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Environmental quality determines finder-joiner dynamics in socially foraging three-spined sticklebacks (*Gasterosteus aculeatus*)

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Abstract

Animals that forage in groups have access to social information concerning the quality and location of food resources available. The degree to which individuals rely on social information over their own private information depends on a myriad of ecological and social factors. In general, where resources are patchy in space and/or time, individuals that use social information and join others at previously identified food patches can reduce both search times and the variance in finding food. Here, we explore social foraging dynamics of shoals of three-spined sticklebacks (*Gasterosteus aculeatus*) and investigate when fish tend to use private information and find food themselves, or rely on social information and attend to the food discoveries of others. We show that fish's allocation to alternative foraging tactics (i.e. finding or joining) can be explained by environmental quality. In environments with large food patches, fish experience a reduced finder's share and tend to adopt joining foraging tactics; in environments with small food patches, fish rely on private information and tend to discover their own food patches. However, we found that finding and joining do not result in equal foraging returns as predicted by theory, and instead payoffs were higher for fish adopting finding tactics in all environments we studied. These unequal payoffs may be explained, in part, by consistent inter-individual differences in the amount of food fish consumed per

foraging event and by heavier fish consuming more food. Overall, our simple experimental approach suggests that socially foraging three-spined sticklebacks do show a degree of behavioural flexibility that enables them to efficiently exploit food patches under a range of environmental conditions.

Keywords: finder-joiner dynamics, social foraging, information sharing, three-spined sticklebacks

Statement of Significance

Animals must continually make decisions to secure resources to survive and reproduce, however, inherent variability in the spatio-temporal distribution of resources means that the best decision is not fixed. How do animals ensure they respond effectively to variation? For animals that live and forage in groups, how do environmental conditions determine whether they use private information or social information to meet these challenges? These are important questions in behavioural ecology and have great significance to animals' ability to deal with unheralded environmental change. Here, we show empirically that three-spine sticklebacks flexibly and adaptively switch between behavioural tactics to acquire foraging resources in accordance with the abundance and distribution of forage in their environment, establishing a new model system to extend and build our understanding of social foraging dynamics and how animal groups optimally function in a variable world.

Introduction

Social animals can gather 'personal information' directly from environmental cues and 'social information' from the behaviour of conspecifics (Dall et al. 2005). In a foraging context, where resources are patchy in space and/or time, those individuals that use social information (i.e. attend to cues that provide information about the foraging success of conspecifics) can reduce both search times and the variance in finding food (Caraco 1981; Caraco and Giraldeau 1991; Clark and Mangel 1984; Ranta et al. 1993; Ruxton et al. 1995). However, the payoff for an individual relying upon social information decreases with an increasing number of conspecifics also using social information (Clark and Mangel 1986; Vickery et al. 1991; Barta and Giraldeau 2001; Beauchamp 2008; Kurvers et al. 2012). This is best understood by considering individuals that rely on personal information to 'find' food patches, and those relying on social information to 'join' others at food patches (Coolen et al. 2001). The more individuals choosing to join others at food patches, the greater the payoff to finding your own patch and acquiring a greater share of the resource (termed the 'finder's share') (Giraldeau and Caraco 2000).

If foraging animals can simultaneously search for and find food, while also monitoring the behavior of conspecifics for joining opportunities, then the system can be classified as an 'information sharing' system with foragers considered 'opportunists' (Clark and Mangel 1984; Vickery et al. 1991; Giraldeau and Caraco 2000). Conversely, if finding and joining are incompatible tactics, or doing both is costly, then individuals may adopt the tactic that provides the greatest expected returns; this is considered a 'producer-scrounger' system (Barnard and Sibly 1981; Giraldeau and Caraco 2000). In producer-scrounger systems, the adoption of either tactic is frequency dependent, whereby the payoffs for scrounging decrease with increasing number of individuals adopting this tactic (Caraco and Giraldeau 1991). Accordingly, individuals are expected to converge to an equilibrium ratio of 'producers' and 'scroungers' in which both tactics attain the same payoff (Mottley and Giraldeau 2000).

The decision of socially foraging animals to either gather their own information and act as producers or rely on others' information and act as scroungers, is affected by a myriad of ecological and social factors. The single most important factor, however, is the quality and distribution of food resources (Giraldeau and Caraco 2000). If food resources in the environment are dispersed and of low value, then the finder's share will be large and consequently, the majority of a population should independently search for food and rely on personal information. In contrast, where food resources are clumped (i.e. low density) and of high value, then this should promote the use of social information by foraging individuals. Recent theoretical work promoting the use of a simulation model based on individual learning, and the associated empirical test of this model, show that scrounging should also increase in environments where patch quality is variable (Afshar and Giraldeau 2014; Afshar et al. 2015). The use of either tactic does not need be fixed, however, and socially foraging animals may also flexibly respond to both personal and social information and adopt either tactic. This is predicted to occur when there is little incompatibility to acting as a producer or scrounger, that is, when individual foragers can monitor the behaviour and food discoveries of conspecifics with little cost to their personal rate of food discovery (Vickery et al. 1991). These predictions, generated by agent-based and theoretical work (Waltz 1982; Clark and Mangel 1986; Caraco and Giraldea 1991; Vickery et al. 1991; Barta and Giraldeau 2001; Beauchamp 2004, 2008; Kurvers et al. 2012; Afshar and Giraldeau

2014) are supported by a number of empirical tests (e.g. Koops and Giraldeau 1996; Giraldeau and Livoreil 1998; Coolen et al. 2001; Beauchamp 2013, 2014; Afshar et al. 2015).

Much recent work into social foraging theory has focused on consistent individual differences in tactic use (Beauchamp 2001; Mathot et al. 2009; Morand-Ferron et al. 2011a), and how and when intrinsic differences in dominance (Barta and Giraldeau 1998; Liker and Barta 2002; McCormack et al. 2007; King et al. 2009), metabolism (Mathot et al. 2009), exploratory tendency (Kurvers et al. 2010; Kurvers et al. 2012), sex (Pfeffer et al. 2002; King et al. 2009) and kinship (Vickery et al. 1991; Tóth et al. 2009; Mathot and Giraldeau 2010), may lead to an individual focusing on one foraging tactic over the other. Other work has looked at frequency dependent reward dynamics and how rewards from past foraging decisions will affect subsequent decisions (Giraldeau 1984; Giraldeau and Caraco 2000; Giraldeau and Dubois 2008; Katsnelson et al. 2008; Morand-Ferron and Giraldeau 2010; Morand-Ferron et al. 2011b; Dubois et al. 2012).

Although social foraging theory is now well developed a vast majority of empirical tests have been conducted on birds in captive environments (Beauchamp 2013), with only a handful of tests on birds foraging in their natural environment (e.g. Morand-Ferron et al. 2007: *Quiscalus lugubris;* Beauchamp 2014: *Calidris pusilla*) and some investigations into social foraging theory in wild primates (e.g. King et al. 2009: *Papio ursinus*; Bicca-Marques and Garber 2004: *Saguinus* sp; Di Bitetti and Janson 2001: *Cebus apella*). The main reason for this bias in species and context is that distinguishing the tactic used by an animal, the boundaries of patches, and the individual pay-offs for discrete foraging events are experimental/observational hurdles that can prove difficult to clear. Consequently, much experimental work in laboratory settings looking at finder-joiner behaviour involves constraining individuals to one of the two tactics using specially designed apparatus (Mottley and Giraldeau 2000), or training a proportion of individuals in a foraging task so that when combined with naïve individuals only the trained individuals can express the finding foraging tactic (Ólafsdóttir et al. 2014). While this is extremely valuable and often necessary when testing predictions from producer-scrounger theory, it is less likely to represent social foraging behaviour in the wild, where animals may well perform both tactics either in consecutive foraging events or simultaneously (King et al. 2009).

Fish have a long history of being used as subjects for empirical explorations of foraging theory, particularly in relation to competition theory (reviewed by Ward et al. 2006) and ideal free distribution theory (reviewed by Milinski 1988). However, fish have rarely been used to explore finder-joiner dynamics (but see Hamilton and Dill 2003; Ólafsdóttir et al. 2014). There are considerable benefits to using fish to explore finder-joiner dynamics: (1) foraging behaviour of individual fish in shoals has been shown to be flexible in response to changes in the distribution of resources in the environment (e.g. Ryer and Olla 1992, 1995), (2) the experimental manipulation of individual state, group composition and the environment is relatively simple, and (3) they are found in a vast array of habitats and hence have diverse morphology and behaviours. Finally, (4) the experimental arenas for fish are often smaller than for other vertebrates and an entire experimental space can recorded by video, enabling an observer to explore how an individual's behaviour is affected by its conspecifics at any given time. Three-spined sticklebacks (*Gasterosteus aculeatus*) are often used in foraging studies (Ranta and Juvonen 1993; Ólafsdóttir et al. 2014) and have recently been used as a model system to explore social learning and the trade-off between using private and social information (Webster and Hart 2006; Laland et al. 2011; Webster and Laland 2012). As such they are a good choice of fish to extend and build our understanding of finder-joiner dynamics.

Here we explore the finder-joiner dynamics of socially foraging three-spined sticklebacks and ask to what degree fishes' allocation to alternative foraging strategies can be explained by patch size and distribution (which we termed 'environmental quality'). We expected that the relative frequency of finding behaviour should decrease in environments with large and/or clumped food patches as a result of a reduced finder's share (prediction 1) (Giraldeau et al. 1990; Giraldeau and Livoreil 1998) resulting in more fish exploiting patches (i.e. larger foraging group size) in these environments (prediction 2) (Afshar and Giraldeau 2014). In accordance with negative frequency dependent use of foraging tactics, we also expected approximately equal foraging returns for the use of either finding or joining tactic in response to changing environments (prediction 3) (Mottley and Giraldeau 2000).

Methods

Study Animals

Subjects were N=48 three-spined sticklebacks (*Gasterosteus aculeatus*), wild-caught on Swansea University campus, Wales, UK (mean weight wet ± SD = 1.12±0.26g). Subjects were kept in a holding tank (30 x 39 x 122 cm) containing gravel substrate, plants and driftwood for 8 weeks prior to the experiment at a consistent temperature of 17°C at 8L:16D photoperiod regime. On day 1 of the experiment, 24 fish were weighed and a 6 mm diameter circular plastic identification tag was placed on their first dorsal spine (Webster and Laland 2009) (Fig. 1a). Fish were randomly allocated to groups of n=6 according to their identification tags (six blue, black, green, white, blue-white and yellow tags were used) resulting in four groups of 6 fish: A, B, C or D before being placed into individual 2.8L (9.5x 16 x 18.5 cm) gravel-lined, aerated tanks. The following day (day 2) this procedure was repeated with another 24 fish and they were randomly allocated to groups E, F, G or H. Fish remained in these individual tanks for the experimental period when not being assayed. Water was changed every two days and all fish were fed 5 defrosted bloodworms (Chironomid larvae) at 9am every day that they were not being assayed. Two days after being housed in individual tanks, fish were habituated to the experimental arena (see below) in their allocated groups for 60 min.

Setup and Environmental Treatments

Four identical experimental arenas were placed next to each other on the laboratory floor. The arenas were created by inserting a plastic grid structure into a clear plastic tank (50 x 65 x 12 cm) (see Webster and Laland 2012) for a description of a similar set-up). The plastic grid structure was made up of 10 x 10 cm squares that were 6 cm deep. We filled the grid with 3 cm of white gravel leaving 3 cm of the grid visible (Fig. 1a). We filled the test arena with aged aerated water to 4 cm above the grid structure, meaning the maximum depth was 7 cm. Defrosted bloodworms could be placed onto the gravel within any grid square to create distinct foraging patches. This key feature of our experimental design meant that the head of a fish had to be within the grid square for it to be able to see the bloodworms (Webster and Laland 2012), and thus, we defined our grids as ‘patches’. White card was placed between the four arenas and all four arenas were surrounded by white screen (PhotoSEL BK13CW White Screen) held up by a custom built metal frame (Fig. 1b). Four photographer’s lights (each with 4 x 25w 240v 6400K True Day light bulbs) lit the arenas from outside the white sheet, dispersing light evenly over the four arenas. Experiments were filmed using 2 Panasonic HDC-SD60 HD video cameras, each filmed two arenas (Panasonic Corporation of North America, Seraucus, NJ, USA) mounted above the arenas (Fig. 1b).

We used a 2x2 experimental design to vary the foraging environment. Factor 1 was 'patch size' and had two levels - small (2 bloodworms per patch) and large (6 bloodworms per patch). Factor 2 was 'patch distribution' and also had two levels – clumped and dispersed. In the clumped distribution there were three clumps of three patches. The three clumps were separated by two grid squares, and the three patches within the clumps were all directly next to each other. In the dispersed treatment, all 9 patches were separated by one grid square (Fig. 1c). Therefore the 4 environmental treatments were: small and clumped (SC), small and dispersed (SD), large and clumped (LC) and large and dispersed (LD) (Fig. 1c). All fish were left for 2 days in their individual tanks before they were habituated to the experimental arena in their allocated groups for 60min. A day later, each group was then assayed once in each of the 4 treatments, with a day's rest in-between assays. Trial order was controlled for each group.

Experimental Procedure

At 13:00h the day prior to the experimental assay the arenas were set-up and filled with aged aerated water. At 9:30h on the day of the experimental assay bloodworms were distributed in each of the experimental arenas according to the allocated environmental treatment (see above). The group of fish was then placed into a clear plastic container, placed at one end of the arena for 10 min before being released into the arena and allowed to forage for 30 min. The fish were released from the container by pulling on a monofilament line, extending outside of the experimental arenas and surrounding screen. The container was removed from the arena as the fish were released. After 30 min the fish were returned to their individual tanks and the arenas were cleaned and set-up for the next day's assay.

Data Collection

Videos were played back in VirtualDub (v 1.10.4, 1998-2012, Avery Lee) and each fish's behaviour was scored (one fish observed at a time). Every time a fish entered a patch containing bloodworm it was recorded. Following (Coolen et al. 2001), entering an unoccupied patch (by other fish) was considered "finding", whereas entering an occupied patch was considered "joining". If a fish entered an unoccupied patch and ingested at least one bloodworm, it was defined as a "finding event". If it failed to ingest the bloodworm, i.e. it pecked at it or if it subsequently spat the worm out after ingesting it (sticklebacks tend to do this as a means of manipulating the food to be able to swallow it), this was considered a "failed finding event". If a fish entered into a patch that was already occupied and ingested a worm, stole a worm out of a conspecific's mouth, or ingested a worm spat out by a conspecific, this was defined as a "joining event". If the fish entered an occupied patch but failed to ingest any bloodworm, or it attempted to steal but failed to ingest the worm, it was defined as a "failed joining event". If a conspecific had entered the patch beforehand, but the patch was unoccupied when the focal fish entered the patch and ate a bloodworm, this was still considered finding behaviour since it was not possible to know for sure whether the focal fish had attained information on the patch being previously discovered. However, if the focal fish made a directed movement towards a patch whilst a conspecific in that patch was feeding, and the focal fish subsequently ate a bloodworm from that patch then it was defined as joining behaviour (Table 1).

For each foraging event recorded, we recorded: the time that the event occurred, the patch location, and the number and identity of all other fish on the patch (where this was a joining event) as well as the identity of near-neighbours (i.e. fish within one grid square). We also recorded the number of bloodworms available at the patch before the foraging event, the event payoff (i.e. the number of bloodworms ingested by the fish), and the number of bloodworms available at the patch after the event. For an unknown reason, Group H did not engage with the foraging trials (they did not eat nor did they explore the arena to any great extent) and so we could not use their data and removed them from all analyses. In the remaining 7 groups, out of a total of 42 fish, there were 5 fish that did not have a foraging event in one of the two small patch treatments; likely because food was depleted quickly by the other fish. These 5 fish and all other fish had foraging events and consumed bloodworms in the large patch treatments.

Statistical Analyses

We used mixed effect models fitted in R (R Development Core Team, 2014, R i386 3.1.2) using *lme4* and g*lmer* packages (Bates et al. 2014) by maximum likelihood t-tests and used Satterthwaite approximations for degrees of freedom to approximate p-values to test our predictions. In all models, we included Group (A-G) as a random effect since our groups are drawn from a larger population that could (in principle) have been selected, and included fish identity (1-42) as a random effect to allow individuals to vary in their responses (see e.g. Carter et al. 2012; Fürtbauer et al. 2015).

To test whether finding behaviour decreased in environments with large and/or clumped food patches (prediction 1) we fitted a LMM with the percentage of an individual's feeding events classified as "finding" as our response variable. We fitted patch size (small, large) and patch distribution (dispersed, clumped) as fixed effects. To further explore the dynamics of joining, we fitted a LMM with the percentage of an individual's "joining events" that were classified as steals (Table 1) as our response variable, and patch size (small, large), patch distribution (dispersed, clumped) and fish weight (g) as fixed effects.

To test whether fish form larger foraging groups in large and/or clumped food patch environments (prediction 2), we fitted a LMM with group size on the patch at each foraging event as the response variable. We fitted patch size (small, large) and patch distribution (dispersed, clumped) as fixed effects.

To test whether fish received approximately equal foraging returns for the use of either finding or joining tactic (prediction 3) we explored variation in individual foraging returns at the event level. We fitted a generalized linear mixed model (GLMM) with Poisson error structure and ran the model separately for small and large patch trials. Event payoff (bloodworms consumed) was included as the response variable, and foraging decision (find, join) and weight (g) were fitted as fixed effects.

We also calculated the finder's share, a/F, where a = finder's advantage, which is the difference in the amount of food items eaten when an individual finds compared to when it joins, and F = number of food items (Giraldeau and Caraco 2000) across our four environmental treatments, and tested for differences across treatments using Wilcoxon signed rank test in SPSS (IBM® SPSS® Statistics, Version 20).

To minimize observer bias, blinded methods were used when all behavioural data were recorded and analysed.

Results:

In all trials all patches were found and exploited by the fish. In the small patch treatments, all 18 bloodworms provided were eaten, except for group C in the small-clumped environment where they only ate 14. In the large patch environmental treatments, no groups ate all the available 54 bloodworms, and on average 36±7 and 38±7 (mean ± SD) bloodworms were eaten in the large-clumped and large-dispersed environmental treatments respectively (Table 2).

Fish used the finding tactic (mean%±SD) in 46%±0.09 of foraging events in the large-clumped environment, 45%±0.08 in the large-dispersed environment, 60%±0.11 in the small-clumped environment and 55%±0.06 in the small-dispersed environment. Consequently, the finder tactic was significantly less common in large patch environments in accordance with our first prediction (LMM: $t_{(1,121.19)}$= 3.306, p=0.001; Table 3a), but the distribution of resources (i.e. clumped of dispersed) had no effect (LMM: $t_{(1,121.27)}$= -1.083, p=0.28; Table 3a). The finder's share was significantly smaller in environments with large patches (Median=-0.02) compared to environments with small patches (Median=0.25) (T=1, r=0.89, p=0.018; Fig. 2), but was not significantly different between clumped (Median=0.15) and dispersed (Median=0.16) environmental treatments (T=10, r=-0.26, p=0.5).

Increased frequency of joining tactics in large patch environments resulted in larger group sizes at patches (LMM: $t_{(1,1019.2)}$= -2.008, p=0.04; Table 3b) in accordance with our second prediction, but there was no significant effect of patch distribution (LMM: $t_{(1,1023.5)}$= 1.512, p=0.13; Table 3b). When joining, the likelihood that fish actively stole the food from another fish already in the patch was higher in large patch environmental treatments (LMM: $t_{(1,111.02)}$=-2.253, p=0.026; Table 3c), but larger fish did not steal more food (LMM: $t_{(1,41.74)}$= -1.494, p=0.1427; Table 3c), and the distribution of resources (clumped versus dispersed) also had no significant effect on stealing (LMM: $t_{(1,112.41)}$= 1.954, p=0.0531; Table 3c).

Contrary to our third prediction, we found unequal foraging returns for tactic use, with the event payoff being greater for 'finding events' in both environments with small patches (GLMM: z = -3.549, p=0.0004; Table 4a), and larger patches (GLMM: z= -2.868, p=0.004; Table 4b). In the environments with large patches, heavier individuals also had a significantly greater event payoff (GLMM: z= 1.995, p=0.046; Table 4b), meaning bigger fish ate more worms.

Discussion:

Our investigations into the finder-joiner dynamics of socially foraging three-spined sticklebacks suggest that fish adaptively switched between finding and joining behaviour to acquire foraging resources in accordance with the abundance and distribution of forage in their environment. In line with our first prediction, we found finding tactics were more frequent in environments with small patches compared to environments with large patches, which is coherent with the significantly greater finder's share in environments with small patches (Giraldeau and Livoreil 1998; Giraldeau and Caraco 2000). This process resulted in larger group sizes at patches in large patch environments in support of our second prediction. Although the effect of patch size on finder-joiner dynamics matched expectations, the effect of patch distribution did not (see Giraldeau and Livoreil 1998) and patch distribution (clumped or dispersed) did not alter the use of the finding tactic. Although initially surprising, it appears that the time/cost to travel between food items on what we termed 'clumped' and 'dispersed' was minimal (as reflected in equivalent finder's advantages, see above) and so future experiments exploring finder-joiner dynamics in three-spined sticklebacks (and other small fish) should use a larger arena, where patch distribution can be manipulated to ensure the costs of travel between patches is realised. Given that the distribution of patches did not influence foraging dynamics in our experiments, we focus the rest of our discussions upon patch size.

Given that fish altered their tactic use in accordance with the patch size in the environment, we expected that these adjustments should result in approximately equal foraging returns for the use of either tactic. Instead, we found that per foraging event, finding was significantly more profitable. Unequal pay-offs can arise when foragers attain different payoffs when using the same tactic. For example, dominant individuals may receive a larger reward when scrounging than more subordinate individuals (Barta and Giraldeau 1998; Stahl et al. 2001; Bugnyar and Kotrschal 2002; Liker and Barta 2002; McCormack et al. 2007; King et al. 2009; Held et al. 2010; Jolles et al. 2013). Whilst we did not observe overt aggression among individuals, for example, where dominant individuals use aggression to stop the joiner from using the resource (Ólafsdóttir et al. 2014), we did find that bigger (heavier) fish could ingest more food, and it is known that larger sticklebacks have an increased probability of successful food capture and eat at a faster rate (Gill and Hart 1996).

The lack of any role for aggression in our study may lie in the prior information fish had, and/or patch types used. In our study there was a level of uncertainty due to our experimental treatment and randomisation of the location of patches in trials. Additionally, patches were relatively quickly depleted. Together, this may make resouces in our experiment more difficult to defend (Dubois and Giraldeau 2007; Overington et al. 2008). Indeed, in Ólafsdóttir et al.'s 2014 study, dominant individuals were those trained to expect food from a certain patch before foraging partners were released into the arena. We were, however, able to distinguish between tolerated access to patches and stealing behaviour as fish would often attempt to steal food from a conspecific's mouth or consume food that a fish had momentarily spat out, even though food was available elsewhere in the environment. This was particularly evident in the large patch environmental treatment where a greater proportion of "joining" events were steals (fish weight had no effect) and food at a single patch was rapidly consumed by a minority of individuals before being kleptoparasitized by others. We believe that, here, size determined the rate of consumption for individuals with larger individuals quickly consuming bloodworms, but often regurgitating them, providing opportunities for conspecifics to steal. It is also possible that satiation effects were prevalent here and that larger fish were able to consume more before becoming satiated. Overall, given that finding is more profitable and bigger fish were able to acquire a greater share of the resources, it would be interesting to further investigate the consequences of these differences for shoaling preferences and homophily, for example, size-assortative shoaling (Croft et al. 2009).

These findings therefore represent an information sharing system, with fish flexibility adopting finding and joining tactics according to their environment. Flexible foraging by fish has been previously reported (Abrahams and Dill 1989; Ryer and Olla 1992, 1995; Hill et al. 2002; Mittlebach 2002), in particular, work with juvenile walleye Pollock (*Theragra chalcagramma*) showed that fish exposed to clumped food or dispersed food for four weeks adjusted their foraging behaviour by increasing and decreasing their use of social information respectively (Ryer and Olla 1995). In our experiments, fish could only see a food item when they swam over it or whilst a conspecific was handling it. We are aware that the fish would likely be able detect the food via olfactory cues in the arena, but considering the density of the food, it would be unlikely fish were able to use olfactory cues alone to precisely locate the food (Webster et al. 2007). Moreover, fish never made strong directional movements towards a food item until they were within the patch itself. Seemingly then, fish in this environment could swim around monitoring other conspecifics whilst individually searching for food and opportunistically eating food items when they became aware of them, either from an unoccupied patch or from an occupied patch. It is important to note, however, that fish did not always eat a food item when they swam over it. It is not known whether this is because they did not see the food item, however, it is not because the fish ignored the food item due to satiation as often they would subsequently join and eat from a patch where conspecifics were feeding.

Overall, we have shown that fishes' allocation to alternative foraging strategies can be explained by environmental quality (patch size) (reduced finder's share: (Giraldeau et al. 1990; Giraldeau and Livoreil 1998)), resulting in larger group sizes on the patches in these environments. However, each tactic does not result in equal foraging returns, instead payoffs for finding are greater in all the scenarios we investigated. Based on our set of experiments we suggest two areas where we believe considerable progress in social foraging theory can be made using this fish system. First, considering the increased use of three-spine stickleback in social learning theory (Laland et al. 2011) we suggest that future experiments explore how joining behaviour affects social learning (Giraldeau and Caraco 2000; Caldwell and Whiten 2003; Humle and Snowdon 2008; Thornton and Malapert 2009; Ilan et al. 2013). Second, fine-scale tracking of multiple agents should allow for empirical tests of how spatial properties and approximations of the fish's field of view (Strandburg-Peshkin et al. 2013) affect tactic use and finder's advantage (Giraldeau et al. 1990; Barta et al. 1997; Di Bitetti and Janson 2001; Mathot and Giraldeau 2008; Beauchamp 2013). In conclusion, we have shown empirically that three-spine sticklebacks flexibly and adaptively switch between behavioural tactics to acquire foraging resources in accordance with the abundance and distribution of forage in their environment, establishing a new model system to extend and build our understanding of social foraging dynamics and how animal groups optimally function in a variable world.

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Compliance with Ethical Standards

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Ethics approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed, and experiments were approved by Swansea University Ethics Committee (Reference IP-1213-3).

References

Abrahams MV, Dill LM (1985) A determination of the energetic equivalence of the risk of predation. Ecology 70:999-107

Afshar M, Giraldeau L-A (2014) A unified modelling approach for producer-scrounger games in complex ecological conditions. Anim Behav 96:167-176

Afshar M, Hall CL, Giraldeau L-A (2015) Zebra finches scrounge more when patches vary in quality: experimental support of the linear operator learning rule. Anim Behav 105:181-186

Aplin LM, Farine DR, Mann RP, Sheldon BC (2014) Individual-level personality influences social foraging and collective behaviour in wild birds. Proc R Soc B 281:20141016

Aplin L, Farine D, Morand-Ferron J, Cole E, Cockburn A, Sheldon B (2013) Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). Ecol Lett 16:1365-1372

Aplin L, Farine D, Morand-Ferron J, Sheldon B (2012) Social networks predict patch discovery in a wild population of songbirds. Proc R Soc Lond B 279:4199-4205

Barnard CJ, Sibly RM (1981) Producers and scroungers: a general model and its application to captive flocks of house sparrows. Anim Behav 29:543-550

Barta Z, Flynn R, Giraldeau L-A (1997) Geometry for a selfish foraging group: a genetic algorithm approach. Proc R Soc Lond B 264:1233-1238

Barta Z, Giraldeau L-A (1998) The effect of dominance hierarchy on the use of alternative foraging tactics: a phenotype-limited producing-scrounging game. Behav Ecol Sociobiol 42:217-223

Barta Z, Giraldeau L-A (2001) Breeding colonies as information centers: a reappraisal of information-based hypotheses using the producer—scrounger game. Behav Ecol 12:121-127

Bates D, Mächler M, Bolker B, Walker S (2014) Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:14065823

Beauchamp G (2001) Consistency and flexibility in the scrounging behaviour of zebra finches. Can J Zool 79:540-544

Beauchamp G (2004) On the use of public information by social foragers to assess patch quality. Oikos 107:206-209

Beauchamp G (2008) A spatial model of producing and scrounging. Anim Behav 76:1935-1942

Beauchamp G (2013) Social predation: how group living benefits predators and prey. Elsevier, London.

Beauchamp G (2014) A field investigation of scrounging in semipalmated sandpipers. Behav Ecol Sociobiol 68:1473-1479

Bicca-Marques JC, Garber PA (2004) Use of spatial, visual, and olfactory information during foraging in wild nocturnal and diurnal anthropoids: a field experiment comparing *Aotus*, *Callicebus*, and *Saguinus*. Am J Primatol 62:171-187

Bugnyar T, Kotrschal K (2002) Scrounging tactics in free-ranging ravens, *Corvus corax*. Ethology 108:993-1009

Caldwell CA, Whiten A (2003) Scrounging facilitates social learning in common marmosets, *Callithrix jacchus*. Anim Behav 65:1085-1092

Caraco T (1981) Risk-sensitivity and foraging groups. Ecology 62:527-531

Caraco T, Giraldea L-A (1991) Social foraging: producing and scrounging in a stochastic environment. J Theor Biol 153:559-583

Carter A, Goldizen A, Heinsohn R (2012) Personality and plasticity: temporal behavioural reaction norms in a lizard, the Namibian rock agama. Anim Behav 84:471-477

Clark CW, Mangel M (1984) Foraging and flocking strategies: information in an uncertain environment. Am Nat 123: 626-641

Clark CW, Mangel M (1986) The evolutionary advantages of group foraging. Theor Popul Biol 30:45-75

Coolen I, Giraldeau L-A, Lavoie M (2001) Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. Anim Behav 61:895-903

Croft DP, James R, Krause J (2008) Exploring animal social networks. Princeton University Press, Princeton

Croft DP, Krause J, Darden SK, Ramnarine IW, Faria JJ, James R (2009) Behavioural trait assortment in a social network: patterns and implications. Behav Ecol Sociobiol 63:1495-1503

Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. Trends Ecol Evol 20:187-193

Di Bitetti MS, Janson CH (2001) Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. Anim Behav 62:47-56

Dubois F, Giraldeau L-A (2007) Food sharing among retaliators: sequential arrivals and information asymmetries. Behav Ecol Sociobiol 62:263-271

Dubois F, Giraldeau L-A, Réale D (2012) Frequency-dependent payoffs and sequential decision-making favour consistent tactic use. Proc R Soc Lond B 279:1977-1985

Fürtbauer I, Pond A, Heistermann M, King, AJ (2015) Personality, plasticity and predation: linking endocrine and behavioural reaction norms in stickleback fish. Funct Ecol 29:931-940

Gill AB, Hart PJB (1996) How feeding performance and energy intake change with a small increase in the body size of the three-spined stickleback. J Fish Biol 48:878-890

Giraldeau L-A (1984) Group foraging: the skill pool effect and frequency-dependent learning. Am Nat 124:72-79

Giraldeau L-A, Caraco T (2000) Social foraging theory. Princeton University Press, Princeton

Giraldeau L-A, Dubois F (2008) Social foraging and the study of exploitative behavior. Adv Stud Behav 38:59-104

Giraldeau LA, Hogan JA, Clinchy MJ (1990) The payoffs to producing and scrounging: what happens when patches are divisible? Ethology 85:132-146

Giraldeau L-A, Livoreil B (1998) Game theory and social foraging. In: Dugatkin LA, Reeve HK (eds) Game theory and animal behavior, 1st edn. Oxford University Press, New York, pp 16-37Hamilton IM, Dill LM (2003) Group foraging by a kleptoparasitic fish: a strong inference test of social foraging models. Ecology 84:3349-3359

Held SD, Byrne RW, Jones S, Murphy E, Friel M, Mendl MT (2010) Domestic pigs, *Sus scrofa*, adjust their foraging behaviour to whom they are foraging with. Anim Behav 79:857-862

Hill S, Burrows MT, Hughes RN (2002) Adaptive search in juvenile plaice foraging for aggregated and dispersed prey. J Fish Biol 61: 1255-1267

Humle T, Snowdon CT (2008) Socially biased learning in the acquisition of a complex foraging task in juvenile cottontop tamarins, *Saguinus oedipus*. Anim Behav 75:267-277

Ilan T, Katsnelson E, Motro U, Feldman MW, Lotem A (2013) The role of beginner's luck in learning to prefer risky patches by socially foraging house sparrows. Behav Ecol: 24:843-850

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

Katsnelson E, Motro U, Feldman MW, Lotem A (2008) Early experience affects producer–scrounger foraging tendencies in the house sparrow. Anim Behav 75:1465-1472

King AJ, Clark FE, Cowlishaw G (2011) The dining etiquette of desert baboons: the roles of social bonds, kinship, and dominance in co-feeding networks. Am J Primatol 73:768-774

King AJ, Isaac NJ, Cowlishaw G (2009) Ecological, social, and reproductive factors shape producer–scrounger dynamics in baboons. Behav Ecol 20:1039-1049

Koops MA, Giraldeau L-A (1996) Producer–scrounger foraging games in starlings: a test of rate-maximizing and risk-sensitive models. Anim Behav 51:773-783

Krause J, Lusseau D, James R (2009) Animal social networks: an introduction. Behav Ecol Sociobiol 63:967-973

Kurvers RHJM, Hamblin S, Giraldeau L-A (2012) The effect of exploration on the use of producer-scrounger tactics. PLoS ONE 7:e49400

Kurvers RHJM, Prins HHT, van Wieren SE, van Oers K, Nolet BA, Ydenberg RC (2010) The effect of personality on social foraging: shy barnacle geese scrounge more. Proc R Soc Lond B 277:601-608

Laland KN, Atton N, Webster MM (2011) From fish to fashion: experimental and theoretical insights into the evolution of culture. Philos T Roy Soc b 366:958-968

Liker A, Barta Z (2002) The effects of dominance on social foraging tactic use in house sparrows. Behaviour 139:1061-1076

Mathot KJ, Giraldeau L-A (2008) Increasing vulnerability to predation increases preference for the scrounger foraging tactic. Behav Ecol 19:131-138

Mathot KJ, Giraldeau L-A (2010) Within-group relatedness can lead to higher levels of exploitation: a model and empirical test. Behav Ecol 21:843-850

Mathot KJ, Godde S, Careau V, Thomas DW, Giraldeau L-A (2009) Testing dynamic variance-sensitive foraging using individual differences in basal metabolic rates of zebra finches. Oikos 118:545-552

McCormack JE, Jablonski PG, Brown JL (2007) Producer-scrounger roles and joining based on dominance in a free-living group of Mexican jays (*Aphelocoma ultramarina*). Behaviour 144:967-982

Milinski M (1988) Games fish play: making decisions as a social forager. Trends Ecol Evol 3:325-330

Mittlebach G (2002) Fish foraging and habitat choice: a theoretical perspective. In: Hart P, Reynolds J (eds) Handbook of Fish Biology and Fisheries, 1st edn. Blackwell Publishing Ltd, Oxford, UK, pp 251-266

Morand-Ferron J, Giraldeau L-A (2010) Learning behaviorally stable solutions to producer–scrounger games. Behav Ecol 21:343-348

Morand-Ferron J, Giraldeau L-A, Lefebvre L (2007) Wild Carib grackles play a producer–scrounger game. Behav Ecol 18:916-921

Morand-Ferron J, Varennes E, Giraldeau L-A (2011a) Individual differences in plasticity and sampling when playing behavioural games. Proc R Soc Lond B 278:1223-1230

Morand-Ferron J, Wu G-M, Giraldeau L-A (2011b) Persistent individual differences in tactic use in a producer–scrounger game are group dependent. Anim Behav 82:811-816

Mottley K, Giraldeau L-A (2000) Experimental evidence that group foragers can converge on predicted producer–scrounger equilibria. Anim Behav 60:341-350

Ólafsdóttir GÁ, Andreou A, Magellan K, Kristjánsson BK (2014) Divergence in social foraging among morphs of the three-spined stickleback, *Gasterosteus aculeatus*. Biol J Linn Soc 113:194-203

Overington SE, Dubois F, Lefebvre L (2008) Food unpredictability drives both generalism and social foraging: a game theoretical model. Behav Ecol 19:836-841

Pfeffer K, Fritz J, Kotrschal K (2002) Hormonal correlates of being an innovative greylag goose, *Anser anser*. Anim Behav 63:687-695

Ranta E, Juvonen SK (1993) Interference affects food-finding rate in schooling sticklebacks. J Fish Biol 43:531-535

Ranta E, Rita H, Lindström K (1993) Competition versus cooperation: success of individuals foraging alone and in groups. Am Nat 142:42-58

Ruxton G, Hall S, Gurney W (1995) Attraction toward feeding conspecifics when food patches are exhaustible. Am Nat 145:653-660

Ryer CH, Olla BL (1992) Social mechanisms facilitating exploitation of spatially variable ephemeral food patches in a pelagic marine fish. Anim Behav 44:69-74

Ryer CH, Olla BL (1995) Influences of food distribution on fish foraging behaviour. Anim Behav 49:411-418

Stahl J, Tolsma PH, Loonen MJ, Drent RH (2001) Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. Anim Behav 61:257-264

Strandburg-Peshkin A, Twomey CR, Bode NW, Kao AB, Katz Y, Ioannou CC, Rosenthal SB, Torney CJ, Wu HS, Levin SA (2013) Visual sensory networks and effective information transfer in animal groups. Curr Biol 23:R709-R711

Thornton A, Malapert A (2009) Experimental evidence for social transmission of food acquisition techniques in wild meerkats. Anim Behav 78:255-264

Tóth Z, Bókony V, Lendvai ÁZ, Szabó K, Pénzes Z, Liker A (2009) Effects of relatedness on social-foraging tactic use in house sparrows. Anim Behav 77:337-342

Vickery WL, Giraldeau L-A, Templeton JJ, Kramer DL, Chapman CA (1991) Producers, scroungers, and group foraging. Am Nat 137:847-863

Waltz EC (1982) Resource characteristics and the evolution of information centers. Am Nat 119:73-90

Ward AJW, Thomas P, Hart PJB, Krause J (2004) Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). Behav Ecol Sociobiol 55:561-568

Ward AJ, Webster MM, Hart PJB (2006) Intraspecific food competition in fishes. Fish Fish 7:231-261

Webster MM, Atton N, Ward AJW, Hart PJB (2007) Turbidity and foraging rate in threespine sticklebacks: the importance of visual and chemical prey cues. Behaviour 144: 1347-1360

Webster MM, Hart PJB (2006) Subhabitat selection by foraging threespine stickleback (*Gasterosteus aculeatus*): previous experience and social conformity. Behav Ecol Sociobiol 60:77-86

Webster MM, Laland K (2009) Evaluation of a non-invasive tagging system for laboratory studies using three-spined sticklebacks *Gasterosteus aculeatus*. J Fish Biol 75:1868-1873

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

Figure Legends

Fig 1 Experimental set-up. (a) Still-shot from experimental video of two arenas each with, individually marked fish (n=6) and (b) view of the experimental arenas and filming setup. (c) Shows the four experimental arenas and distribution of bloodworms in each of the 4 treatments: large and clumped (LC), large and dispersed (LD), small and clumped (SC) and small and dispersed (SD)

Fig 2 Boxplot representing the finder's share for the groups (n=7) in the large patch and small patch treatments. Finders share = a/F, where a = finder's advantage, that is, the difference in amount of food items eaten when an individual finds and when it joins, and F = number of food items (Giraldeau & Caraco (2000). Boxes represent first and third quartiles and whiskers extend to the highest value that is within 1.5 times the inter-quartile range. The dot point represents an outlier observation, a data point outside the whiskers

Table Legends

Table 1 Definitions of behavioural tactics

Table 2 Descriptive statistics of the number of bloodworms eaten by finding (F) and joining (J) for each group in each treatment

Table 3 The effect of patch size and distribution on (a) the percent of total events that were 'finding events', (b) the proportion of 'joining' events that were steals, and (c) the effect of size and distribution treatments on mean group size on patches. The reference category for patch size was 'large' and the reference category for patch distribution was 'dispersed'. All results are estimated from linear mixed models. Group and fish identity were fitted as random effects. Significant p-values are presented in bold

Table 4 The effect of tactic; 'finding event' (F; reference category) or 'joining event' (J), and weight on the event payoff (number of bloodworms consumed) as estimated from a generalised linear mixed model. Separate models were run on the for the (a) small patch treatment and (b) the large patch treatment. Group and fish identity were fitted as random effects. Significant p-values are presented in bold

Table 1

Tactic	Success	Description of behaviour
Finding	Successful	-Focal fish enters an unoccupied patch and ingests ≥ 1 bloodworm
	Failed	-Focal fish enters an unoccupied patch and does not ingest a bloodworm, i.e. pecks at it or spits worm out
Joining	Successful	-Focal fish enters an occupied patch and ingests ≥ 1 bloodworm
		-Focal fish steals a worm out of a conspecifics mouth
		-Focal fish ingests a worm spat out by a conspecific
	Failed	-Focal fish enters an occupied patch and does not ingest a bloodworm, i.e. pecks at it or spits worm out
		-Focal fish attempts to steal a bloodworm from a conspecific but does not ingest it
		-Focal fish attempts to ingest a bloodworm spat out by a conspecific but does not ingest it

Table 2

Number of Bloodworms Eaten												
	Small						**Large**					
	Clumped			**Dispersed**			**Clumped**			**Dispersed**		
Group	**F**	**J**	**Total**	**F**	**J**	**Total**	**F**	**J**	**Total**	**F**	**J**	**Total**
A	16	2	18	13	5	18	22	19	41	29	18	47
B	12	6	18	15	3	18	12	18	30	19	21	40
C	11	3	14	11	7	18	27	20	47	19	25	44
D	9	9	18	12	6	18	14	21	35	24	16	40
E	12	6	18	10	8	18	27	13	40	16	22	38
F	13	5	18	12	6	18	15	16	31	8	21	29
G	10	8	18	11	7	18	18	9	27	19	9	28
Mean	11.86	5.57	17.43	12.00	6.00	18.00	19.29	16.57	35.86	19.14	18.86	38.00
StDev	2.28	2.51	1.51	1.63	1.63	0.00	6.16	4.28	7.13	6.52	5.21	7.14
Min	9	2	14	10	3	18	12	9	27	8	9	28
Max	16	9	18	15	8	18	27	21	47	29	25	47
Range	7	7	4	5	5	0	15	12	20	21	16	19

Table 3

<table>
<tr><td colspan="6">(a) Percentage 'finding events'</td></tr>
<tr><th></th><th>Estimate</th><th>Standard Error</th><th>DF</th><th>t-value</th><th>Pr (>|t|)</th></tr>
<tr><td>(Intercept)</td><td>45.48</td><td>3.57</td><td>131.67</td><td>12.74</td><td></td></tr>
<tr><td>Patch Size</td><td>12.51</td><td>3.78</td><td>121.19</td><td>3.31</td><td><0.002</td></tr>
<tr><td>Patch Distribution</td><td>-4.10</td><td>3.78</td><td>121.27</td><td>-1.08</td><td>0.280</td></tr>
<tr><td colspan="6">(b) Percentage joining events that were ‘steals’</td></tr>
<tr><th></th><th>Estimate</th><th>Standard Error</th><th>DF</th><th>t-value</th><th>Pr (>|t|)</th></tr>
<tr><td>(Intercept)</td><td>0.67</td><td>0.13</td><td>49.1</td><td>5.03</td><td></td></tr>
<tr><td>Patch Size</td><td>-0.13</td><td>0.06</td><td>111.02</td><td>-2.25</td><td>0.026</td></tr>
<tr><td>Patch Distribution</td><td>0.11</td><td>0.06</td><td>112.41</td><td>1.95</td><td>0.053</td></tr>
<tr><td>Fish weight</td><td>-0.17</td><td>0.11</td><td>41.74</td><td>-1.50</td><td>0.142</td></tr>
<tr><td colspan="6">(c) Mean group size on patches</td></tr>
<tr><th></th><th>Estimate</th><th>Standard Error</th><th>DF</th><th>t-value</th><th>Pr (>|t|)</th></tr>
<tr><td>(Intercept)</td><td>1.77</td><td>0.06</td><td>13.9</td><td>28.31</td><td></td></tr>
<tr><td>Patch Size</td><td>-0.17</td><td>0.09</td><td>1019.2</td><td>-2.01</td><td>0.030</td></tr>
<tr><td>Patch Distribution</td><td>0.09</td><td>0.06</td><td>1023.5</td><td>1.51</td><td>0.130</td></tr>
</table>

Table 4

(a) The event payoff in the small patch treatment				
	Estimate	**Standard Error**	**z-value**	**Pr (>|z|)**
(Intercept)	0.03	0.30	0.11	
F or J	-0.48	0.14	-3.55	**<0.001**
Weight	0.10	0.24	0.43	0.669
(b) The event payoff in the large patch treatment				
	Estimate	**Standard Error**	**z-value**	**Pr (>|z|)**
(Intercept)	-0.70	0.24	-2.88	
F or J	-0.25	0.09	-2.87	**<0.005**
Weight	0.36	0.18	2.00	**0.046**

Figures

Figure 1:

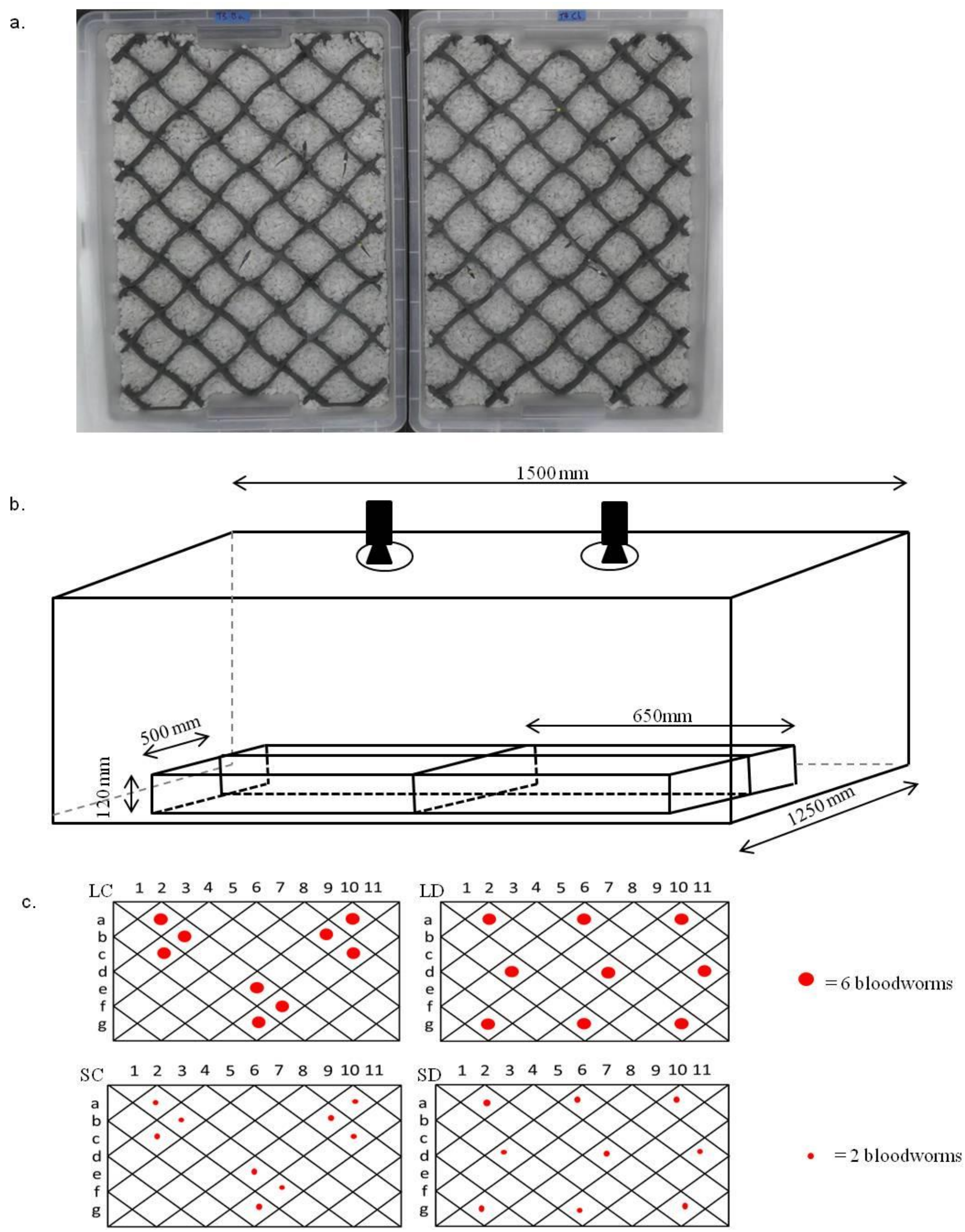
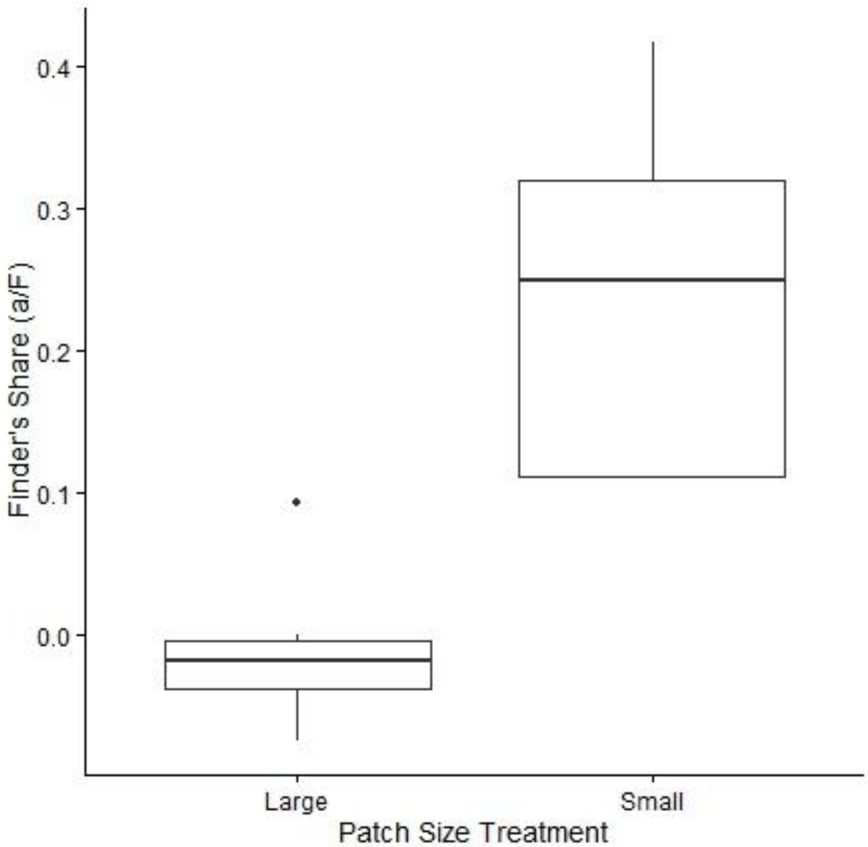


Figure 2:



0.4
0.3
0.2
0.1
0.0
Finder's Share (a/F)
Large
Small
Patch Size Treatment