Social learning enhances search image acquisition in foraging brook trout

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Abstract Brook trout feed primarily on prey items for which they have developed a search image. Periodically, fish are required to update their search images to match temporal variability in prey abundance. It is currently unknown how brook trout develop search images, but there is evidence to suggest that it could be influenced by social learning, wherein a fish learns a novel behavior through observation alone. Here we demonstrate that adult brook trout use social learning to quickly develop search images for novel prey. We trained a set of demonstrators to develop a search image for canned mealworms and subsequently moved demonstrators to treatment pools that contained naïve bystanders. We also had control pools that contained naïve bystanders and sham demonstrators that had not been trained on mealworms. Over an 8-day period, bystanders in treatment pools consumed 68 % of mealworms, compared to only 36 % in control pools. Moreover, social learning of search images was rapid as bystanders in treatment pools began feeding on mealworms in less than 1 day, whereas it took 7 days for bystanders in control pools to feed heavily on mealworms. Social learning of search images confers an adaptive advantage by reducing energetic costs of foraging.

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Introduction

The process by which a predator develops a preference for novel prey is referred to in general ecological literature as 'search image acquisition' (Pyke 1984). The term has been applied to drift-feeding salmonids (Ware 1971; Ringler 1979) to describe the situation where fish will not accept novel, nutritious, prey until it has been presented repeatedly (Bannon and Ringler 1986; Brown and Laland 2001). We use the term 'search image' in that context.

It is presently unknown how trout develop a search image, but there is evidence to suggest that social learning can be involved (Gowan 2007; Warburton and Hughes 2011). Social learning is the acquisition of information or behaviors through observation of others (Brown and Laland 2003). Because social learning is through observation, energetic costs to the individual are low (Laland et al. 2003; Oliveira 2012). Furthermore, social learning allows multiple types of information to be gathered simultaneously (Reader et al. 2003), thereby expediting the development and discovery of new behaviors (Galef and Laland 2005; Ward et al. 2012). Social learning was once thought restricted to higher-order vertebrates, but it has been demonstrated that many fish species use social learning to recognize predators (Kelley and Magurran 2003; Griffin 2004), select a mate (Brown and Laland 2003), determine conspecific rival rank (Grosenick et al. 2007; White and Gowan 2013), and select optimal habitat locations (Reader et al. 2003).

Social learning of foraging behavior in fishes has been fairly well documented in several species (Brown and Laland 2003; Brown et al. 2011), but all studies to date have been in laboratories (Warburton and Hughes 2011). Furthermore, all studies of salmonids have involved hatchery-reared juveniles (Suboksi and Templeton 1989; Brown and Laland 2001; Sundström and Johnsson 2001). Together, these studies provide evidence that naïve fish readily learn about novel prey sources from trained demonstrators. However, it is still unknown if social learning operates in the wild, and whether dietary preference of adult salmonids can be influenced by social learning (Brown and Laland 2003; Galef and Laland 2005).

The objective of this study was to determine if wild adult brook trout (*Salvelinus fontinalis)* use social learning to develop search images for novel prey items. For 10 days, we trained a set of demonstrators to develop a search image for canned mealworms. We then relocated those trained demonstrators to treatments pools and placed untrained sham demonstrators in control pools, and documented the length of time it took naïve bystanders in treatment and control pools to develop a search image for mealworms.

Methods

Study area

The study was completed at Fridley Run, a second-order mountain stream located in the George Washington National Forest in Virginia. Our study area included 14 pools (two for training demonstrators and 12 to serve as treatments and controls) in a 1,220-m-long stream reach.

On 24 June 2008, we collected fish from each pool using multiple-pass backpack electrofishing with blocknets installed at the upstream and downstream ends of each pool. Fish were anesthetized using MS-222 and fish ≥125 mm total length (i.e. adults, Hudy et al. 2010) were tagged with colored ribbon tags unique to each fish (see Gowan and Fausch 2002 for details). Feeding behavior of marked and unmarked fish was monitored from permanent streambank blinds installed in locations that allowed the observer to enter the blind without disturbing fish.

Throughout the study, we used specially designed feeders (see Gowan (2007)) to deliver a novel prey source: canned mealworms sold commercially as reptile food (Zoo Med Laboratories, San Luis Obispo, CA, USA). Mealworms weighed an average of 0.96 g (SE=0.002) each and provided 490 J (SE=0.75) of energy, which was an order of magnitude more than typical prey items found in mountain streams (Gowan 2007). Thus, once a fish developed a search image for mealworms, it tended to exploit that prey preferentially over natural prey. Feeders were designed to deliver one mealworm every 5 min.

Demonstrator training

Demonstrator training lasted from 30 June to 15 July and occurred in two pools, each of which contained three feeders. We monitored fish feeding behavior daily to determine the number of mealworms each individual fish consumed. At the end of this training period, over 65 % of mealworms were being consumed, and so we assumed all fish in the training pools had developed search images and thus could be used as knowledgeable demonstrators (this turned out not to be the case, as described later).

On 17 July, we re-captured fish from the two training pools and three demonstrators were transplanted into each of six randomly selected treatment pools. Twelve untrained fish (sham demonstrators) were captured from pools not included in the study, tagged, and two were transplanted into each of the remaining pools to serve as controls.

Although treatment and control pools were randomly assigned, the specific demonstrators placed into each pool were not. In order for demonstrators to provide social information to bystanders, they had to be large enough to defend territory, but not large enough to dominate all fish and block access to feeders even after other fish had developed a search image. Therefore, the largest transferred fish was always the third or fourth largest fish in the pool. The average size of bystanders was 172.60 mm (SE=6.65) and demonstrators 177.20 mm (SE=10.60).

Bystander testing

One feeder was installed in each treatment and control pool and turned on 24 h after demonstrators were transplanted to the pool. From 19 July to 25 July, each pool was observed for 1 h in the morning and in the afternoon, with the order of observations randomized each day. During each observation period, the number

of mealworms consumed by each fish in the pool was quantified. A mealworm was considered uneaten if it floated out of the pool or sunk to the bottom because we never saw fish take mealworms from the substrate.

Data analysis

The original experimental design was balanced with six treatment pools and six control pools. However, some intended knowledgeable demonstrators did not feed on mealworms after being transferred to treatment pools (these were always subordinate fish during the training period that apparently did not develop a search image), and several knowledgeable demonstrators moved out of treatment pools immediately after transplanting. Moreover, some intended bystanders moved out of the study reach altogether. As a result, we established the criteria that true treatment pools had to contain at least one knowledgeable demonstrator that fed on mealworms shortly after transplanting and remained in the pool for at least 5 days, and at least one bystander. Control pools had to have at least one sham demonstrator that stayed in the pool, one bystander, and must not have ever contained a knowledgeable demonstrator. Based on these criteria, we determined that three pools received knowledgeable demonstrators and five pools received sham demonstrators. The treatment pools contained an average of 6.60 bystanders (SE=1.69) and control pools contained an average of 9.00 bystanders (SE=1.45). Two treatment pools had four demonstrators, and one treatment pool had two demonstrators. After the initial movement of demonstrators, the composition of pools remained largely constant throughout the study.

If search images were acquired via social learning, we would expect more mealworms to be taken by bystanders in treatment pools with knowledgeable demonstrators than by bystanders in control pools with sham demonstrators. To test this hypothesis, we modeled the percentage of mealworms that were either taken or competed for by bystanders in treatment and control pools on each date. For each pool ($n=3$ treatment pools and $n=5$ control pools) for each day, we calculated the percentage of all worms taken or competed for by bystanders, and used these values as the dependent variable in the analysis. We considered a bystander to have competed for a worm if it charged the worm simultaneously with one or more other fish,

but did not get the worm. The independent variables used to construct the model were date and treatment. The model was a generalized estimating equation (GEE), which uses a semiparametric approach to analyze non-normal data collected with repeated-measures (Liang and Zeger 1986). The percentage of mealworms (arcsine square root transformed) consumed or competed for by bystanders was modeled using a Gaussian distribution with identity link and an autoregressive correlation structure. Due to low samples sizes, we also used a jackknife variance estimator. Significance of the independent variables was tested using a type-III Wald chi-square statistic with $\alpha=0.05$. All analyses were completed with the R v2.14 statistical programing language (R Development Core Team 2012) using functions from packages geepack (Halekoh et al. 2006) and car (Fox and Weisberg 2011).

To better understand how social learning in treatment pools occurred, we analyzed the percentage of mealworms consumed by bystanders compared to knowledgeable demonstrators over time. We expected that initially demonstrators would consume more mealworms, but that, as the larger bystanders developed a search image, they would outcompete demonstrators for worms. To test this hypothesis, we modeled the percentage of mealworms consumed by bystanders and demonstrators in treatment pools over time using the same methods detailed above.

Results

During testing, bystanders in treatment pools consumed or competed for an average of 68.3 % (SE=5.3) of mealworms, which was significantly higher than the 35.7 % (SE=9.8) of mealworms consumed or competed for by bystanders in control pools ($X^2=8$, d.f.=1, $p=0.005$). There was also an effect of date ($X^2=209$, d.f.=7, $p<0.001$). These effects were attributable to bystanders in treatment pools immediately consuming high percentages of mealworms, but those in control pools not consuming mealworms at a high rate until the seventh day of testing (Fig. 1). In treatment pools, the larger bystanders began taking more mealworms than the smaller demonstrators after 1 day, and continued to take a higher percentage of mealworms thereafter ($X^2=13.0$, d.f.=1, $p=0.003$). The exception was 23 July when a heavy storm interrupted normal foraging (Fig. 2).

Discussion

Foraging brook trout used social learning to develop search images. Over 7 days, bystanders in the presence of a knowledgeable demonstrator took almost twice as many mealworms as bystanders with only an untrained, sham demonstrator. In addition, bystanders with a knowledgeable demonstrator developed search images in less than a day, whereas bystanders without a knowledgeable demonstrator took about 7 days. In total, this indicates that feeding behavior and prey preference can be transmitted socially in wild, adult brook trout, and the time required for information transfer is less than 1 day.

It has been suggested that salmonids are opportunistic foragers that consume different prey in proportion to relative abundance (Syrjänen et al. 2011), and therefore feed primarily on the most abundant prey species (Elliott 1973; Allan 1981; Johnson et al. 2007). If so, then search image acquisition is not an important part of the foraging process. However, by using a completely novel prey item and monitoring fish daily, we show that salmonids do not immediately switch to novel prey, even when the new prey are conspicuous and abundant. We interpret this behavior to indicate trout must develop a search image for new prey, and that the process can be accelerated through social learning.

Social learning has theoretically and empirically been shown to confer an adaptive advantage (Galef and Laland 2005). Asocial learning requires individuals to personally sample the environment in an attempt to find
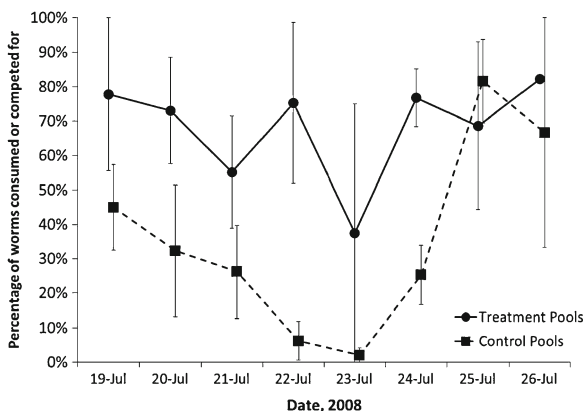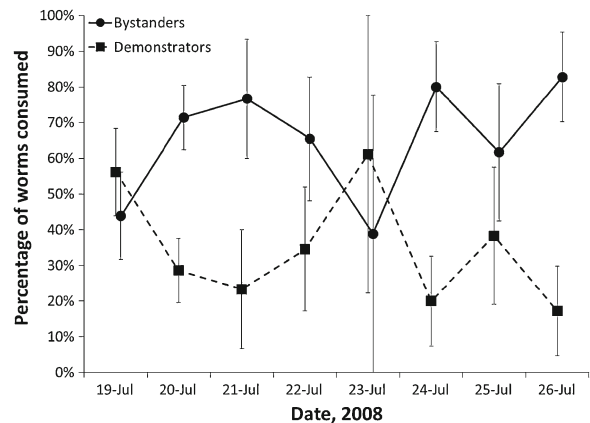

Fig. 2 Percentage of consumed mealworms taken by bystanders (*solid line*) and demonstrators (*dashed line*) in three treatment pools during the 8-day testing period. *Error bars* represent ±1 SE

the most advantageous behavior, a discovery that may never be realized in temporally-variable environments (Magnhagen and Staffan 2003; Laland 2004; Galef and Laland 2005). With social learning, individuals bypass a potentially lengthy trial-and-error process and move directly to profitable behaviors (Brown and Laland 2003; Ward et al. 2012). The result is decreased predation risk, less energy devoted to searching for food, and more time feeding (Suboksi and Templeton 1989; Brown and Laland 2001; Webster and Laland 2012).

Bystanders in control pools took 6 days longer to develop a search image for mealworms than bystanders in treatment pools, meaning that bystanders in control pools did not exploit a highly profitable food source even when it had been continuously available for nearly a week. This lag period could be very consequential in the wild because trout in Appalachian streams are food-limited with positive growth restricted to a brief period between late May and early July (Ensign et al. 1990; Utz and Hartman 2009). As such, failure to capitalize on energy-rich prey even for just a few days during the critical growth period could decrease survival and lifetime growth and reproduction (Hughes et al. 1992).

Social learning involved more than simply development of a search image. It also influenced foraging location, as bystanders moved to the feeders once they developed a search image, and it involved a change in dietary preference because fish began focusing on mealworms to the exclusion of other prey. We demonstrate these effects for the first time in the wild (Warburton and Hughes 2011) where the availability of natural prey and

Fig. 1 Percentage of worms either consumed or competed for by bystanders in treatment (*solid line*; *n*=3) and control pools (*dashed line*; *n*=5) during the 8-day testing period. *Error bars* represent ±1 SE

other variables could have hindered the ability of a fish to learn. Along with Gowan (2007) and White and Gowan (2013), this study suggests that social learning is a major mechanism of information transfer among trout in size-mediated dominance hierarchies.

The adaptive significance of social learning is best considered in the context of fish movement. Population models that incorporate stream-fish movement make what had seemed to be the over-simplified assumption that trout moving to a new pool bear no energetic cost when evaluating their position in the dominance hierarchy and locating energetically profitable foraging locations (Railsback et al. 1999; Gowan and Fausch 2002; Railsback and Harvey 2002). But, results of our study indicate that the assumption may be largely valid because trout use low-cost social learning to quickly locate novel prey and determine dominance status (White and Gowan 2013). As such, because social learning lowers the cost of movement, the adaptive advantages of moving (including finding better foraging locations and colonizing new habitats) are increased. This may explain why some populations of brook trout contain many mobile individuals (Gowan and Fausch 1996).

An individual's behavior is derived asocially via genetics and personal experience and socially via observation of conspecifics (Hughes et al. 1992; Galef and Laland 2005). No one individual has the behavioral repertoire necessary for responding to all possible environmental conditions. However, the population as a unit has a much larger suite of adaptive behaviors, and movement of individuals disseminates information across the landscape. As such, fish movement is the vehicle through which behaviors are transferred, via social learning, from the individual to the population.

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