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Heritability of the algal-foraging ability: an indirect benefit of female mate preference for males' carotenoid-based coloration in the guppy, *Poecilia reticulata*

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Abstract Several sexual selection theories assume certain benefits of female mate preference. The direct benefit, i.e., the direct contribution from males to their offspring and females, has been well tested empirically. However, the indirect benefit, i.e., the male's genetic contribution to their offspring, has been poorly demonstrated. Female preference for males' carotenoid-based coloration is known in some animals. Since animals must acquire carotenoids through foods, it is often hypothesized that the brightness of the carotenoid-based coloration is a reliable indicator of the male's foraging ability. Hence, females' indirect benefits, such as greater foraging ability in their offspring, through mate preference for the carotenoid-based coloration are assumed. However, the heritability of the foraging ability for foods that serve as carotenoid resources has not been tested. In this study, a maze experiment was performed in guppies (*Poecilia reticulata*) to examine the heritability of the foraging ability for algae, carotenoid resources in nature. The latency for completing algal-foraging tasks in this experiment showed high individual variation. Heritable estimates of the foraging ability were substantial ($h^2 = 0.57 - 0.66$) and significant, suggesting a genetic contribution to the foraging ability from fathers to their offspring. This result may support the hypothesis that indirect benefits influence the evolution of female choice.

Keywords Coloration · Foraging ability · Heritability · Indirect benefit · Sexual selection

Introduction

Direct and/or indirect benefits of female mate preference are often hypothesized in several evolutionary theories of

sexual selection (Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Andersson 1994; Kokko et al. 2003). Direct benefits, in which males directly contribute to offspring survival or female fecundity, have been empirically demonstrated in many studies such as those pertaining to males' nuptial gifts (Gwynne 1984; Rutowski et al. 1987) and paternal care (Petrie 1983; Knapp and Kovach 1991). On the other hand, it is also assumed that females obtain indirect benefits from their mates through genetic contribution from the males to their offspring (Zahavi 1975; Andersson 1994; Houde 1997; Hill 2002). Although indirect benefits have also been tested empirically in some cases (e.g., the barn swallow *Hirundo rustica*; Møller 1994), the indirect benefits of the female's mate preference for male characteristics are still poorly understood. For example, the indirect benefits of the female preference for carotenoid-based coloration have hardly been examined empirically although such indirect benefits have been suggested (Andersson 1994; Houde 1997; Hill 2002).

It is well known that in some birds and fishes, the females choose their mates on the basis of the males' carotenoid-based coloration (Milinski and Bakker 1990; Johnson et al. 1993; Houde 1997; Craig and Foote 2001; Hill 2002). Since animals cannot synthesize carotenoids de novo, they must obtain carotenoids through their foods such as plants and algae (Krinsky et al. 1989; Olson and Owens 1998). Therefore, the brightness of the carotenoid-based coloration is often regarded as a signal of the male's foraging ability for carotenoid-rich foods (Endler 1980; Houde 1997). In addition, carotenoids play several important roles in a variety of physiological systems in animals (Krinsky et al. 1989; Lozano 1994; Olson and Owens 1998). Hence, it can be considered that females can obtain indirect benefits, e.g., greater foraging ability for carotenoid-rich foods and consequently higher viability of their offspring, by choosing males expressing brighter coloration as their mates (Endler 1980; Kodric-Brown 1989; Houde 1997; Karino and Haijima 2004). Nevertheless, the heritability of the foraging ability for foods that serve as carotenoid resources has not been demonstrated thus far. In the present study, we examined the heritability of an aspect of the foraging

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ability for foods that serve as carotenoid resources in the guppy, *Poecilia reticulata*.

Guppies are live-bearing poeciliid fish native to the streams of Trinidad (Houde 1997) and they show remarkable sexual dichromatism, i.e., the males assume bright spots of orange, black, and iridescent coloration on their bodies. Female guppies often prefer males with brighter coloration (the greater degree of color saturation) of orange spots as their mates (Kodric-Brown 1989; Houde and Torio 1992; Grether 2000). Because the male's orange coloration depends on dietary carotenoids, the brightness of the orange coloration is regarded as an indicator of the male's foraging ability for algae, i.e., carotenoid resources in nature (Endler 1980; Kodric-Brown 1989; Grether et al. 1999). Therefore, if we can detect significant heritability of the algal-foraging ability in guppies, it would support the assumption that indirect benefits influence the evolution of female preference for the males' carotenoid-based coloration.

Methods

We collected guppies in March and September 2001 and March and October 2002, from the Hiji River (26°43'N, 128°11'E) located in the northern part of Okinawa Island, Japan. In this population, male secondary sexual traits, such as the size of orange spots, show high individual variation (Karino and Haijima 2001) with the similar degree with those of the native populations (e.g., Houde and Endler 1990). Female guppies in this population prefer males expressing brighter orange coloration as their mates (Karino and Shinjo 2004), similar to females of other populations (Kodric-Brown 1989; Houde and Torio 1992; Grether 2000). The collected specimens and their descendants were reared in 40–60 l aquariums with circulating water at 26–28°C with 12 h light and 12 h dark photoperiods in the laboratory of Tokyo Gakugei University. We used the first and second generation descendants for this experiment.

We conducted a simple maze experiment to examine the foraging ability of guppies. The experimental apparatus was divided into three compartments by two opaque boards (Fig. 1). A part of each opaque board (5 cm width) could be removed by a nylon filament. We measured the

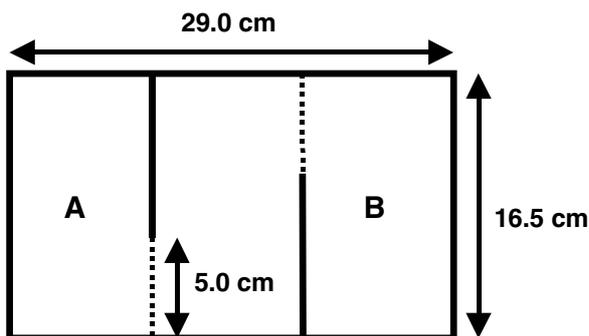


Fig. 1 Apparatus used for the maze experiment to examine the foraging ability of the guppy

time required to reach and peck algae, which were present within one side compartment, by each fish (latency) that had started out from the other side compartment. The test fish could not see the algae from the starting point; therefore, this maze experiment examined their ability to search for algae with respect to their exploration ability within the novel environment and their sensitivity to the chemical cue from algae. We added 2–3 cm gravel at the bottom of the aquarium and placed opaque boards on three sides of the aquarium to avoid disturbance. A 15-watt daylight lamp was placed 10 cm above the aquarium, and the water temperature was maintained at 26–28°C. Trials were conducted from 1200 to 1800 h. In order to obtain algae of similar quality, we placed 4 cm × 4 cm plastic fine mesh sheets in the container filled with both dechlorinated water and water from the original river for a period of 4 weeks. After 4 weeks, the mesh sheets were equally covered by a species of green algae (Karino and Haijima 2004). In order to accustom the test fish to the algal diet, they were fed algae on mesh sheets as well as commercial fish food starting 30 days prior to the experiment.

To evaluate the foraging ability of individual fish, we performed six trials on different days. The test fish were not fed from the day prior to the trial in order to ensure a high-motivation level for searching foods. This preparation did not appear to affect the health of any of the test fish. We placed a test fish into one side compartment of the experimental aquarium and a mesh sheet covered by algae was placed into the other side compartment. The mesh sheet with algae was located at the bottom of the centre of the compartment (e.g., A in Fig. 1). After a 10-min acclimation period, we carefully removed the removable parts of the opaque partitions when the test fish was located at the centre of the compartment (e.g., B in Fig. 1). Subsequently, we recorded the fish behaviour during a 30-min experimental period using a digital video camera (Sony DCR-TR30) and measured the time (s) required by the fish to peck the algae on the mesh sheet. If the test fish did not peck algae during the experimental period, their score of the latency for completing the algal-foraging task was 1800 s. We reversed the locations of the test fish and algae at the start of the next trial. Therefore, in three trials an individual fish started from A in Fig. 1 and in the other three trials it started from B. The mean value of the latencies for completing the foraging tasks in six trials was calculated as the score of the foraging ability of the test fish.

We conducted this maze experiment for 23 virgin females and 23 males. After the trials, a particular female and male were reared within a small aquarium (14 cm × 14 cm × 10 cm). When the female delivered offspring, the male and female parents were removed from the aquarium. The offspring were fed newly hatched brine shrimp nauplii and commercial fish food. When the secondary sexual traits (e.g., gonopodiums of males; Houde 1997) appeared, we chose two females and two males from a single brood and they were reared separately until maturity (ca. 3 months after birth). They were fed with the algae on the mesh sheet 30 days prior to the trials. We performed six trials of the maze experiment for each individual offspring and calculated

the mean latency for completing the algal-foraging tasks. Of the 23 female parents, one female delivered only male progeny; therefore, the female offspring from the other 22 broods were used for the experiment.

The heritability estimates (h^2) were calculated by parent-offspring regression analysis (Falconer and Mackay 1996). For the parent-offspring regression, we averaged the latencies for completing algal-foraging tasks of two male progeny from a single brood as the score of sons and those of two female progeny as the score of daughters. We also calculated the mean score among these four offspring as the midoffspring value; the midparent value of their sire and dam was also calculated. All data showed normal distributions (Kolmogorov-Smirnov one-sample test, $P>0.2$). When the parent-offspring regression is positively significant, it suggests a heritable component to the variation of the foraging ability (Falconer and Mackay 1996). The magnitude of the heritable component was estimated by twice the slope of regression when only one parent was analysed or by the slope of regression when analysis was conducted using the midparent value (Falconer and Mackay 1996; Lynch and Walsh 1998). Although we chose parental pairs at random, the mean latency for completing the algal-foraging tasks of the male parent and that of the female parent were significantly correlated ($r^2=0.213$, $P=0.03$ in parents of sons and $r^2=0.210$, $P=0.03$ in parents of daughters). Therefore, we corrected the heritability estimates for assortative mating according to the method of Falconer and Mackay (1996).

Results

The latencies from the start until to peck algae showed high individual variation for both male parents (mean \pm SD=1264.7 \pm 524.6 s; range=352.0–1800.0 s) and female parents (1484.6 \pm 534.4 s; range=195.6–1800.0 s). Similarly, the latencies varied individually among the male offspring (1285.4 \pm 444.4 s; range=283.3–1759.5 s) and the female offspring (1400.6 \pm 393.1 s; range=198.6–1800.0 s). The sexual difference in terms of the time required to peck algae was not significant in both the parents (t -test, $t_{44}=1.4$, $P=0.17$) and the offspring ($t_{88}=1.1$,

Table 1 Heritability estimates (h^2) of the latency for completing the algal-foraging tasks by guppies

	n_p	n_o	$h^2\pm SE$	P
Father-son	23	46	0.66 \pm 0.21	0.005
Father-daughter	22	44	0.57 \pm 0.19	0.007
Father-midoffspring	22	88	0.62 \pm 0.18	0.003
Mother-son	23	46	0.57 \pm 0.22	0.01
Mother-daughter	22	44	0.61 \pm 0.18	0.002
Mother-midoffspring	22	88	0.59 \pm 0.18	0.003
Midparent-son	23	46	0.61 \pm 0.17	0.002
Midparent-daughter	22	44	0.59 \pm 0.14	<0.001
Midparent-midoffspring	22	88	0.60 \pm 0.14	<0.001

n_p : number of parental pairs, n_o : number of offspring

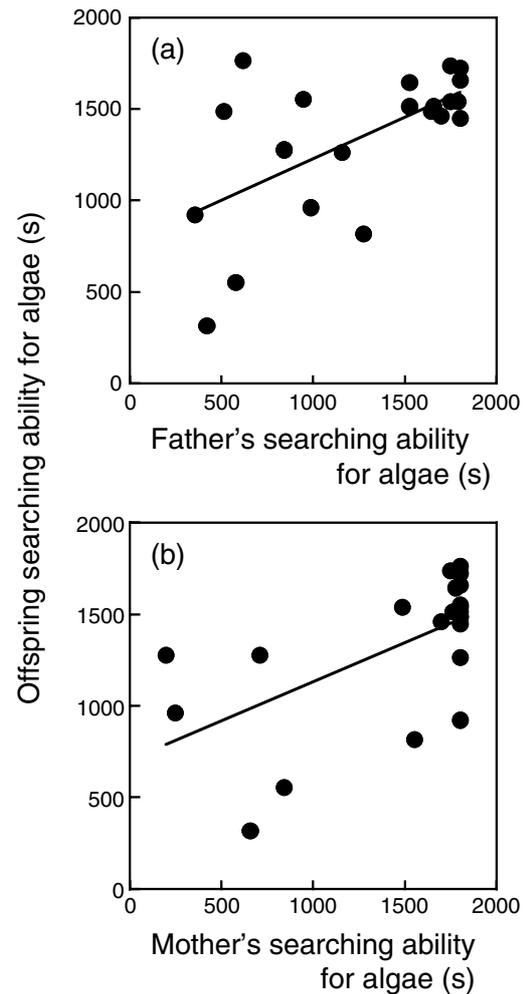


Fig. 2 Relationships of the latency for completing the algal-foraging tasks between midoffspring value and their male parents (a) and female parents (b) in the guppy

$P=0.26$). Male parents could reach and peck algae rapidly in accordance with the number of trials (Spearman's rank correlation coefficient $r_s=-0.25$, $n=138$, $P=0.004$). However, a significant correlation was not found in female parents ($r_s=-0.10$, $n=138$, $P=0.24$). Male offspring also required a shorter time to peck algae in the later trials ($r_s=-0.15$, $n=276$, $P=0.01$) whereas female offspring did not ($r_s=-0.09$, $n=264$, $P=0.15$). This suggests that males rapidly learned the location of algae within the experimental environment or could conform to the novel environment faster than females.

The heritability estimates of the latency for completing the algal-foraging tasks between the male parents and both the sons and the daughters were substantial and significant (Table 1). The father-midoffspring regression showed a positive relationship (Fig. 2a) and the heritability estimate was highly significant (Table 1). The heritability estimates of the latency to peck algae between the female parents and their offspring were significant (Table 1; Fig. 2b), suggesting that there were genetic contributions to offspring

foraging ability from both males and females. With respect to the midparent values, the estimated heritabilities of the foraging ability were substantial and highly significant for both the sons and the daughters (Table 1). In addition, the heritability estimate of the foraging ability between the midparent and midoffspring was also highly significant (Table 1). These results indicate a heritable component to the variation of the algal-foraging ability in guppies.

Discussion

Carotenoid-based coloration is one of the major sexual signals in animals (Andersson 1994; Olson and Owens 1998; Hill 2002). In guppies, it is well known that the females choose their mates on the basis of the males' carotenoid-based coloration (Kodric-Brown 1989; Houde and Torio 1992; Grether 2000; Brooks and Endler 2001; Karino and Shinjo 2004). Because animals have to obtain carotenoids through their foods, carotenoid-based coloration is regarded as a reliable indicator of the individual's foraging ability for carotenoid-rich foods (Endler 1980; Andersson 1994). Indeed, in guppies, the intake of an algal diet that serves as carotenoid resources enhances the brightness of the orange spot coloration in males (Grether et al. 1999; Karino and Haijima 2004). Therefore, it is often assumed that females can obtain indirect benefits, such as greater foraging ability in their offspring, through mate preference on the basis of the males' carotenoid-based coloration (Endler 1980; Kodric-Brown 1989; Houde 1997). Nevertheless, a part of this hypothesis, i.e., whether the foraging ability of males is a heritable component, has not been demonstrated empirically. The results of the present study indicate high individual variation in guppies, with regard to this aspect of the algal-foraging ability, namely, the ability to search within a novel environment. Because male guppies spent significantly less time to peck algae in the later trials, the score of the algal-foraging tasks in this study also suggests learning ability. Moreover, this study clearly demonstrates the inheritance of the algal-foraging ability. Therefore, the results of the present study may support the hypothesis that the indirect benefits, i.e., genetic contribution of males to the foraging ability of their offspring, influence the evolution of female mate preference for the males' carotenoid-based coloration (Endler 1980; Kodric-Brown 1989; Houde 1997).

In the present study, the sexual difference in the latency for completing algal-foraging tasks was not detected. On the other hand, unlike males, a negative correlation between the number of trials and the latency to peck algae was not found in females. Reader and Laland (2000) have reported a greater learning ability in female guppies, in comparison with males, in regard to foraging sites within maze experimental environments. This contradiction may be due to the difference in the design of their experiments and ours. Reader and Laland (2000) examined patterns of the spread of foraging information among a group of guppies ($n=20$ individuals in a group). In contrast, we examined the forag-

ing ability of an individual fish. Therefore, fish in this study could not learn foraging information from other individuals. It is probable that, in guppies, some sexual differences exist between the degree of learning ability for information from other individuals and that from exploring novel environments themselves.

Results of this study suggest the indirect benefit of mate preferences of female guppies in terms of the foraging ability from males to their offspring and may support the hypothesis that the evolution of female preferences for exaggerated male traits occurs through the indirect benefit (Endler 1980; Kodric-Brown and Brown 1984; Andersson 1994). However, further evidences will be needed to totally demonstrate the indirect benefit of female mate preferences through the males' foraging ability. First, it is required to determine whether the variation in the foraging ability documented in this study affects the intake of algae to a level where it would influence both the orange coloration and mating success of the males. Since males in this study fed algae freely 1 month prior to the experiment to accustom to the algal diet, it is possible that their orange coloration might be enhanced regardless of their searching ability for algae. Therefore, further examination with different experimental design is recommended to clarify the relationship between the algal-searching ability of male guppies and the degree of the brightness of their orange coloration as well as that of their attractiveness to females. Second, it is still unclear whether individuals with higher foraging ability documented in this study are more successful in obtaining algae and in mating with females in nature. In the wild, foraging success may be also influenced by many other variables (Wootton 1998). For example, the foraging ability of individuals in the natural situation may be affected by social factors, such as learning ability from environmental components (Reader and Laland 2000). Moreover, it is probable that the foraging ability examined in this study, such as the high movement within the novel environment, may increase the vulnerability of the fish to predators in environments with a high predation risk. By examining these relationships among the algal-foraging ability and other variables, the influence of the algal-foraging ability on the indirect benefit of female preferences for carotenoid-based coloration of males will be further clarified.

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