

# Space-use and sociability are not related to public-information use in ninespine sticklebacks

M. M. Webster<sup>1</sup> · K. N. Laland<sup>1</sup>

Received: 30 July 2014 / Revised: 9 March 2015 / Accepted: 9 March 2015  
© Springer-Verlag Berlin Heidelberg 2015

**Abstract** There has been much recent interest in both public information use, and the evolutionary origins and ecological consequences of animal personalities but surprisingly little integration of these two fields. Personality traits may impact upon the extent to which individuals respond to public information in a number of different ways. As a first step towards addressing some of these questions, in this study, we asked whether personality traits predicted public information use in ninespine sticklebacks (*Pungitius pungitius*). Over a 33-day period, subjects were scored twice for a number of behavioural traits, including measures of activity, exploration and shoaling tendency, and were exposed multiple times to a public information use foraging task, in which they were required to select the richer of two prey patches based upon the foraging success of two demonstrator groups. The repeatable ( $r=0.38-0.58$ ) behavioural traits were reduced to two principle components describing space use and sociability. Neither of these was found to be related to either of two measures of public information use. While the personality traits that we considered did not co-vary with public information use in this species, they may well indirectly affect opportunity for exposure to public information, and this is an obvious avenue for further research.

**Keywords** Behavioural syndrome · Bold-shy · Innovation · Producer-scrounger · Social learning strategies · Temperament

Communicated by J. Lindström

✉ M. M. Webster  
mike.m.webster@gmail.com

<sup>1</sup> School of Biology, University of St Andrews, Harold Mitchell Building, Fife KY16 9TS, UK

## Introduction

Animals can acquire public information about their surroundings through observing or interacting with other individuals (Heyes 1994; Hoppitt and Laland 2008). The use of public information, and social learning, has been described in many animal species representing a diverse range of taxa (Avital and Jablonka 2000; Leadbeater and Chittka 2007; Hoppitt and Laland 2013). It is thought that such behaviour may benefit animals by allowing them to minimise the costs associated with sampling the environment, enabling them to acquire information about the distribution and nature of resources, travelling routes, mates, competitors or threats efficiently (Heyes and Galef 1996; Galef and Giraldeau 2001; Valone and Templeton 2002; Danchin et al. 2004; Dall et al. 2005; Valone 2007).

Given the apparent adaptive advantages of social learning, there is currently significant research interest in the costs and benefits of public information use and the conditions that determine when individuals should copy the behaviour of others (Laland 2004; Laland et al. 2011; Rendell et al. 2011; Rieucou and Giraldeau 2011; Hoppitt and Laland 2013). While the majority of these studies have considered only the effects of external conditions, such as those pertaining to the physical and social environment perceived by the individual, a number of researchers have begun to investigate the role of individual behavioural variation, including personality traits, in determining individual's propensity to use public information (Nomakuchi et al. 2009; David et al. 2011; Webster and Ward 2011; Aplin et al. 2013; Jolles et al. 2013). Personality refers to stability or consistency in the expression of one or more behavioural traits over a given time period. Much as for social learning, personality traits have been described in a diverse range of different species, and their evolutionary origins and their fitness consequences are currently receiving a great deal

of interest from researchers (Wilson et al. 1994; Wilson 1998; Gosling and John 1999; Sih et al. 2004a, b; Réale et al. 2007; Sih and Bell 2008; Bell et al. 2009; Conrad et al. 2011).

Broadly speaking, personality might affect public information use in two ways. First, personality traits might affect the opportunity to acquire public information. Most obviously, more sociable individuals, who spend more time with their group mates, or which interact widely with many individuals, may be more likely to be exposed to public information than individuals which do not frequently spend time near or interacting with others (Sih and Bell 2008). Other personality traits, such as activity levels or tendency to explore, might also affect exposure to public information, by influencing the likelihood that individuals will encounter others as they move through the environment. Second, personality traits might predict the use of public information once the animal is exposed to it. Though the mechanisms linking personality traits and tendency to use public information are not clear, such effects have been documented in some species. In great tits (*Parus major*) for example, individuals that were independently categorised as ‘faster explorers’ were found to be more likely to visit feeders where they saw conspecifics feeding compared to ‘slower explorers’, suggesting a link between exploration and scrounging behaviour (Marchetti and Drent 2000). In barnacle geese (*Branta leucopsis*), neophobia was seen to be related to scrounging behaviour, with more neophobic individuals being more likely than less neophobic conspecifics to scrounge the food discoveries of others (Kurvers et al. 2010a). Individual neophobia measures were also found to be positively correlated with social information use under binary choice conditions in this species (Kurvers et al. 2010b).

In the current study, we focused upon the second of these two ideas that personality traits might be related to the use of public information. Focussing upon ninespine sticklebacks (*Pungitius pungitius*), we specifically sought to determine whether public information use about foraging patches, assayed multiple times for each individual, was related to individual behavioural variation in other contexts under conditions in which all individuals had equal exposure to public information cues. We focussed upon four behavioural measures: activity, thigmotaxis (a measure of cover use), a measure of exploration rate and time spent grouping with conspecifics. These behavioural measures were selected because, together, they allow us to quantify how the animals move through space and, by extension, how likely they are to encounter resources and other conspecifics. We used the ninespine stickleback, an emerging model organism in behavioural ecology and evolution (Merilä 2013), because they are facultatively social and are known to use public information when foraging (Laland et al. 2011; Webster and Laland 2011, 2012, 2013). Furthermore, this species has been used as a study system for exploring inter- and intra-population variation in personality traits (Herczeg et al. 2009; Webster et al. 2009).

We made no explicit predictions as to how these behaviours might be related to public information use, instead focussing on two broad aims. Our first aim was to identify any correlations between public information use and personality traits that might form the basis for future research into potential social foraging strategies used by animals. Our second aim was to identify relationships between personality traits and the weighting given to different sources of information—here more recently available public information versus earlier-acquired private information—when the two conflict with one another. To achieve this, we tested one set of subjects that were naïve to the distribution of resources in the public-information test, and another set of experienced subjects, that had pre-existing information about the distribution of resources that conflicted with the public information that they received in the public-information test. These aims fall within our broader interest in social foraging and the conditions which influence how animals use public information.

## Methods

### Subjects

Ninespine sticklebacks were collected from Melton Brook, Leicestershire, UK (52° 39' 43" N, 1° 06' 49" W) in August 2011 (pilot study and the first four of six batches tested in the experiment proper) and again in August 2012 (the final two batches). In the laboratory, they were initially held in groups of 30 in 90-L aquaria. Each aquarium contained a layer of coarse sand, an external filter and artificial vegetation for cover. The light/dark regime was held at 12:12 h, and the temperature was maintained at 8 °C. The fish were fed daily with frozen bloodworms.

Sixty fish were used as test subjects, and around 80 more were used as demonstrators or stimulus fish in the experiments described below. A further 40 fish were used in a pilot study, also described below. Testing took place between September 2011 and November 2012. Neither test subjects nor stimulus fish were sexed, and no fish were tested while in reproductive state. Reproductive state can be inferred from the presence of nuptial colouration in males and the presence of an egg mass in females. Previous research has shown that gravid females and reproductive males differ from one another and from non-reproductives in their use of public information, while non-reproductive males and females do not differ in this regard (Webster and Laland 2011). In the closely related threespine stickleback (*Gasterosteus aculeatus*), no sex differences in boldness, sociality or social-exploratory behaviour were detected between non-reproductive males and females (Ward et al. 2004).

## General methods

For each of 60 ninespine sticklebacks, we quantified PI use on three occasions, and shoaling and (within the same assay) activity, thigmotaxis and exploration on two occasions each. The PI use, sociability and activity, thigmotaxis and exploration assays are described in detail in the subsections below. Of the 60 test subjects, 30 were given prior experience ('pre-training') of finding food in only one of two artificial feeder units. In the subsequent PI-use assays, they were given conflicting public information, in that the feeder to which they had been trained to expect food was manipulated so as to yield less food than it yielded in the PI-use assay, whilst the other (hitherto unproductive) feeder was demonstrated to be the richer of the two. The other 30 fish were fed from both feeders, with one feeder randomly selected to yield food on each day ('sham-training'). Following pre-training/sham training, the two treatment groups are referred to as experienced and naïve. More details of these training procedures are given below.

Fish were tested according to the schedule in Table 1. Test subjects were selected at random from the housing tanks. They were trained and tested in six batches of ten fish each, with five fish receiving pre-training and five sham training within each batch. Test subjects were randomly allocated to the pre- and sham-training conditions. Test subjects were first weighed with digital scales to the nearest 0.01 g (blotted mass) and measured using callipers to the nearest 0.1 mm. We used fish measuring 34.7 to 47.5 mm in standard length. Condition factor ( $1000 \times (\text{mass}/\text{length}^3)$ ) was included as covariates in the statistical analyses described below. Weighing and measuring took place 24 h after feeding. Each fish was then housed alone in a 45-L aquarium. Each aquarium contained a gravel substrate and plastic plants and was attached to its own external filter. Two feeder units were also present, in the left and right corners along the longer axis of each aquarium. These were placed opposite the filter inlet, which was located in the centre of the facing wall. The feeder units were used for prey

delivery, as described below, in the pre-training/sham-training subsection. Each aquarium was visually and chemically isolated from the others. Ninespine sticklebacks are facultatively social, and being housed alone is not likely to be a major stressor. While housed under these conditions, they were fed five bloodworms per day each. They were never fed less than 24 h prior to being tested. On test days, they were fed around 1 h after testing. On the final day of the testing period, they were measured and weighed again (prior to being fed). This allowed us to quantify growth and any change in body condition over the duration of the study period. There were no differences in body mass or condition factor between fish assigned to the naïve and experienced treatment groups at the start of the experiment (one-way ANOVAs, log<sub>10</sub> transformed mass,  $F_{(1, 59)}=0.60$ ,  $P=0.44$ ; condition factor,  $F_{(1, 59)}=1.79$ ,  $P=0.19$ ). Condition factor did not change significantly over the course of the study (paired samples *t* test,  $t=-1.36$ ,  $df=59$ ,  $P=0.83$ ), and the degree of change did not differ between the two treatment groups (one-way ANOVA,  $F_{(1, 59)}=0.01$ ,  $P=0.96$ ).

The test schedule in Table 1 contains some randomisation of testing orders but is not fully randomised. This is because we wished to standardise the time between pre- or sham-training and the three PI-use tests, so that all the subjects were tested at the same time following training exposure. Similarly, we wished to maintain a 2-week timespan between the first and second sociability and activity, thigmotaxis and exploration tests. For each individual then, the timing of the first sociability assay was randomly allocated to days 15 or 18 of the testing period, with the first activity, thigmotaxis and exploration assay occurring on the other day. The second of each of these assays took place 14 days later. All assays took place between 10.00 and 16.00 on the day of testing, with randomised individual test ordering.

### Public-information use assay: pre-training and sham-training

As described above, half of the test subjects were given private information about the location of the prey patch, via a period of pre-training. In the test proper, they were then given conflicting public information. The other half of the test subjects were given no consistent private information.

Test subjects housed in their individual holding aquaria were fed once per day via one of the two feeder units located in the corners of the aquarium. The feeder units consisted of a 4×4-cm base, 30-cm tall tower, constructed from opaque white plastic. The base of the feeder stopped 1 cm short of the substrate, allowing the fish to eat the prey once it had reached the bottom of the feeder. The fish received a daily food ration of five bloodworms each, as described above. Fish in the pre-training treatment group always received their food via the same feeder unit, left or right. The filter inlet, located

**Table 1** Test schedule

Day	Treatment
1	First weighing and measuring, assigned to individual housing aquarium
1–14	Pre-training/sham training
15	Sociability assay I/space use assay I
18	Sociability assay I/space use assay I
22	PI-use assay I
24	PI-use assay II
26	PI-use assay III
29	Sociability assay II/space use assay II
32	Sociability assay II/space use assay II
33	Final weighing and measuring

centrally on the facing wall provided a reference landmark. The feeder which yielded the food was randomly predetermined for each fish. For those fish in the sham-training treatment group, the feeder unit which yielded the prey was selected at random each day. We used feeder location (left or right) rather than feeder characteristics (such as colour) as the focus of training and public information, because previous research has revealed that it is the location of a feature, and not its physical characteristics that forms the basis of learning via public information and local enhancement in this species (Webster and Laland 2013). The pre- and sham-training feeding regimes were continued up until the end of the study, even after the public information trials had been completed.

In order to determine the efficacy of the pre-training protocol, we first ran a pilot study. Twenty randomly selected fish were subjected to pre-training for 14 days, using the procedure described above, and a further 20 received sham-training. In the pre-training treatment group, ten fish were trained to expect food from the left feeder only and ten from the right feeder only. Following this, the fish were tested for feeder preference under binary choice conditions. They were tested in an aquarium identical to the one that they had previously been housed in, including two identical feeder units in the corners and an attached filter unit to prove a landmark reference. The filter was switched off for the duration of the trial. No prey was present in the testing arena at any point during the trial. They were placed within a holding unit, a tower of clear, colourless perforated Perspex measuring  $10 \times 10 \text{ cm} \times 25 \text{ cm}$  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 aquarium and half way between the end walls where the feeder units were located. The fish was held for 10 min in order to acclimatise, before the holding unit was raised 10 cm, releasing the fish and beginning the trial. The trial lasted for 3 min. We point sampled the location of the fish every 6 s, noting whether or not it was within 8 cm of either end of the test tank. This pilot experiment, reported in the results section, revealed that fish pre-trained to the left or the right feeder showed a preference for the feeder on that side. In contrast, the fish in the sham-training treatment showed no such preference. The fish used in this pilot experiment played no further part in the remainder of the study.

## Behavioural assays

### *Public-information use assay*

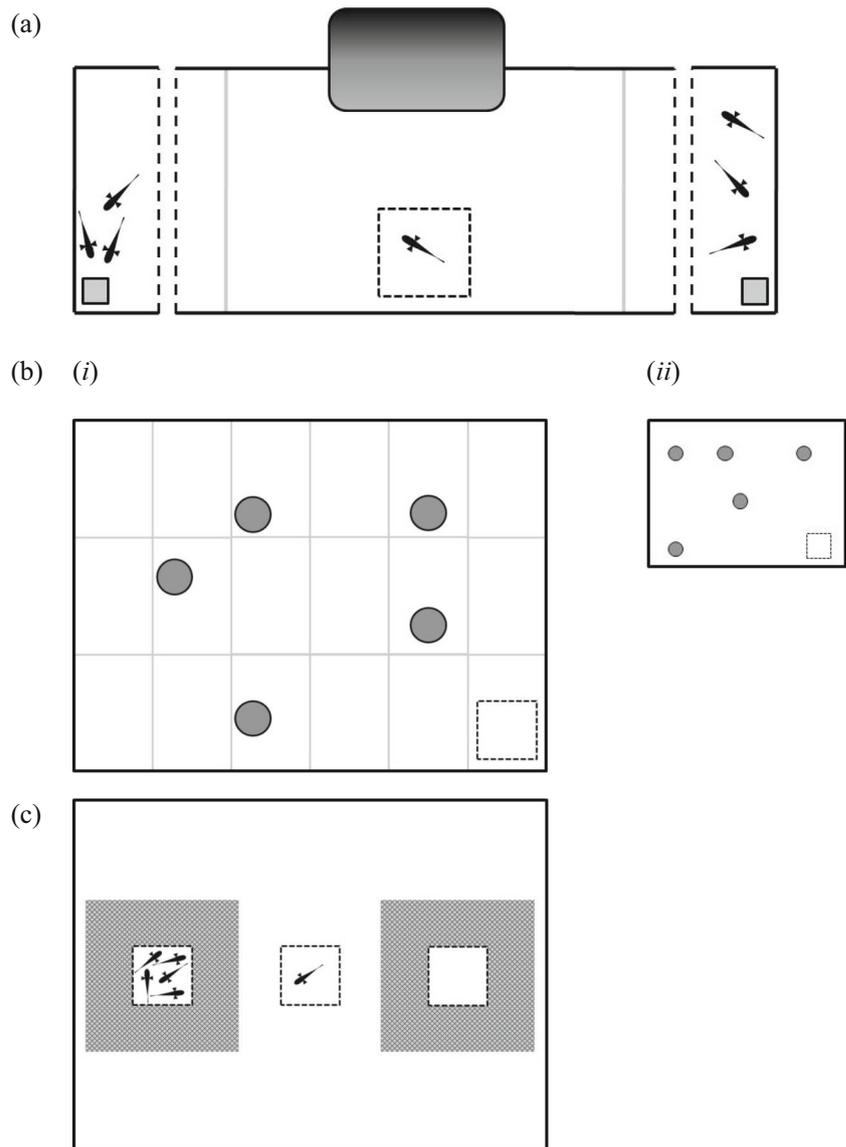
**Test arena** PI use was tested using a binary choice test tank comprising a main observer arena, set between two demonstrator chambers (Fig. 1a). Each demonstrator chamber contained three conspecific demonstrators and a feeder unit.

The feeder units released food at different rates and were designed so that the observer could see the demonstrators' feeding behaviour but could not see or otherwise detect the food itself. The observer was therefore able to estimate patch quality only indirectly, by using public information generated by the feeding demonstrators. Following a demonstration period, opaque barriers were placed between the observer arena and the demonstrator chambers, and the observer was released and allowed to move about the observer arena. A goal zone was present at each end of the arena, adjacent to either demonstrator chamber. The amount of time the observer spent in each goal zone was taken as a measure of its preference for that goal zone. A preference for the zone adjacent to the rich patch is taken as a measure of public-information-mediated patch choice.

We used a glass tank ( $45 \times 30 \times 30 \text{ cm}$ , water depth 12 cm) as the observer arena. At either end of the observer arena, we placed a colourless Perspex demonstrator chamber ( $27 \times 15 \times 12 \text{ cm}$ , water depth 12 cm). These were placed 0.5 cm from the ends of the observer chamber. Each of the three tanks contained a 1 cm deep layer of coarse sand. 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 three zones. These were set 8 cm from either end of the observer arena. The two areas between the end of the tank and the bars were designated the prey patch goal zones. An external hanging filter was attached to the wall of the central tank, so as to match the layout of the holding tanks in which the test subjects were housed during their pre-training or sham training. The filter was not switched on during the trials, but the filter inlet provided a landmark which may have further aided pre-trained fish to orientate between the left and right feeders.

Within each of the demonstrator tanks, we placed a feeder unit. The feeder unit consisted of a  $4 \times 4 \text{-cm}$  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 they could see the prey as it was delivered. The rear wall was white to maximise the visibility of the prey. The side walls were opaque, so that the observer in the central tank could not see the prey. Demonstrators were unable to reach the prey until it sank to the bottom of the feeder but were able to attack it as it fell. The front wall of the feeder stopped 1 cm short of the floor of the tank, allowing the demonstrators to eat the prey once it had reached the bottom of the feeder. Prey deliveries consisted of two 3 mm long pieces of thawed frozen bloodworm. These were small enough to be consumed with minimal handling by the demonstrators, ensuring that the observing focal fish could see the feeding behaviour of the demonstrators, but not the prey itself. Screening on the outside of the test tank prevented the fish from seeing the experimenter as the prey was added. Housing the demonstrators in watertight chambers ensured that no chemical cues originating from

**Fig. 1** Plan views of the experimental arenas used to quantify **a** public information use, **b** measures of space use and **c** shoaling behaviour. *Solid black lines* represent opaque surfaces and *broken black lines* represent colourless transparent surfaces. The *solid grey lines* in **a** and **b** represent the public information use goal zones and the different zones of the arena used to quantify movement respectively. These were level with the substrate surface and did not impede fish movement. The *grey squares* in **a** represent the feeder units and the *large grey rectangle* represents the filter unit. The *circles* in **b** represent landmark features. **b** (*i* and *ii*) represents the two landmark configurations used in the successive space use assays. The *hatched areas* in **c** represent the zones in which fish were deemed to be shoaling. See main text for full details and procedures

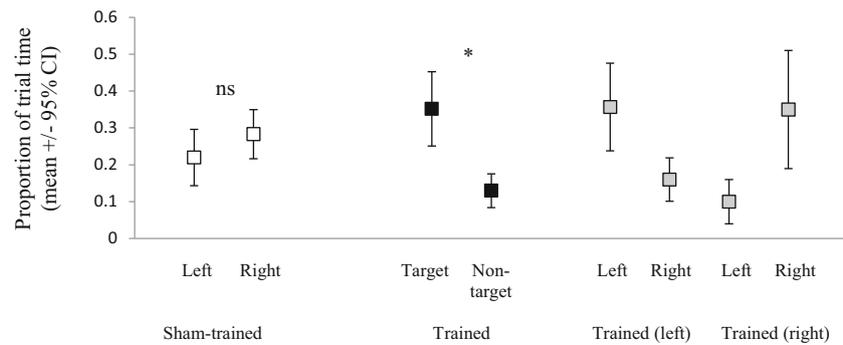


the prey were available to observer, since these may provide direct information about feeder location and prey density (Webster et al. 2007a). This ensured that observer could only base their patch choices upon visual cues received during the demonstration phase. No prey was present in the central arena at any point during the trial.

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, colourless perforated Perspex measuring  $10 \times 10 \times 15$  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, opposite the wall with the filter inlet attached, and half way between the end walls that faced the demonstrator chambers.

We used two opaque black plastic screens measuring  $30 \times 30$  cm square  $\times 3$  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 simultaneously slid into place between the tanks without causing any vibration that might stress the observer. The exterior walls of both the observer arena and demonstrator chambers were screened in black plastic. Trials were recorded via a webcam fixed 90 cm above the tank.

The demonstrators measured between 40 and 45 mm in length. Due to limitations in the numbers of available fish of this size range, the demonstrators were drawn from a pool of around 80 fish. No demonstrator was used more than once in any 3-day period. Observers were only tested once, and no observers were subsequently used as demonstrators, or vice versa. We did not use demonstrators that had previously been housed with the test subjects, in order to remove any potential



**Fig. 2** A pilot experiment run to test the efficacy of pre-training fish to expecting food from one of two feeders (*left* or *right*). The white points show the amount of time (mean±95 % CI) spent in the left and right feeder goal zones by sham-trained fish, where food had been randomly assigned to the left or right feeder on each day of testing. The black points show amount of time spent in the target (i.e., the side to which they were

trained) or non-target feeder goal zones by pre-trained fish, where food had been consistently delivered to the left or right feeder only on each day of testing. \* $P < 0.05$ . *ns* no significant difference. The grey points show a breakdown of the pre-training data into fish trained to the left feeder and fish trained to the right feeder

effects of familiarity (Ward and Hart 2003; Griffiths and Ward 2011).

**Test procedure** The demonstrators and focal fish were deprived of food for 24 h before testing in order to ensure that they were motivated to feed. Three randomly selected demonstrators were added to each demonstrator chamber and allowed to settle for 10 min before the focal fish was added to the central holding unit and allowed to settle for a further 10 min. The demonstration phase lasted for 6 min and ran as follows. At the beginning of the first, third and fifth minute of

the trial, prey suspended in 1 cm<sup>3</sup> of tank water were added to the feeder in the designated rich patch, using a pipette. During the first and third minutes of the trial, the poor patch received no prey. A ‘blank’ consisting of 1 cm<sup>3</sup> of tank water was added to the feeder at the same time that the rich feeder received prey. During the fifth minute, the poor feeder also received prey. This ensured that while prey was delivered at a 3:1 ratio, the focal fish was unable to select a prey patch simply on the basis of it being the last place it saw fish feeding. The demonstrators consumed all of the offered prey in each trial.

For trials involving test subjects held under the pre-training condition, the rich feeder was always located on the opposite side to which they had been trained, providing them with public information that contradicted their previous experience. In trials of subjects held under the sham-training condition, which had no previous experience of one feeder being superior to the other, one side was randomly selected for the location of the rich feeder and was then used for all three public information trials. This was performed so as to ensure that fish in both the pre- and sham-training treatments received demonstrations that were otherwise identical.

After the 6-min demonstration phase, the opaque black screens were simultaneously slid into place between the observer arena and the two demonstrator chambers. This took approximately 10 s and did not appear to stress the observer. The observer was allowed to settle for a further 1 min before being released from the holding unit. The observer was

**Table 2** Comparing behavioural trait scores between experienced and naïve treatment groups (repeated measures GLM)

	$F_{(1, 58)}$	$P$ value	$\eta^2$
Activity			
Measure	0.01	0.91	<0.01
Treatment	0.29	0.58	0.01
Measure × treatment	0.05	0.82	0.01
Latency to enter 50 % of arena			
Measure	1.09	0.30	0.02
Treatment	0.19	0.65	0.01
Measure × treatment	0.28	0.59	0.01
Thigmotaxis			
Measure	0.01	0.97	<0.01
Treatment	0.64	0.43	0.01
Measure × treatment	0.58	0.49	0.01
Shoaling			
Measure	0.01	0.92	<0.01
Treatment	0.01	0.91	<0.01
Measure × treatment	0.01	0.93	<0.01

Measure describes within-subjects comparisons between the first and second trial. Treatment describes conditions where fish either had or had not received feeder preference training. Refer to main text for further details

**Table 3** Consistency of behavioural measures (Spearman’s rank correlation)

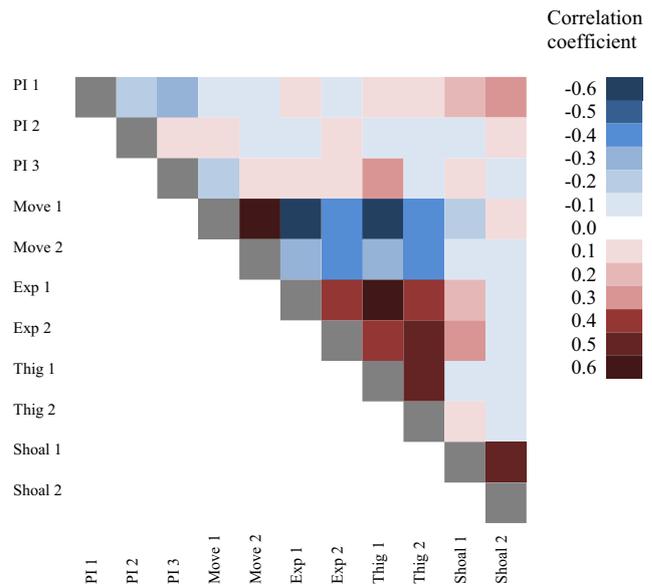
Behaviour	Number	$r$	$P$ value	95 % CI
Activity	60	0.58	<0.001	0.41, 0.71
Thigmotaxis	60	0.42	<0.001	0.25, 0.58
Latency to enter 50 % of arena	60	0.38	<0.001	0.14, 0.58
Time shoaling	60	0.44	<0.001	0.21, 0.62

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. During the choice phase, we recorded the location of the observer every 6 s (whether it was within either goal zone or the central neutral zone, yielding a total of 50 data points) and the first goal zone it entered. A fish was deemed to have entered the goal zone if its entire head passed over the delineating yellow goal zone bar.

### Activity, thigmotaxis and exploration

We quantified activity, thigmotaxis, and exploration in fish placed within a novel arena. This consisted of an arena within an opaque black plastic container measuring 80 cm long  $\times$  60 cm wide  $\times$  35 cm deep and with a water depth of 20 cm. A grid consisting of 1 cm wide bars set in the substrate and level with its surface was used to divide the test arena into 18 areas measuring 20  $\times$  13 cm each (Fig. 1b). These did not impede the movement of the fish and were used to quantify exploration, as described below. Two test arena configurations were used. Each test subject was tested once in each, in a randomly determined order. This ensured that each test occurred in a novel arena. The first configuration contained a sand substrate and the second a coarse gravel substrate, both 1 cm deep. Each contained five landmarks, consisting of a 19 cm tall, 6 cm wide clear plastic cup filled with sand (in the sand substrate configuration) or small rocks (in the gravel substrate configuration). The layout of these varied between the two configurations, as shown in Fig. 1b (*i* and *ii*). A holding unit was placed in one corner of the test arena. This consisted of a tower of clear, colourless perforated Perspex measuring 10  $\times$  10 cm  $\times$  25 cm tall. It was attached via a monofilament line to a 15 cm long arm clamped to the wall of the observer arena, allowing the holding unit to be raised by the experimenter.

The test subject was added to the holding unit and allowed to acclimate for 10 min. Following this, the observer was released by raising the holding unit 10 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 test subject. This began the trial, which ran for 15 min. We recorded three behaviours: activity, thigmotaxis and the latency of the test subject to visit half of the zones. Activity was point sampled at 15-s intervals, giving a total of 60 observations. For each sampling instance, we noted whether the fish was swimming or whether it was stationary, either in the water column or on the substrate. Thigmotaxis or wall-following behaviour was also sampled at 15-s intervals. Thigmotaxis was used as a measure of cover use, represented here by the walls and landmarks (Webster and Laland 2011, 2012). For



**Fig. 3** A heatmap showing correlation coefficients obtained from Spearman rank correlations for all combinations of the behaviours measured in the study. *PI 1–3* refers to the time allocation scores (time in rich patch – time in poor patch) in the three public information use trials. *Move* refers to the amount of time spent moving in the two novel arena assays. *Exp* refers to the latency to enter 50 % of the zones of the arena floor in the two novel arena assays. *Thig* refers to the measures of thigmotaxis, the proportion of time the fish remained within 5 cm of the walls and landmarks in the two novel arena assays. *Shoal* refers to the proportion of time that the fish spent shoaling in the two shoaling assays. *Red* and *blue* cells indicate positive and negative correlations, respectively

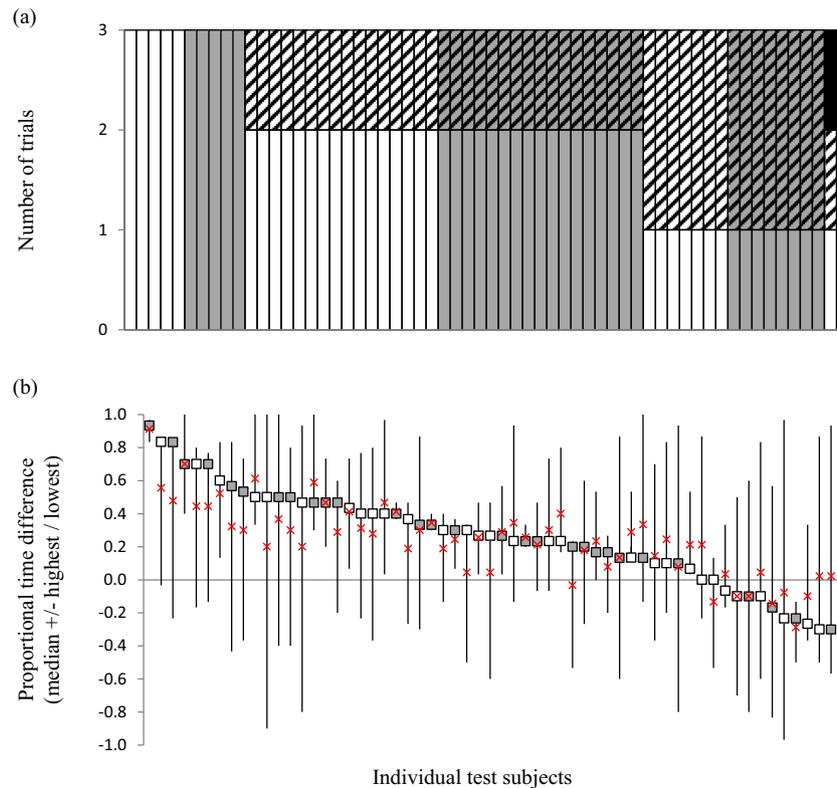
each sampling instance, we recorded whether the fish was within 5 cm of either the side wall of the arena or one of the five landmarks within the arena interior. Finally, latency to enter half of the arena zones was recorded as a continuous variable, to the nearest second. Fish failing to enter half of the zones were given a ceiling score of 900 s.

### Shoaling assay

We established a binary choice test arena measuring 80 cm long  $\times$  60 cm wide  $\times$  35 cm deep, with a water depth of 20 cm in an opaque black plastic container (Fig. 1c). The arena contained a 2 cm deep layer of coarse sand. Ten centimetres from either end of the arena, we placed a 10 cm square, 25 cm

**Table 4** PCA loadings of behavioural measures

Behavioural measure	PC1 'space use' (54.6 % of variance)	PC2 'sociability' (25.1 % of variance)
Activity measure	−0.86	−0.12
Latency to enter 50 % of arena measure	0.86	0.06
Thigmotaxis measure	0.83	−0.06
Shoaling measure	−0.10	0.99



**Fig. 4** **a** The number of times out of three trials in which each fish first entered the rich patch goal zone. The grey and white sections show first entries into the rich patch by fish in the experienced and naïve treatments, respectively. The hatched section of the bar shows first entries into the poor patch goal zone. Black sections indicate trials in which the fish failed to enter either goal zone. Each bar represents one fish. These are arranged in order of most to fewest first entries into the rich patch goal zone. There was no difference in rich patch goal zone entries by fish in the experienced and naïve treatment groups. **b** The time allocation scores to the rich patch (time in rich patch goal zone – time in poor patch goal zone) for each of three trials per fish. The points show the time allocation for the

median ranked trial, and the error bars show the highest and lowest time allocation scores for each individual. The red cross symbols show the mean time allocation score for each individual. Where error bars are absent, the median and highest/lowest scores were identical. Grey and white points represent fish from the experienced and naïve treatments, respectively. Data are arranged in order of highest to lowest median time allocation to the rich patch goal zone. Analyses were performed for both median and mean time allocation scores. There was no difference in rich patch goal zone entries by fish in the experienced and naïve treatment groups

tall stimulus chamber. This was constructed from colourless, perforated plastic. A webcam was fixed above the arena, allowing observations to be made. To one of the stimulus chambers, we added five unsexed, non-reproductive sticklebacks measuring 40–45 mm in length. Together, these formed the stimulus shoal. The chamber holding the stimulus shoal was selected at random, and the other was left empty. The stimulus shoal was allowed to settle for 10 min before the test subject was added to the tank and was changed after every trial. They were drawn from the pool of approximately 80 stimulus fish. No stimulus fish was used twice in the same 48-h period. As in the PI assay, we did not use demonstrators which had previously been housed with the test subjects, in order to remove any potential effects of familiarity (Ward and Hart 2003; Griffiths and Ward 2011).

The test subject was placed within a holding unit attached to a pulley mechanism, as described above. The test subject was allowed to acclimatise for a further 10 min before the trial began. Following this, the holding unit was raised 10 cm from

the base of the arena, also as described above. The trial lasted for a further 20 min, during which time we recorded the proportion of time that the test subject spent within 8 cm, approximately two average body lengths, of either stimulus chamber. This distance was selected as it corresponds to the inter-individual shoaling distance seen in free-moving shoals (Webster et al. 2007b).

**Table 5** Summary of an ordinal regression investigating the effects of condition factor and behavioural trait variables, and naïve/experienced treatment upon the number of times entered the rich goal zone first in PI use trials

Variable	$\chi^2$	<i>df</i>	<i>P</i> value	Parameter estimate	95 % CI
Condition factor	2.21	1	0.17	90.43	–10.80, 241.52
PC ‘space use’	1.71	1	0.15	0.34	–0.01, 1.04
PC ‘sociability’	2.14	1	0.12	–0.07	–0.98, 0.14
Treatment	1.50	1	0.22	–0.13	–1.81, 0.42

## Statistical analyses

In the pilot experiment, we used paired-sample *t* tests to compare time spent in the goal zone of the target and non-target feeders in the trained-treatment fish and in the left versus the right goal zone in the sham-trained treatment group. Data were normalised using arcsine transformation before analyses were performed.

We compared the first and second measures of the four behavioural traits—activity, thigmotaxis, latency to enter 50 % of the test arena and time spent shoaling—between the naïve and experienced groups using repeated measures ANOVAs. Proportional data (activity, thigmotaxis and shoaling) were normalized with arcsine transformation, while count data (latency to explore 50 % of the arena) were transformed using log10 transformation before analyses were performed.

We used Spearman rank correlations to test for consistency of responses between measures for each of these traits, as well as for correlations between all possible combinations of behavioural measure and the three-time allocation measures of public information use. These behaviours were then collapsed into two principle components describing ‘space use’ and ‘sociability’ using a principle components analysis, as described below.

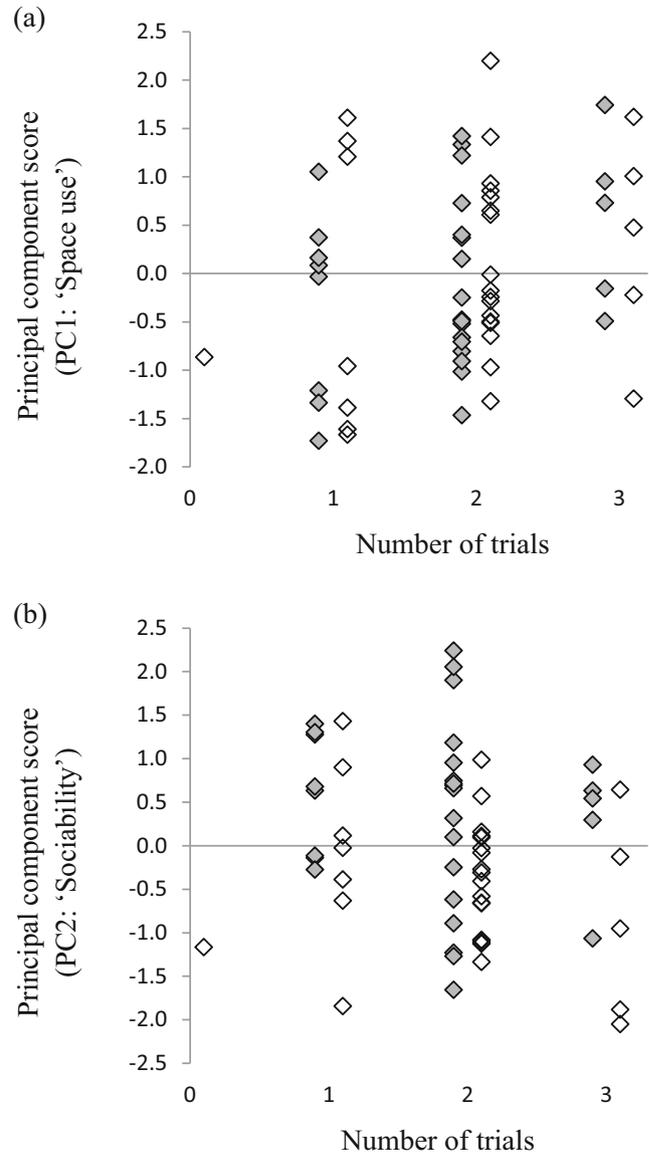
Next, we compared public information use between the naïve and experienced groups. We used the first goal zone that each fish entered to determine a first choice score consisting of the number of trials in which it entered the rich patch goal zone first over the three public information tests. We also calculated a time allocation score using the proportion of time spent in the rich goal zone minus the mean proportion of time spent in the poor goal zone in each of the three trials. We used an independent samples *t* test and a repeated measures ANOVA respectively to compare these scores between the naïve and experienced treatment groups.

Finally, we sought to determine the relationship between the space use and sociability measures and the two metrics of PI use. In order to determine whether either of the two principle components were related to the first goal zone choice of the fish over the three public information assays, we performed an ordinal regression using, with first choice score, an ordinal category of 0, 1, 2 or 3, assigned as the dependent variable. Treatment was included as a fixed factor and starting body mass and condition factor, and the space use and sociability principle components were included as covariates, fitted using stepwise backward elimination. In order to test for effects of either of the two principle components upon time allocation, we ran two general linear models using Gaussian error distributions. These used the mean and median time allocation respectively as the dependent variable. In both cases, treatment was included as a fixed factor and starting body mass and condition factor, and space use and sociability were included as covariates.

## Results

### Pilot experiment

Fish that had been pre-trained to feed from one of two feeders (left or right) spent more time in the goal zone surrounding the feeder to which they had been trained (paired samples *t* test,  $t=3.84$ ,  $df=19$ ,  $P=0.001$ ). Naïve fish that had been sham trained, subject to the same training procedure but with food randomly allocated to either feeder on any given day, showed no feeder goal zone preference ( $t=-1.17$ ,  $df=19$ ,  $P=0.26$ , Fig. 2). The



**Fig. 5** **a** Scatterplot showing the number of first entries into the rich patch goal zone plotted against the principle component scores describing space use. **b** The number of first entries into the rich patch goal zone plotted against the principle component scores describing sociability. Grey and white points represent fish from the experienced and naïve treatments, respectively. No relationship was seen between these variables

results of the pilot experiment demonstrate that the 14-day training period was sufficient to generate a learned bias for one of the two feeders.

### Behavioural trait measures

We saw no differences in the four behaviours (activity, thigmotaxis, latency to enter 50 % of the test arena and time spent shoaling) between fish from the naïve and experienced treatment groups (Table 2).

Because the behavioural trait scores between experienced and naïve treatment groups did not differ, we pooled these data when looking at consistency. The four behaviours were all found to be positively correlated over the two sampling periods (Table 3 and Fig. 3). Moreover, we saw that the two measures of activity were negatively correlated with the measures of latency to explore 50 % of the arena and thigmotaxis. These latter two measures were positively correlated with one another (Fig. 3).

In the shoaling assay, fish spent more time within two body lengths of the chamber holding the stimulus shoal than they did within two body lengths of the empty chamber (naïve and experienced treatment group data pooled, paired samples *t* tests on arcsine transformed data, first assay,  $t=12.77$ ,  $df=59$ ,  $P<0.001$ ; second assay,  $t=9.54$ ,  $df=59$ ,  $P<0.001$ ).

### Principle components analysis of behavioural traits

A PCA was used to reduce the four behaviour measures—activity, thigmotaxis, latency to enter 50 % of the test arena and time spent shoaling—into a minimal number of

components. This yielded two components, describing 54.6 and 25.1 % of the variation respectively (Kaiser-Meyer-Olkin measure 0.71; Bartlett's test of sphericity,  $X^2=58.12$ ,  $df=6$ ,  $P<0.001$ ). PC1, hereafter 'space use', described negative correlations between activity and thigmotaxis and between activity and latency to explore half of the arena, and a positive correlation between thigmotaxis and latency. PC2, hereafter 'sociability', contained the measure of time spent shoaling. The loadings of these behavioural measures onto the two PCs are given in Table 4.

### Public-information use

We saw no differences between naïve and experienced fish in the number of times that they first entered the goal zone demonstrated in the trial to be rich, or in the mean time difference spent in the rich versus the poor goal zone (independent samples *t* test: first entered rich goal zone,  $t=-0.18$ ,  $df=58$ ,  $P=0.85$ , Fig. 4a; repeated measures ANOVA: time in goal zone, performance over the three trials,  $F_{(1, 58)}=0.49$ ,  $P=0.58$ ,  $\eta^2=0.008$ ; performance between training treatments  $F_{(1, 58)}=0.27$ ,  $P=0.60$ ,  $\eta^2=0.005$ ; performance across trials  $\times$  training treatments  $F_{(1, 59)}=0.31$ ,  $P=0.54$ ,  $\eta^2=0.06$ ; Fig. 4b).

Pooling data from the naïve and experienced treatment groups, we saw that fish entered the rich patch first more often than they entered the poor patch across the three trials (paired samples *t* test,  $t=4.41$ ,  $df=59$ ,  $P<0.001$ ). They also spent more time there compared to the poor patch (mean time allocation across the three trials per individual,  $t=-7.88$ ,  $df=59$ ,  $P<0.001$ ).

**Table 6** Summary of a GLM investigating the effects of condition factor and behavioural trait variables, and naïve/experienced treatment upon (a) mean and (b) median time allocation to the rich goal zone in PI-use trials (time in rich goal zone – time in poor goal zone)

Variable	<i>df</i>	Mean square	<i>F</i>	<i>P</i> value	<i>B</i>	95 % CI	$\eta^2$
<b>A</b>							
Model	4	28.63	0.58	0.67			0.04
Intercept	1	113.53	2.32	0.13	4.64	-2.16, 7.46	0.04
Condition factor	1	12.39	0.25	0.62	191.11	-252.40, 634.63	0.01
PC 'space use'	1	19.05	0.39	0.53	0.59	-1.24, 2.44	0.01
PC 'sociability'	1	63.25	1.29	0.26	1.07	-0.77, 2.92	0.02
Treatment	1	55.58	1.14	0.29	-1.08	-4.83, 2.66	0.02
Total	60						
Corrected total	59						
<b>B</b>							
Model	4	22.72	0.27	0.89			0.02
Intercept	1	186.99	2.22	0.14	6.85	-2.09, 9.80	0.04
Condition factor	1	3.71	0.04	0.83	121.75	-460.47, 703.98	0.01
PC 'space use'	1	6.31	0.07	0.78	0.36	-2.06, 2.78	0.01
PC 'sociability'	1	27.89	0.33	0.57	0.93	-1.49, 3.35	0.01
Treatment	1	81.98	0.97	0.33	-1.90	-6.82, 3.02	0.02
Total	60						
Corrected total	59						

## Personality and public-information use

An ordinal regression revealed that the number of trials in which fish first entered the rich patch was unrelated to space use or sociability PC scores, nor to their training or body condition (Table 5, Fig. 5a, b). Confidence intervals for the effect of condition factor were wide, suggesting that an effect of condition factor on prey patch first choice may still be possible, but were narrow for mass, treatment and the space use and sociability principal components, suggesting that a large effect of these variables is implausible.

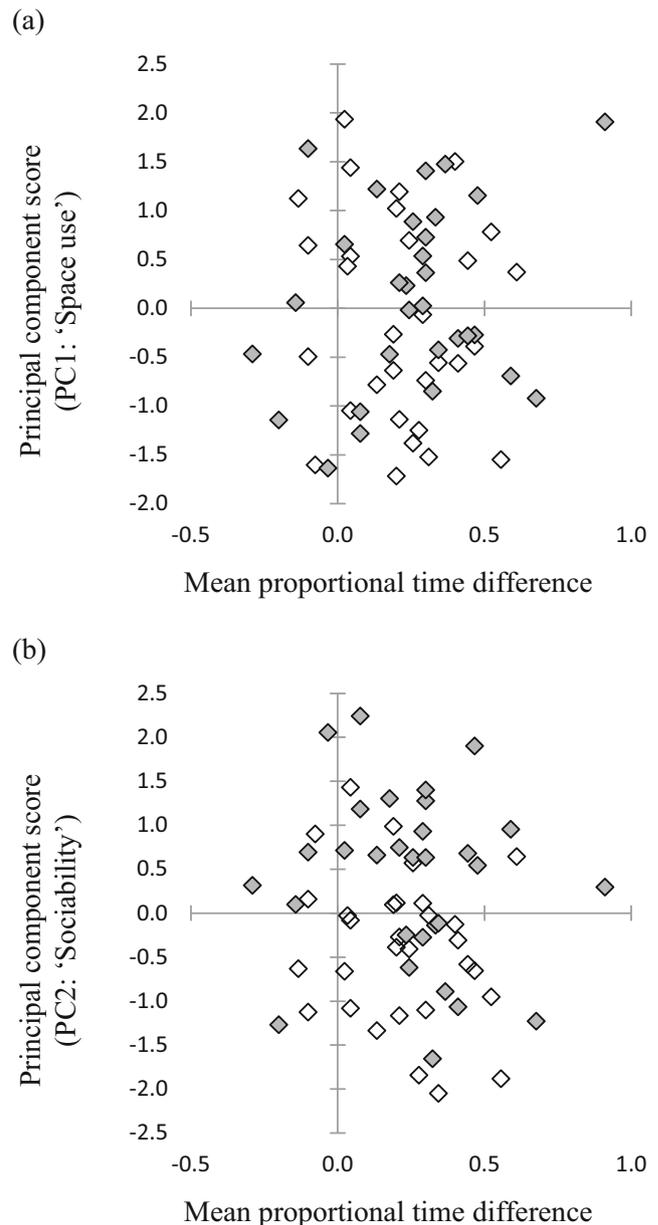
Similarly, GLMs showed that the mean proportional difference in time spent between the rich and poor patches was not related to space use or sociability nor related to training or body condition. This was true when both mean and median time allocation scores were used as dependent variables (Table 6, Fig. 6a, b). Effect sizes were small (0.04 or lower in all cases), suggesting that biologically meaningful effects of prior experience, space use or sociability are unlikely.

## Discussion

Our study revealed individual consistency in activity, exploration, thigmotaxis and time spent shoaling in ninespine sticklebacks, measured over a period of several weeks, but found that these traits were unrelated to either of two measures of PI use. In addition to this, we saw no effect of experience with regard to where to forage in our experiment—while we were able to train fish to prefer one of two feeders, trained fish were just as likely to be influenced by (conflicting) PI as were naïve fish when they were tested. Effect sizes here were seen to be small (Tables 5 and 6) suggesting that this finding reflects a true absence of any substantial effect of these behaviours upon PI use, rather than being an artefact of insufficient power to detect such a relationship.

Overall, the majority of fish were net PI users, being more likely to first enter and to spend more time in the PI-demonstrated rich patch in most of their successive trials. This is consistent with the findings of earlier work on PI use in this species carried out in our laboratory (Laland et al. 2011). Individual consistency in PI-use over the three trials was low, however, with moderate negative correlations in net time allocation to the rich prey patch seen between the first and second and first and third assays (Fig. 3), although no decline in PI use over successive trials was evident at the treatment group level.

Our finding that measures of activity, exploration, thigmotaxis and time spent shoaling were consistent across trials within individuals corresponds with the findings of other studies reported in the literature. These and similar behaviours have previously been shown to be correlated across exposures in a wide variety of different species and are considered to be



**Fig. 6** **a** Scatterplot showing the mean time allocation to the rich patch goal zone (time in rich patch goal zone – time in poor patch goal zone) plotted against the principle component scores describing space use. **b** Mean time allocation to the rich patch goal zone plotted against the principle component scores describing sociability. Grey and white points represent fish from the experienced and naïve treatments, respectively. No relationship was seen between these variables

common sources of personality variation in non-human animals, though potentially with different underlying mechanisms (reviewed by Réale et al. 2007; Sih and Bell 2008; Bell et al. 2009; Conrad et al. 2011).

Our primary finding that PI use was unrelated to any of the behavioural traits that we looked at contrasts with those of some previous studies, such as Marchetti and Drent (2000), Kurvers et al. (2010a, b) and David et al. (2011), where similar behavioural traits were seen to be linked to scrounging

behaviour and PI use, respectively. We note of course that these studies were carried out in different species and using differently designed assays. On the other hand, our findings are consistent with those from studies investigating different forms of social information use in the threespine stickleback (Webster et al. 2007c; Harcourt et al. 2010). In these studies, attraction to feeding conspecifics alone (Webster et al. 2007c) and attraction to feeding conspecifics and response to other social cues (Harcourt et al. 2010) were not seen to be related to measures of boldness or exploratory behaviour. This suggests that such relationships between public learning and foraging and other behavioural traits are probably species, and context, specific, and that attempts to generalise across species may sometimes be misleading.

The absence of a relationship between PI use and the behavioural traits considered in this study could be due to a number of factors. For example, theoretical analyses have shown that discriminatory use of public information is generally adaptive (Rendell et al. 2010). While ninespine sticklebacks are not an obligatorily shoaling species and were seen in this study to vary in their sociability, they are nevertheless generally social. All individuals are therefore likely to be exposed to PI at different times throughout their lives and may all therefore have had ample opportunity to learn to associate conspecific feeding behaviour with the presence of food prior to being used in our experiments. If conspecific feeding behaviour is a reliable indicator of prey availability, then we might expect all individuals to respond to such cues, irrespective of any variation between them in other behaviours.

Finally, it remains plausible that variation in space use or sociability or other behavioural traits might indirectly affect how individuals use PI, by affecting their exposure to it. This possibility was deliberately excluded by our experimental design, as we sought to determine whether PI use co-varied with these personality traits when opportunity for exposure was standardised. It seems intuitive that, for example, individuals that spend more time interacting with others, or which are more strongly attracted to large groups of conspecifics, might be exposed to PI more frequently or from a greater variety of different sources. Individuals that are more active or exploratory, or which interact more frequently with novel elements in their environment, might themselves be more likely to encounter other individuals and thus be exposed to PI more frequently too. At the same time, those individuals might also be more likely to privately acquire information about the nature and distribution of resources in the environment. Given this, it seems clear that personality traits that affect how individuals move through their environment and encounter and interact with others might affect how they acquire information from both private and social sources. In principle, such effects can be quantified via information-diffusion experiments, in which groups of freely moving individuals are monitored as they interact and uncover hidden resources. Social network

analysis can be used to quantify the structure of social interactions (Croft et al. 2008; Wilson et al. 2013), which in turn can be used to inform network-based diffusion analysis (NBDA) models which attempt to identify the effects of social structure and other variables upon the rate and order at which individuals acquire information about resources such as food patches (Franz and Nunn 2009; Hoppitt et al. 2010). This approach has recently been used to quantify social effects on information acquisition in fish (Atton et al. 2012, 2014; Webster et al. 2013). Useful further research could account for individual level variation in a range of different behavioural traits that might conceivably affect how likely individuals are to encounter resources and interact with others. Such work could prove useful in revealing the importance of the behavioural traits which comprise personalities in the acquisition and spread of information.

**Acknowledgments** This work was funded by a European Research Council advanced grant (EVOCULTURE 232823) to KNL.

**Ethical standards** The experiments described in the article were performed in accordance with the current laws of the UK.

## References

- Aplin LM, Farine DR, Morand-Ferron J, Cole EF, Cockburn A, Sheldon BC (2013) Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecol Lett* 16:1365–1372
- Atton N, Hoppitt W, Webster MM, Galef BG, Laland KN (2012) Information flow through threespine stickleback networks without social transmission. *Proc R Soc B* 279:4272–4278
- Atton N, Galef BJ, Hoppitt W, Webster MM, Laland KN (2014) Familiarity affects social network structure and discovery of prey patch locations in foraging stickleback shoals. *Proc R Soc B* 281:20140579
- Avital E, Jablonka E (2000) Animal traditions: behavioural inheritance in evolution. Cambridge University Press, Cambridge
- Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis. *Anim Behav* 77:771–783
- Conrad JL, Weinersmith KL, Brodin T, Saltz JB, Sih A (2011) Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *J Fish Biol* 78:395–435
- Croft DP, James R, Krause J (2008) Exploring animal social networks. Princeton University Press, Princeton
- Dall SR, Giraldeau LA, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. *Trends Ecol Evol* 20:187–193
- Danchin E, Giraldeau LA, Valone TJ, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. *Science* 305:487–491
- David M, Cézilly F, Giraldeau LA (2011) Personality affects zebra finch feeding success in a producer–scrounger game. *Anim Behav* 82:61–67
- Franz M, Nunn CL (2009) Network-based diffusion analysis: a new method for detecting social learning. *Proc R Soc B* 276:1829–1836
- Galef BG, Giraldeau LA (2001) Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim Behav* 61:3–15

- Gosling SD, John OP (1999) Personality dimensions in nonhuman animals a cross-species review. *Curr Dir Psychol Sci* 8:69–75
- Griffiths SW, Ward A (2011) Learned recognition of conspecifics. In: Brown C, Laland K, Krause J (eds) *Fish cognition and behavior*. Wiley Blackwell, Oxford
- Harcourt JL, Biau S, Johnstone R, Manica A (2010) Boldness and information use in three-spined sticklebacks. *Ethology* 116:440–447
- Herczeg G, Gonda A, Merilä J (2009) Predation mediated population divergence in complex behaviour of nine-spined stickleback (*Pungitius pungitius*). *J Evol Biol* 22:544–552
- Heyes CM (1994) Social learning in animals: categories and mechanisms. *Biol Rev* 69:207–231
- Heyes CM, Galef BG (1996) *Social learning in animals: the roots of culture*. Academic Press, London
- Hoppitt W, Laland KN (2008) Social processes influencing learning in animals: a review of the evidence. *Adv Study Behav* 38:105–165
- Hoppitt W, Laland KN (2013) *Social learning: an introduction to mechanisms, methods, and models*. Princeton University Press, Princeton
- Hoppitt W, Boogert NJ, Laland KN (2010) Detecting social transmission in networks. *J Theor Biol* 263:544–555
- Jolles JW, Ostojić L, Clayton NS (2013) Dominance, pair bonds and boldness determine social-foraging tactics in rooks, *Corvus frugilegus*. *Anim Behav* 85:1261–1269
- Kurvers RH, Adamczyk VM, van Wieren SE, Prins HH (2010a) The effect of boldness on decision-making in barnacle geese is group-size-dependent. *Proc R Soc B* 277:601–608
- Kurvers RH, Van Oers K, Nolet BA, Jonker RM, Van Wieren SE, Prins HH, Ydenberg RC (2010b) Personality predicts the use of social information. *Ecol Lett* 13:829–837
- Laland KN (2004) Social learning strategies. *Learn Behav* 32:4–14
- Laland KN, Atton N, Webster MM (2011) From fish to fashion: experimental and theoretical insights into the evolution of culture. *Philos Trans R Soc B* 366:958–968
- Leadbeater E, Chittka L (2007) Social learning in insects—from miniature brains to consensus building. *Curr Biol* 17:703–713
- Marchetti C, Drent PJ (2000) Individual differences in the use of social information in foraging by captive great tits. *Anim Behav* 60:131–140
- Merilä J (2013) Nine-spined stickleback (*Pungitius pungitius*): an emerging model for evolutionary biology research. *Ann N Y Acad Sci* 1289:18–35
- Nomakuchi S, Park PJ, Bell MA (2009) Correlation between exploration activity and use of social information in three-spined sticklebacks. *Behav Ecol* 20:340–345
- Réale D, Reader SM, Sol D, McDougall PT, Dingemans NJ (2007) Integrating animal temperament within ecology and evolution. *Biol Rev* 82:291–318
- Rendell L, Boyd R, Cownden D, Enquist M, Eriksson K, Feldman MW, Fogarty L, Ghirlanda S, Lilliecrap T, Laland KN (2010) Why copy others? Insights from the social learning strategies tournament. *Science* 328:208–213
- Rendell L, Fogarty L, Hoppitt WJ, Morgan TJ, Webster MM, Laland KN (2011) Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends Cogn Sci* 15:68–76
- Rieucou G, Giraldeau LA (2011) Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. *Philos Trans R Soc B* 366:949–957
- Sih A, Bell AM (2008) Insights for behavioral ecology from behavioral syndromes. *Adv Study Behav* 38:227–281
- Sih A, Bell A, Johnson JC (2004a) Behavioral syndromes: an ecological and evolutionary overview. *Trends Ecol Evol* 19:372–378
- Sih A, Bell AM, Johnson JC, Ziemba R (2004b) Behavioral syndromes: an integrative overview. *Q Rev Biol* 79:241–277
- Valone TJ (2007) From eavesdropping on performance to copying the behavior of others: a review of public information use. *Behav Ecol Sociobiol* 62:1–14
- Valone TJ, Templeton JJ (2002) Public information for the assessment of quality: a widespread social phenomenon. *Philos Trans R Soc B* 357:1549–1557
- Ward AJW, Hart PJB (2003) The effects of kin and familiarity on interactions between fish. *Fish Fish* 4:348–358
- Ward AJW, Thomas P, Hart PJB, Krause J (2004) Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behav Ecol Sociobiol* 5:561–568
- Webster MM, Laland KN (2011) Reproductive state affects reliance on public information in sticklebacks. *Proc R Soc B* 278:619–627
- 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 (2013) The learning mechanism underlying public information use in nine-spined sticklebacks (*Pungitius pungitius*). *J Comp Psychol* 127:154–165
- Webster MM, Ward AJW (2011) Personality and social context. *Biol Rev* 86:759–773
- Webster MM, Atton N, Ward AJW, Hart PJB (2007a) Turbidity and foraging rate in threespine sticklebacks: the importance of visual and chemical prey cues. *Behaviour* 144:1347–1360
- Webster MM, Goldsmith J, Ward AJW, Hart PJB (2007b) Habitat-specific chemical cues influence association preferences and shoal cohesion in fish. *Behav Ecol Sociobiol* 62:273–280
- Webster MM, Ward AJW, Hart PJB (2007c) Boldness is influenced by social context in threespine sticklebacks (*Gasterosteus aculeatus*). *Behaviour* 144:351–371
- Webster MM, Ward AJW, Hart PJB (2009) Individual boldness affects interspecific interactions in sticklebacks. *Behav Ecol Sociobiol* 63:511–520
- Webster MM, Atton N, Hoppitt WJ, Laland KN (2013) Environmental complexity influences association network structure and network-based diffusion of foraging information in fish shoals. *Am Nat* 181:235–244
- Wilson DS (1998) Adaptive individual differences within single populations. *Philos Trans R Soc B* 353:199–205
- Wilson DS, Clark AB, Coleman K, Dearstyne T (1994) Shyness and boldness in humans and other animals. *Trends Ecol Evol* 9:442–446
- Wilson ADM, Croft DP, Krause J (2013) Social networks in elasmobranchs and teleost fishes. *Fish Fish* 15:676–689