators from becoming satiated.

Within the observer arena, the observer was held within a holding unit for the duration of the settling period and demonstration phase. The holding unit consisted of a tower of clear, colorless perforated Perspex measuring 10 × 10 cm × 15 cm tall. It was attached via a monofilament line to a 15-cm-long arm clamped to the top of the observer arena, allowing the holding unit to be raised by the experimenter. The holding unit was placed 5 cm from the side wall of the observer arena and half way between the end walls that abutted the demonstrator chambers. We used 2 opaque black plastic screens measuring 30 × 30 cm square by 2 mm thick to separate the observer arena from the demonstrator chambers during the choice phase of the trial. These were designed so that they could be slid into place between the tanks without causing any significant vibration that might alarm the observer. The exterior walls of both the observer arena and demonstrator chambers were screened in black plastic. Observations were made via a webcam fixed 90 cm above the tank and connected to a laptop computer.

## Subjects

In total we tested 6 species of fish for social information use, using threespine sticklebacks as demonstrators in all of these experiments. Neither demonstrators nor observers were sexed. Within trials the demonstrators were matched to each other by body length to within 3 mm. Since the demonstrators were drawn from a limited pool of available fish some demonstrators were used in multiple trials. No individual was used more than once in any 3-day period. In between testing days, each observer was held within a 30 × 30 × 30 cm aquarium containing a 2-cm-deep sand substrate, an artificial plant and an air stone. These were visually and chemically isolated from each other.

## Procedure

The demonstrators and observers were deprived of food for 24 h before testing in order to ensure that they were motivated to forage. The demonstrators were added to the demonstrator chambers and allowed to settle for 30 min before the observer was added to the holding unit in the central test and allowed to settle for a further 10 min. During this period opaque black screens were placed between the observer arena and the 2 demonstrator chambers, and the observers could not see the demonstrators.

The demonstration phase lasted for 6 min and ran as follows. The prey stimulus consisted of a 10-s presentation of the laser pointer. This was performed at the beginning of the first, third, and fifth minute of the demonstration period of both the demonstration and the choice phase for the "rich" patch demonstrator groups (treatments Feeding A–D), both demonstrator groups in Group size A and in the rich patch of the Prey stimulus only treatment. The prey stimulus was also presented during the first 10 s of the fifth minute of each phase in the "poor" patch for treatments Feeding C and D. This ensured that while prey stimuli were presented at a 3:1 ratio in these treatments, the focal fish was unable to select a patch simply on the basis of it being the last place it saw others feeding. The location of the rich patch, either to the left or to the right of the observer arena, was randomly selected for each trial.

After the 6-min demonstration phase, the opaque black screens were slid into place between the observer arena and the 2 demonstrator chambers. This took approximately 10 s and did not appear to stress the observer or demonstrators. These were retained for the remainder of the trial in treatments Feeding B and D. In all other treatments they were held in place for 10 s and then removed again. The observer was allowed to settle for a further 1 min before being released from the holding unit. The observer was released by raising the holding unit 5 cm from the base of the arena, using the pulley mechanism. The base of the holding unit was left suspended beneath the water surface, so as not to disturb the surface of the water and startle the observer. This commenced the choice phase of the trial, which lasted for 5 min. Using the videos of the choice phase of the trial we recorded the location of the observer every 6 s, whether within either goal zone or the central neutral zone, yielding a total of 50 data points.

## Treatments

Each fish was tested 7 times, once in each of the treatments described below. We adopted a repeated measures design, with the order of testing in each treatment randomized for each subject. Fish were tested every 3 days and were fed daily, but never less than 24 h before being tested.

### Feeding A, 5|5 demonstrators visible, prey 3:0
Two groups of 5 demonstrators were used. One group was presented with the prey stimulus 3 times during the demonstration phase whereas the other group exhibited no feeding behavior. The demonstrators were still visible whereas the observers were allowed to move between patches during the choice phase, and the feeding group of demonstrators was presented with the prey stimulus a further 3 times during this period.

### Feeding B, 5|5 demonstrators hidden, prey 3:0
This treatment was performed as described above, except that the opaque barriers were placed in between the observer and demonstrator tanks after the demonstration phase and before the choice phase, preventing the observer from seeing the demonstrators during this period.

### Feeding C, 5|5 demonstrators visible, prey 3:1
Two groups of 5 demonstrators were used. One group was presented with the prey stimulus 3 times during the demonstration phase whereas the other group was presented with it once. The demonstrators were still visible whereas the observers were allowed to move between patches during the choice phase, and the 2 groups

of demonstrators were presented with the prey stimulus again at the same ratio during this period.

### Feeding D, 5|5 demonstrators hidden, prey 3:1

This treatment was performed as described above for Feeding C, except that the opaque barriers were placed in between the observer and demonstrator tanks after the demonstration phase and before the choice phase, preventing the observer from seeing the demonstrators during this period.

### Group size A, 8|2 demonstrators visible, prey 3:3

A group of 8 and a group of 2 demonstrators were used. Both groups were presented with the prey stimulus 3 times during the demonstration phase. The demonstrators were still visible whereas the observers were allowed to move between patches during the choice phase, and both groups of demonstrators were presented with the prey stimulus a further 3 times during this period. This condition allowed us to determine whether any of the species were attracted to larger (or smaller) groups of demonstrators, which many indicate a general shoaling preference.

### Group size B, 8|2 demonstrators visible, prey 0:0

A group of 8 and a group of 2 demonstrators were used. Neither groups were presented with the prey stimulus during the demonstration phase. The demonstrators were still visible whereas the observers were allowed to move between patches during the choice phase. This condition allowed us to check for a general shoaling preference in any of the observer species, and complements the Group size A condition by removing any confounding effects of demonstrator feeding behavior.

### No social stimulus control, 0|0 demonstrator chambers visible, prey 3:0

No demonstrators were present in either demonstrator chamber. The prey stimulus was delivered 3 times to one feeder only during the demonstration phase and 3 times during the choice phase of the trial. These treatment was performed to determine whether the

observers could perceive the prey stimulus by any means (such as via reflected light from within the feeder unit).

## Statistical analyses

For each trial we subtracted the number of sampling instances (out of a total of 50 possible) spent in the poor goal zone from that spent in the rich goal zone. These data were used as the dependant variable in a repeated measures GLM with Poisson distribution. Treatment was used as the within subject variable, with species included as a between subjects factor. We used simple contrasts to compare each of the treatments and the treatment × species interaction to the *no social stimulus control* treatment. In order to test for differences between species within the different treatments we also performed one-way Anovas with Tukey post hoc tests for each treatment.

## Ethical statement

These procedures were reviewed and approved by the Ethics Committee at the University of St Andrews. All of the procedures described above meet the ABS/ASAB guidelines for ethical treatment of animals.

## RESULTS

A repeated measures GLM revealed effects of treatment (Wilks $\lambda = 0.41$, $F_{(6, 113)} = 25.24$, $P < 0.001$), species ($F_{(5, 114)} = 7.48$, $P < 0.001$) and a treatment × species interaction (Wilks' $\lambda = 0.59$, $F_{(6, 113)} = 2.01$, $P = 0.001$, Figure 1). Contrasts compared the difference in the amount of time that fish spent in the rich goal zone relative to the poor one in each treatment against that of the *no social stimulus control* treatment in which no demonstrators were present (Table 1). These revealed that fish tended to spend more time in the rich goal zone than they did in the control in all but one treatment, Feeding D, in which the observer fish were presented with 2 demonstrator groups attacking prey stimuli at high and low rates and then were allowed to select prey patches after
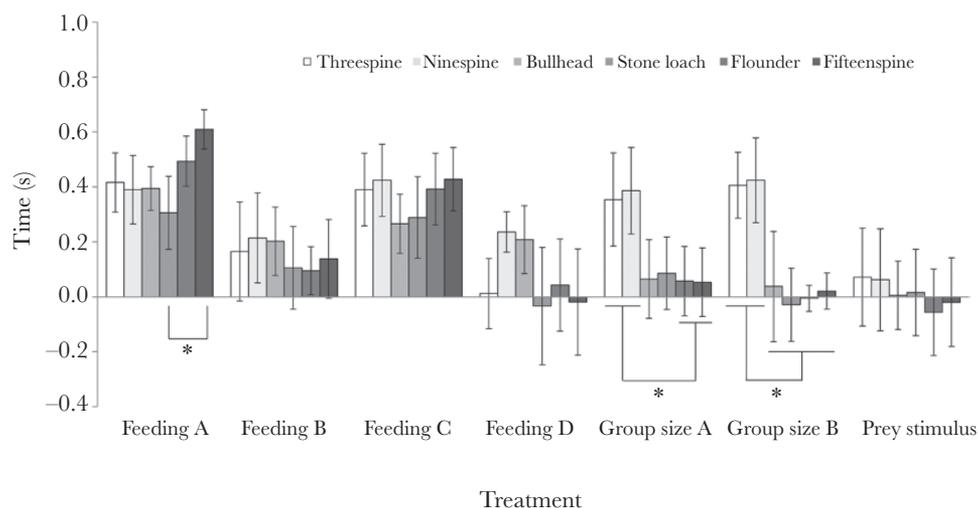


**Figure 1**
Proportional time allocation (time in "rich" goal zone – time in "poor" goal zone, mean ± 95% CI). Here rich goal zone refers to the goal zone associated with the group feeding at the higher rate (Feeding A–D), the larger group (Group size A and B) or the prey stimulus object (Prey stimulus). A positive score indicates that the fish spent more time close to the group of demonstrators feeding at the greater rate (Feeding A–D), or the largest group (Group size A and B). We found effects of treatment, species and a species × treatment interaction (see Results and Table 1). Asterisks indicate differences between species within treatments.

**Table 1**

**Simple contrasts performed as part of a repeated measures GLM used to compare prey patch goal zone preferences for each of 6 experimental social information treatments against a seventh treatment in which no social stimulus was presented (see main text for further details)**

|  | Treatment | df | $F$ | $P$ |
|---|---|---|---|---|
| Treatment | Feeding A | 1 | 86.031 | <0.001 |
|  | Feeding B | 1 | 9.019 | 0.003 |
|  | Feeding C | 1 | 51.696 | <0.001 |
|  | Feeding D | 1 | 0.751 | 0.388 |
|  | Group size A | 1 | 9.908 | 0.002 |
|  | Group Size B | 1 | 7.225 | 0.008 |
| Treatment × species | Feeding A | 5 | 1.991 | 0.085 |
|  | Feeding B | 5 | 0.237 | 0.945 |
|  | Feeding C | 5 | 0.621 | 0.684 |
|  | Feeding D | 5 | 0.697 | 0.627 |
|  | Group size A | 5 | 0.763 | 0.578 |
|  | Group Size B | 5 | 2.025 | 0.080 |

these had been removed from sight. There was also some variation in patch selection between species with treatments, as indicated by the significant effects of species and the treatment × species interaction term, above, although here contrasts revealed no differences between any of the treatments and the *no social stimulus control* treatment (Table 1).

All species showed a preference for the demonstrated richer patch in the treatments where they chose in real time whereas the demonstrators were still visible (Feeding A and C), indicated by positive scores for time in rich patch-time in poor patch, with confidence intervals that did not span zero, Figure 1). When choosing after the demonstrators had been removed from view, in the treatment where one group of demonstrators was attacking the prey stimulus and one was not (Feeding B), all species again showed a preference for the rich patch, with confidence intervals not spanning zero. In the treatment where both demonstrators were attacking the prey stimulus at different rates (Feeding D), only 2 species, ninespines and bullheads, showed a preference for the richer patch. In the 2 treatments where the demonstrator group sizes were varied (Group Size A and B), only the threespines and ninespines (the 2 social species) showed any preference, spending more time close to the larger groups. Finally, in the *no social stimulus control* treatment where prey stimuli were presented in the absence of any demonstrators, no species showed any patch preference.

One-way Anovas revealed no differences between species in the treatments Feeding B, C, and D ($F_{(5, 119)} = 0.12$, $P = 0.98$; $F_{(5, 119)} = 0.99$, $P = 0.43$; $F_{(5, 119)} = 1.51$, $P = 0.18$), and none in the No social stimulus control ($F_{(5, 119)} = 0.65$, $P = 0.66$). We did see differences between species in the other treatments. In Feeding A ($F_{(5, 119)} = 3.91$, $P = 0.003$) fifteenspines spent more time in the rich patch than did stone loaches (Tukey post hoc: $P = 0.002$). In group size A ($F_{(5, 119)} = 4.56$, $P = 0.001$), both threespines ($P = 0.039$ and $0.045$) and ninespines ($P = 0.021$ and $0.025$) spent more time in the rich patch than did flounders or fifteeenspines. Finally, in Group size B ($F_{(5, 119)} = 11.26$, $P < 0.001$), threespines spent more time closer to the larger group of demonstrators than did bullheads, stone loaches, flounders, or fifteenspines ($P = 0.002$ vs. bullheads and <0.001 for the other species). The same pattern was seen for ninespines compared to these species ($P = 0.001$ vs. bullheads and <0.001 for the other species).

## DISCUSSION

Our experiment reveals clear evidence of social information use and social learning non-grouping fishes. When the demonstrators were visible to the observers, all species spent more time in close proximity to the group that was feeding (Feeding A) or which was feeding at the greater rate (Feeding C). When the demonstrators were not visible during the period when the observers were allowed to move throughout the tank, all species spent more time close to the location of the demonstrator group that had been feeding than they did near the group that had not fed, indicating that they had learned the location of this group (Feeding B). Moreover, one species, bullheads, were seen to be capable of recalling which of 2 feeding groups of demonstrators had fed at the greater rate when both were presented with prey-stimuli (Feeding D). This form of public information use has previously been documented in the facultatively social ninespine stickleback, where it has been suggested to be an adaptive specialization for gathering information under predation risk (Coolen et al. 2003).

When considered alongside those of other researchers who have observed social learning in non-group-forming animals such as octopi (Fiorito and Scotto 1992), tortoises (Wilkinson et al. 2010) and lizards (Kis et al. 2015), our findings imply that living a solitary life is no barrier to being an adept user of socially transmitted information. Going further, we suggest that such a link between sociality and social learning performance should not necessarily be expected, since non-group-living does not equate to being nonsocial. Even animals that actively avoid others are likely to be exposed to social cues from territorial neighbors and competitors, and they may be compelled to aggregate with others if they are exploiting patchily distributed resources, particularly if these are scarce. Even when not directly encountering others, non-grouping species may encounter the products of conspecifics, in the form of scent marks, excreted waste, or food items that they have discarded, for example, and these may provide sources of information and even facilitate social learning (e.g., Terkel 1996).

Our study focussed upon cues provided by heterospecifics, and for many animals the other species that they encounter are a potentially major source of social information (Avarguès-Weber et al. 2013). It is plausible that information generated inadvertently by heterospecifics might also be widely used by other species even where these do not actively associate, as seen in the laboratory in our study, and further work here, particularly in the field, would be useful.

Work addressing the question of whether group living is correlated with social learning performance has largely been piecemeal and there is scope for systematic comparative research to be done here. Reader's (1999) and Reader and Lefebvre's (2001) meta-analyses of social learning performance in relation to group size in primates, which found no link between the 2 after controlling for phylogenetic effects, is a nice example of the form that such work might take. It would also be informative to consider multiple aspects of sociality, including the nature and distribution of interactions between group members, rather than simply group size, alongside other factors such as primary functions of grouping in those species that do so, such as to mitigate predation risk or to socially forage, and the context in which social information is used. Finally, Heyes (2012) has argued that proficiency in social learning may be affected by selection acting upon input channels such those governing perception of and attention and motivation towards social cues, even if the underlying cognitive mechanisms

underpinning social learning are unspecialized. A more interesting question than whether non-grouping animals can socially learn then might be one that takes a phylogenetic approach to ask whether more effective social learning is found in lineages with longer evolutionary histories of group living, and whether adaptive specialization, either in input channels or cognitive processing, is seen in these.

## SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

## FUNDING

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Webster and Laland (2017).

**Handling editor:** John Skelhorn

## REFERENCES

Avarguès-Weber A, Dawson EH, Chittka L. 2013. Mechanisms of social learning across species boundaries. J Zool. 290:1–11.

Biederman GB, Davey VA. 1993. Social learning in invertebrates. Science. 259:1627–1628.

Coolen I, van Bergen Y, Day RL, Laland KN. 2003. Species difference in adaptive use of public information in sticklebacks. Proc Biol Sci. 270:2413–2419.

Fiorito G, Scotto P. 1992. Observational Learning in Octopus vulgaris. Science. 256:545–547.

Goodale E, Ratnayake CP, Kotagama SW. 2014. Vocal mimicry of alarm-associated sounds by a drongo elicits flee and mobbing responses from other species that participate in mixed-species bird flocks. Ethology. 120:266–274.

Heyes C. 2012. What's social about social learning? J Comp Psychol. 126:193–202.

Kis A, Huber L, Wilkinson A. 2015. Social learning by imitation in a reptile (*Pogona vitticeps*). Anim Cogn. 18:325–331.

Laland KN, Atton N, Webster MM. 2011. From fish to fashion: experimental and theoretical insights into the evolution of culture. Philos Trans R Soc Lond B Biol Sci. 366:958–968.

Lefebvre L, Giraldeau LA. 1996. Is social learning an adaptive specialization? In: Heyes CM, Galef BG editors. Social learning in animals: the roots of culture. London: Elsevier. pp. 107–128.

Reader SM. 1999. Social learning and innovation: individual differences, diffusion dynamics and evolutionary issues (Doctoral dissertation). Oxford: University of Cambridge.

Reader SM, Lefebvre L. 2001. Social learning and sociality. Behav Brain Sci. 24:353–355.

Seppänen JT, Forsman JT, Mönkkönen M, Thomson RL. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology. 88:1622–1633.

Smith C, Barber I, Wootton RJ, Chittka L. 2004. A receiver bias in the origin of three-spined stickleback mate choice. Proc Biol Sci. 271:949–955.

Sullivan KA. 1984. The advantages of social foraging in downy woodpeckers. Anim Behav. 32:16–22.

Templeton JJ, Kamil AC, Balda RP. 1999. Sociality and social learning in two species of corvids: the pinyon jay (*Gymnorhinus cyanocephalus*) and the Clark's nutcracker (*Nucifraga columbiana*). J Comp Psychol. 113:450–455.

Terkel J. 1996. Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). In: Heyes CM, Galef BG editors. Social learning in animals: the roots of culture. London: Elsevier. pp. 17–47.

Ward AJ, Holbrook RI, Krause J, Hart PJ. 2005. Social recognition in sticklebacks: the role of direct experience and habitat cues. Behav Ecol Sociobiol. 57:575–583.

Ward A, Webster M. 2016. Sociality: the behaviour of group living animals. Zurich: Springer International Publishing.

Webster MM, Laland KN. 2012. Social information, conformity and the opportunity costs paid by foraging fish. Behav Ecol Sociobiol. 66:797–809.

Webster MM, Laland KN. 2017. Data from: Social information use and social learning in non-grouping fishes. Behavioral Ecology. http://dx.doi.org/10.5061/dryad.kg008.

Webster MM, Ward AJ, Hart PJ. 2008. Shoal and prey patch choice by co-occurring fishes and prawns: inter-taxa use of socially transmitted cues. Proc Biol Sci. 275:203–208.

Wilkinson A, Kuenstner K, Mueller J, Huber L. 2010. Social learning in a non-social reptile (*Geochelone carbonaria*). Biol Lett. 6:614–616.