

Foraging innovation is inversely related to competitive ability in male but not in female guppies

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Foraging success is likely to affect hunger level and motivation to locate and exploit novel food sources in animals. We explored the relationship between scramble competition for limited food and foraging innovation in the guppy (*Poecilia reticulata*), predicting that poor competitors would be more likely to innovate when presented with novel foraging tasks. Among males, we found that latency to complete novel foraging tasks was correlated both with weight gain and number of food items consumed, suggesting that poor competitors are more likely to innovate. However, among females there was no relationship between innovative tendency and either weight gain or foraging success. We suggest that this sex difference may reflect parental investment asymmetries in males and females, and we predict similar sex differences in other species. *Key words*: animal proto-culture, foraging, guppies, innovation, *Poecilia reticulata*, scramble competition. [*Behav Ecol* 10:270–274 (1999)]

Animals often respond to novel ecological and social challenges, or physiological stresses, with new or modified acquired behavior patterns, or innovations (Kummer and Goodall, 1985; Lee, 1991). Innovation is an important component of behavioral plasticity, vital to the survival of individuals in species with generalist or opportunistic lifestyles (Lefebvre et al., 1997). Moreover, the diffusion of a new behavior through a population is typically thought to follow from the innovation of a single individual. However, despite being fundamental to several significant research programs, including those investigating foraging behavior, behavioral plasticity, and the social learning and transmission of information, little is known about which individuals form new behavior patterns or what ecological variables influence innovation (Kummer and Goodall, 1985; Lee, 1991). It is unclear whether animal innovation should be regarded as a personality trait (associated with particularly clever or creative individuals), a state-dependent variable (e.g., foraging innovation may be driven by hunger), or whether it results from exposure to pertinent ecological stimuli (e.g., a sudden change in the environment).

The best known examples of innovation in animal populations are novel behavior patterns that facilitate the extraction, preparation, and processing of food. These include the washing of potatoes and wheat by Japanese macaques, *Macaca fasciata*, tool use in chimpanzees, *Pan troglodytes*, and other primates, and milk-bottle-top opening by British titmice, *Parus* spp. (Beck, 1980; Frigaszy and Visalberghi, 1990; Goodall, 1964; Hinde and Fisher, 1951; Kawai, 1965; McGrew, 1994). Lefebvre et al. (1997) described 322 separate cases of feeding innovation in birds. In all such examples, a novel food source is used, or exploited more efficiently, as a result of the innovation. Other examples of innovation function in a social domain. For example, Goodall (1986) described a male chimpanzee that augmented his threat display by banging together

empty kerosene cans, a behavior that coincided with a dramatic rise in dominance status.

Although compelling evidence is scarce, observations of natural animal populations suggest that particular classes of individuals may be prone to innovation. There is at least anecdotal evidence that innovators often differ from the remainder of the group in some characteristic, such as rank, age, or sex. Katzir (1982, 1983) found that mid- to low-ranking jackdaws, *Corvus monedula*, were first to enter a novel space or eat a new food, with top-ranking birds typically being second or third. Primate studies appear to indicate that innovators are frequently on the outskirts of the social group (Kummer and Goodall, 1985). For instance, Sigg (1980) found that peripheral female hamadryas baboons, *Papio hamadryas hamadryas*, were significantly better at learning novel tasks than central females. In their review of novel tool use tasks among capuchins, Frigaszy and Visalberghi (1990) found no evidence for individuals possessing a “characteristic propensity” to show innovative behavior.

To date, virtually all of the relevant empirical data on innovation in animals stems from observations of natural populations. Inevitably such reports have an anecdotal quality. In several instances, the novel behavior has been observed only once, and in a single individual (Kummer and Goodall, 1985). Some behavior patterns are slightly idiosyncratic, and many such reports require clarification before it can be certain that the behavior concerned is more than a random or accidental event, or that it serves the function attributed to it. There are numerous experimental studies demonstrating that particular individuals, or species, are capable of solving a novel problem (Köhler, 1925; Tomasello et al., 1987; Visalberghi and Frigaszy, 1990); however, the majority of such experiments have not investigated within-species variation in problem-solving ability, and there are surprisingly few experimental studies of problem solving that focus on sex, age, or dominance-rank differences (Hutt, 1973).

We explored the hypothesis that hungry individuals or poor competitors may be driven by hunger to innovate to locate food by investigating the correlation between innovation and past foraging success in small populations of guppies. Guppies are an excellent model system for research into animal innovation. Social transmission of foraging information has

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been clearly demonstrated in guppies (Laland and Williams, 1997), and it would be valuable to establish which individuals are most likely to generate the foraging innovations. Social learning in guppies is also implied in other contexts, such as mate choice (Dugatkin and Godin, 1993) and avoidance learning (Sugita, 1980). In addition, guppies have been found to exhibit significant variation in the tendency to inspect unfamiliar predators (Magurran et al., 1993), which may reflect variation in a more general response to novel situations and thereby influence foraging innovation. For instance, if guppies exhibit variation in boldness or risk aversion, which is expressed in a number of different contexts, this variability might influence innovation to locate and exploit novel foods. Moreover, in addition to the substantial behavioral literature on guppies, they have a number of practical advantages: they are easy and inexpensive to keep in small populations as a consequence of their small size and simple feeding requirements. In the wild, the guppy feeds on several prey types in varied locations (Dussault and Kramer, 1981) and prefers to live in groups of conspecifics (Magurran et al., 1995). Our experimental paradigm imitates a scenario in which individuals move away from the shoal to locate a novel food source.

We predicted that those fish least successful at scramble competition would be the individuals most likely to innovate when presented with novel foraging tasks. We tested the hypothesis directly by (1) monitoring over a 2-week period the change in weight of individuals in two mixed-sex populations of guppies, (2) recording the success of each individual at scramble competition, and (3) introducing into each population novel maze tasks, recording each fish's time to complete the task. These tasks required subjects to swim a series of mazes to locate hidden food sources. We predicted that there would be a positive relationship between weight gain and time to innovate, as measured by the time taken to complete the novel foraging tasks. We also predicted that there would be a positive relationship between number of food items previously consumed in scramble competition and time to innovate.

METHODS

Subjects and apparatus

Our subjects were 32 adult guppies, 16 male and 16 female, purchased from Neil Hardy Aquatics. Subjects were chosen to represent a range of sizes, with females ranging in mass from 0.13 g to 1.14 g ($\bar{x} \pm SE = 0.57 \pm 0.07$ g) and males varying between 0.15 g and 0.58 g ($\bar{x} \pm SE = 0.35 \pm 0.04$ g). Female fish were thus significantly larger than males (t test: $t_{30} = 2.71$, $p < .025$). Domestic rather than wild guppies were used because their distinctive coloration allows recognition of individuals of both sexes while avoiding stressful marking procedures. We studied two populations to increase the power of the analysis.

Fish were housed in standard 60×30×33 cm aquaria, with a water depth of 30 cm, maintained at 25°C. Novel foraging tasks were presented to populations of fish by introducing the task apparatus into the aquaria. Each novel task involved swimming through a maze apparatus, placed 10 cm from the end of the tank, and into a goal zone containing a floating feeder. The mazes were opaque white PVC dividing partitions, each containing a hole through which the fish could swim to the other end of the tank. A partition 10 cm in front of the maze allowed the apparatus to be set up while excluding the fish, with the raising of this partition signifying the beginning of a trial. A second partition slid directly behind the maze, being pushed down completely to close the hole on the goal-zone side once a trial had ended. The goal zone contained a con-

cealed floating feeder of red plastic 30 mm in diameter and 6 mm deep. Small quantities (approximately four items) of freeze-dried bloodworm were placed in these feeders. For task 1, the maze apparatus was a partition with a 5×5 cm square, centrally located hole at the bottom of the tank. For task 2, the maze was a partition with a plastic, cylindrical, upright tunnel (height 6.5 cm, entrance diam 8 cm) covered in dark green cellophane in front of a square, centrally located 5×5 cm hole at the top of the partition. Here, the fish had to swim up the tunnel and then across through the hole to reach the food source. Dark green cellophane was used to cover the tunnel, as a see-through maze could confuse the fish. Guppies are not known to show any preference for or against the color green. For task 3, the maze apparatus in task two was turned upside down so that fish had to swim downward and then across through a hole at the bottom of the tank. These three tasks were designed to be of increasing difficulty.

Procedure

Subjects were separated into two populations of 16 fish, each with equal numbers of males and females, and a range of different sizes. We weighed each fish and noted its distinctive color markings so that it could be identified. For 14 days food items (a mixture of live bloodworm, *Chironomus* spp., freeze-dried bloodworm, or standard tropical fish flaked food) were dropped into the tanks in a manner designed to enhance scramble competition and to maximize variation in foraging success. This involved dropping food items individually, or in twos or threes, into the central region of the tank. When the food had been consumed, further food items were added in the same manner. Approximately 40 food items were given to each tank on each feed. During each feeding session only one food type was presented in order to minimize the opportunity for individuals to specialize on food types. We fed subjects in this manner three times daily, at 0900, 1300, and 1700 h. On days 10–14, subjects were fed exclusively on freeze-dried bloodworm because this food consisted of small but distinct items, each of which could only be eaten by a single fish. For this 5-day period, as a measure of competitive foraging ability, we recorded which fish ate each food item. After feeding was complete on the 14th day, we weighed all the fish again and recorded their change in weight over the 2-week period.

On days 15–17, at 0900 h, we presented subjects in the two populations with three innovation tests, one a day, and recorded the latency to complete the task for each fish. The maze apparatus was introduced into the tanks at the beginning of each trial and removed immediately after it had been completed. If all fish had not completed the task after 20 min had elapsed the trial was terminated, and unsuccessful fish were allocated this time. We summed the innovation times across the three tasks to minimize any confounding effects generated by completion of a maze by chance or by following another fish. During this 3-day period, once a day, at 1700 h, subjects were given further food items in the same manner as described above.

RESULTS AND DISCUSSION

The number of food items consumed during the 5-day monitoring period ranged from 7 to 87, this 12-fold difference demonstrating significant variation between individuals in foraging success. Similarly, weight change ranged from a loss of 0.04 g to a gain of 0.20 g. Foraging success correlated significantly with weight gain ($r = .476$, $p = .005$), indicating that success in scramble competition was indeed a major factor determining weight change. There was a significant correlation between initial mass and number of food items consumed

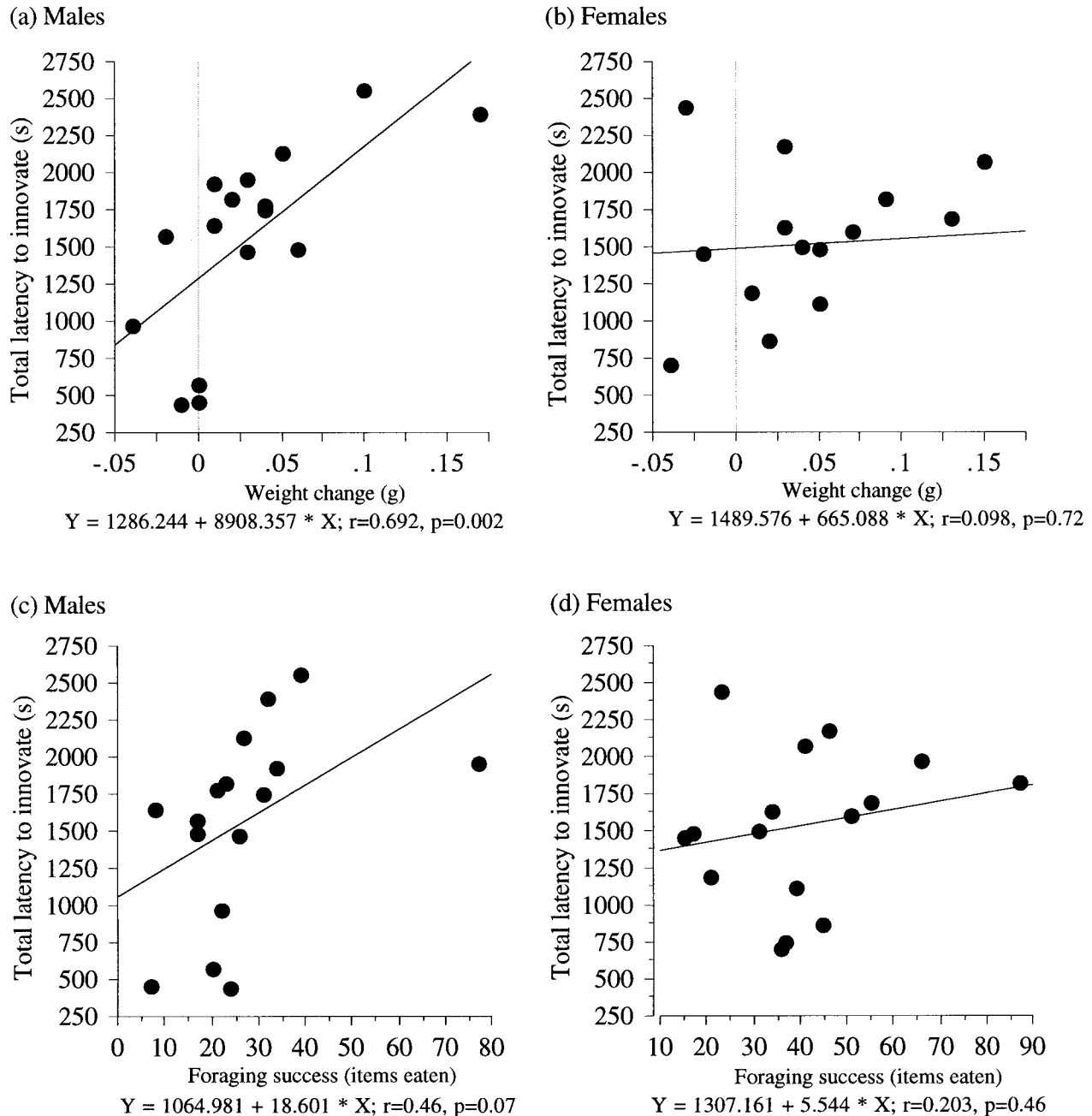


Figure 1

A strong correlation is found between weight change and total time to innovate in males (a), but no relationship is found in females (b). Results are similar for the relationship between past foraging success and total time to innovate in males (c) and females (d).

($r = .486, p = .004$) and between initial mass and weight change ($r = .366, p = .039$), indicating that larger fish out-competed smaller fish in scramble competition. Females ($\bar{x} \pm SE = 40.25 \pm 4.67$) consumed more food items than males ($\bar{x} \pm SE = 26.56 \pm 3.99$; independent t test: $t_{30} = 2.23, p = .03$), but the difference in weight gain between females ($\bar{x} \pm SE = 0.06 \pm 0.02$ g) and males ($\bar{x} \pm SE = 0.03 \pm 0.01$ g) was not significant (independent t test: $t_{30} = 1.36, p = .18, ns$).

The time to complete each of the three innovation tasks was summed to give an overall measure of innovative tendency (total latency to innovate). Across all fish, the correlation between total latency to innovate and weight change approached significance ($r = .336, p = .06$). Similarly, the correlation between total latency to innovate and foraging success

also approached significance ($r = 0.297, p = 0.09$). However, closer inspection reveals that these relationships across all fish result principally from the males (Figure 1). Males showed a strongly significant correlation between total latency to innovate and weight change ($r = .692, p = .002$) and a weaker, but notable, relationship between total latency to innovate and foraging success ($r = .460, p = .06$). Females, in contrast, exhibited no significant relationship between total latency to innovate and weight change ($r = .098, p = .72, ns$) and total latency to innovate and foraging success ($r = .203, p = .46, ns$). Despite this finding, the total latency to innovate for females ($\bar{x} = 1530$ s) was less than that for males ($\bar{x} = 1559$ s), although not significantly so. Males in population 1 showed a strongly significant correlation between total latency to inno-

vate and weight change ($r = .74, p = .04$), and a similar strong correlation was found in population 2 ($r = .63, p = .09$). In contrast, females in both population 1 ($r = .06, p = .88$) and population 2 ($r = .34, p = .41$) did not show a strong correlation between total latency to innovate and weight change. Thus, the two populations, in separation, provide a replication of our main finding.

As guppies are shoaling fish, it is possible that some fish may have followed others through the maze. If fish had followed each other at random, following would not be able to account for the correlations between weight change, foraging success, and total latency to innovate, described above. However, if following was size assortative, or was significantly more frequent in one sex, in theory it might be able to account for some of our findings. Size-assortative shoaling has been reported in guppies (Lachlan et al., 1998). We investigated these possibilities by defining following as any instance when a fish completed a maze 10 s or less after an earlier fish in the same tank. By this criterion, there were 20 instances of following out of the 96 latency times. We observed that, in general, the fish swam the maze alone, but occasionally, a pair or three fish would enter the goal zone together. There was no significant difference between the weight of followers ($\bar{x} \pm SE = 0.48 \pm 0.05$ g) and leaders ($\bar{x} \pm SE = 0.48 \pm 0.05$ g; independent t test: $t_{38} = 0.11, p = .92$, ns), nor any significant correlation between them ($r = .11, p = .64$). There was no evidence that one sex was more likely to follow or be followed than the other. Thirteen of the 20 cases of following were by males ($\chi^2 = 1.8, df = 1, p > .1$, ns); 10 of the 20 leaders were male. Seventeen out of 32 fish followed at some point; 17 out of 32 fish were leaders. Only 6 fish were both followers and leaders, indicating that most followers were not leaders, and vice-versa. When cases of following are removed, the relationship between weight change and total latency to innovate remains strong in males ($r = .58, p = .02$) and not females ($r = .205, p = .45$). Collectively, these findings do not support the hypothesis that the pattern of results are an artifact of following.

Thus males show a strong correlation between weight change and time to innovate, with weight change accounting for nearly 50% of the variance in innovation time. However, females show no equivalent relationship. A similar pattern is found for foraging success, and the results are replicated in the two populations. One interpretation of these findings is that males are indeed driven to innovate by hunger stress, but will devote their energy to mating when they are not subject to such stress. Observations from the laboratory, where, on average, a male displays to females seven times in 5 min (Farr and Herrnkind, 1974), and from the wild, where females receive a sneaky mating attempt every minute (Magurran and Seghers, 1994), certainly suggest that, when able, males will prioritize mating. Consistent with this reasoning is the observation that there is a much weaker correlation between foraging success and weight gain in males ($r = .27, p = .31$) than in females ($r = .52, p = .04$), perhaps suggesting that males burn off energy derived from food in courtship, rather than investing in growth. In contrast, females are constantly searching for new food sources, irrespective of past foraging success. Among guppies, females have indeterminate growth, and there is a strong link between energy intake, growth and fecundity, whereas males essentially stop growing when they reach sexual maturity (Constanz, 1989; Dussault and Kramer, 1981). It may be that female guppies are inherently more curious and investigative about their surroundings than males because finding high-quality food has a greater marginal fitness value for females than for males. If this reasoning is correct, we predict similar results in other species where maternal investment significantly exceeds paternal investment, such as

in most mammals. That is, in such species we predict (1) a stronger relationship between competitive ability and foraging innovation in males than in females and (2) greater levels of foraging innovation in females relative to males.

The findings of this study have important implications for research into animal social learning. Theoretical models have reached the conclusion that seemingly broad environmental conditions favor vertically transmitted (i.e., transgenerational) cultural traditions (Boyd and Richerson, 1985, 1988; Feldman et al., 1996). This finding was regarded by Boyd and Richerson (1988) as “troubling” when faced with the apparent rarity of such traditions in animal populations. It is entirely possible that future research will find that stable traditions are not quite as infrequent among animals as is currently believed. However, until such evidence is available, it remains a mystery why vertical cultural transmission is apparently rare among animals.

Kummer and Goodall (1985) found no shortage of innovation in primate populations, but these innovative behaviors rarely spread. The findings of this study suggest that the dearth of examples of stable traditions in animals may be a consequence of the complexities of transmission dynamics in a social group, rather than a reflection on the creativity or cognitive capabilities of animals. Various authors have noted a tendency among fish for poor competitors to be on the outskirts of the shoal or even to leave the shoal, being forced to shuttle between patches (Krause, 1994; Milinski, 1984). Primate studies also appear to indicate that innovators are frequently on the outskirts of the social group (Kummer and Goodall, 1985; Sigg, 1980). On many occasions when ecological and technical innovations occur in primate populations, the innovator is alone, or at least freed from social distractions, and the innovating animal is rarely the dominant or central individual in the population (Fragaszy and Visalberghi, 1990; Kummer and Goodall, 1985). If the twin observations that it is poorer competitors that innovate and that poorer competitors are on the outskirts of aggregations are common to many species, much innovation will tend to be unobserved by other animals, decreasing the chance of the novel behavior pattern spreading. This may be one explanation for both the slow diffusion of new behaviors in the wild (Kummer and Goodall, 1985) and the rarity of stable animal traditions (Boyd and Richerson, 1988).

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