

Age and Experience Affect Female Choice in the Guppy (*Poecilia reticulata*)

Astrid Kodric-Brown^{1,*} and Paul F. Nicoletto^{2,†}

1. Department of Biology, University of New Mexico,
Albuquerque, New Mexico 87131;

2. Department of Biology, Lamar University, Beaumont, Texas 77710

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ABSTRACT: Female choices of males, and how these choices are influenced by ecological and social factors, have been studied extensively. However, little is known about the effects of age and breeding experience on female mating decisions. We used video techniques to examine female mate choice in guppies based on the area of carotenoid (orange) pigmentation on the body. Females were presented with paired images of males, one ornamented and the other plain. Visual preference for each male was measured. Age-related changes in the criteria of choice were examined by comparing the responses of the same mature but sexually inexperienced 6-mo-old and 12-mo-old females. Effects of breeding experience on female choice were examined by comparing mate preferences of 12-mo-old female virgins with their preferences after they had mated and produced a brood. Female preferences for ornamented males with large areas of carotenoid pigment changed with age but not with mating experience. Six-month-old virgin females preferred ornamented males, whereas 12-mo-old virgin and postpartum females did not differentiate between males based on orange coloration. The results are discussed in light of life-history theory and have important implications for studies of sexual selection as well as for the design of mate-choice studies.

Keywords: sexual selection, mate choice, age, experience, guppy.

A basic assumption of both theoretical and empirical studies of sexual selection is that individual females are consistent in their preferences for particular male traits, so these preferences do not change over the reproductive life span (Andersson 1994). Age-related changes in female mating preferences may be important in direction and the

rate of evolution of secondary sexual traits. Although there are a few studies on short-term consistency, measured in days or weeks, in female choice for male traits, the results are equivocal; consistency has been shown in some studies (Godin and Dugatkin 1995; Kodric-Brown and Nicoletto 1997) but not in others (Ligon and Zwartjes 1995; Johnsen and Zuk 1996). No such studies are available for long-term consistency spanning the entire reproductive period of females.

If the ability to discriminate and to choose among potential mates is adaptive, then selection should operate on mate choice behavior as it does on other traits that affect the fitness of individuals. Thus, age-related changes in reproductive effort or reproductive value may result in age-related changes in mate choice. As organisms continue to age after reaching reproductive maturity, their residual reproductive value declines, and typically there is a corresponding increase in their reproductive effort for each breeding episode (Roff 1992; Stearns 1992). Whether selectivity increases or decreases will depend on an organism's life history, such as age at first maturity, age-related changes in fecundity, and expected life span, all of which should influence mate choice.

The importance of female preferences in selecting for and maintaining multiple male secondary sexual traits is widely recognized (Houde and Endler 1990; Howard and Young 1998; Marchetti 1998; Brooks and Couldridge 1999). It is also known that many environmental factors may affect mate choice, among them predation risk (Magnhagen 1991), parasite load (Lopez 1999), and experience gained from previous interactions with males (Collins 1995; Marler et al. 1997). However, the importance of age-related changes in female preferences in contributing to this variation in male traits has yet to be addressed. If females show age-related changes in degree of selectivity on the kinds of traits that they prefer, then this may be a mechanism that selects for variation in male traits.

It is also not clear how mating experience by itself, or in combination with age, affects female preference (Forslund and Pärt 1995). Few studies have investigated the

* E-mail: kodric@unm.edu.

† E-mail: nicoletpf@hal.lamar.edu.

relationship between female age and choice of mates (but see Burley 1977; Burley and Moran 1979; Prosser et al. 1997). In these studies, however, the effects of experience and age usually cannot be distinguished; the observed age-related changes in female reproductive performance may have been due entirely or in part to experience or to an interaction between age and experience.

Changes in female choosiness associated with age, mating experience, or an interaction between age and mating experience should not only affect the strength of selection for particular male traits but also favor the evolution of male mating tactics. Age- or experience-related changes in female preferences may select for changes in the morphological and behavioral components of courtship of males. Thus, one would expect qualitative and quantitative changes in male displays to reflect female age and/or breeding experience.

We studied the effects of age, controlling for experience, and the effect of experience on female choice in the guppy. Specifically, we asked, How does female preference for a male secondary sexual trait vary with age or mating experience? Does a female's tendency to habituate to repeated presentations of males change with age or mating experience? Does age or mating experience affect the short-term consistency of female choice for particular males?

Guppies are small, live-bearing fishes with a polygynous breeding system. Male investment in offspring is limited to providing sperm. Males vary in their colors and display behavior, and females preferentially mate with highly ornamented, vigorously displaying males (Farr 1980; Houde and Endler 1990; Kodric-Brown 1993; Nicoletto 1993). Female preferences for showy males are consistent, at least over short time periods (Godin and Dugatkin 1995; Kodric-Brown and Nicoletto 1997). As in most fishes, female guppies have indeterminate growth, so their reproductive effort increases with age (size). If there is a positive relationship between reproductive effort and choosiness, older females should be more selective than younger ones. In this case, mating experience should reinforce the effects of age, and older experienced females should be choosier than similarly aged but inexperienced females. However, because selection on traits that enhance fitness declines with age, it is also possible that young females would be choosier than older females, and mating experience would not affect mate choice.

Material and Methods

Fish used in our experiments were laboratory-reared, first-generation descendants of females caught at McCauley Spring in the Jemez Mountains near Albuquerque, New Mexico. The population was established by introduction approximately 30 yr previously. It experiences low pre-

reproductive pressure, since there are no piscivorous fish. Males are highly ornamented, with large areas of the body and fins covered with red and yellow (carotenoid), black (melanin), and iridescent (mostly blue and white) spots. Females prefer males with complex color patterns, large areas of carotenoid pigment, and high display rates (Nicoletto 1993, 1995).

We tested the visual preferences of 25 females using video images of showy and dull males presented in a binary choice design. Visual preferences are an accurate predictor of mating preferences (Kodric-Brown 1985). Each female was tested three times: as a 6-mo-old virgin, a 12-mo-old virgin, and then after mating and producing a brood. Since exposure to males during maturation influences subsequent choice of males (Breden et al. 1995; Rosenqvist and Houde 1997), all females were raised in visual contact with males varying in the area of carotenoid spots on their body from 5% to 30%. This coincides with the variation in male ornamentation used in our mate-choice trials.

The utility of video as an experimental tool to study mate choice patterns in fishes has been demonstrated (e.g., Rowland et al. 1995; Rosenthal et al. 1996; Clark and Stephenson 1999; Rosenthal 1999). Female guppies respond similarly to video images of males and to live males (Kodric-Brown and Nicoletto 1997). There are several advantages to using video images of males rather than live males in these experiments. One is that each female as she ages can be presented with the same visual stimuli. Only by using video images could we eliminate effects of temporal variation in male behavior and appearance, which are known to change with age (Rodd and Sokolowski 1995). Another advantage of using video images is that the behavioral interactions between a live male and a female, which may also change with age and experience, are eliminated. By presenting females with images of swimming rather than courting males, one can focus on the importance of male color patterns, especially the area of carotenoid spots, in female choice of males (Kodric-Brown and Nicoletto 1997).

Mate-choice trials were conducted in a small aquarium (20.5 cm × 21 cm) containing natural-color gravel. The front of the aquarium was marked in 5-cm increments so that we could record the female's position during a trial. Two 12.5 × 17.5-cm, high-resolution color Sony monitors (model PVM8033Q) were placed opposite each other, on the right and left sides of the aquarium. Females were introduced into the test aquarium and allowed to habituate for 10 min. The trial began with the simultaneous presentation, on the opposite monitors, of a life-sized image of a showy and a plain male. Each videotape consisted of the following sequence: 5 min of an empty aquarium, followed by 5 min of the first male (either showy or plain), 1 min of an empty aquarium, followed by 5 min of the

second male. The two stimuli were sequentially presented on alternate monitors to control for side bias. For example, showy male on right side and plain male on left side during the first 5 min of the presentation, followed by plain male on left side and showy male on right side during the second 5 min of the presentation. Female preference for a male image was determined by the amount of time she spent within 5 cm of a video monitor during a 10-min observation period. Female motivation was assessed by observing the behavioral responses of females to the male video images. Typically, sexually receptive females respond to male courtship by orienting to the male and gliding toward him. Since the male video images did not show courtship, female responses consisted only of orienting movements. All females were initially tested for the presence of the "orienting" behavior (Baerends et al. 1955) to ensure that they were sexually motivated and that they responded to the video images of males in an appropriate way. Trials in which females spent over 50% of time in the central "neutral" zone of the compartment were discarded.

For the construction of the videotapes, we used 10 males matched for size but contrasting in the proportion of the body covered with carotenoid spots. Showy males had 25%–30% of the body covered with carotenoid spots, whereas plain ones had only 5%–10% of the body covered with carotenoid spots. Videotapes of males were made by recording the swimming behavior of a male in a small aquarium (15 cm × 10 cm × 15 cm), illuminated with a 150-W Dolan-Jenner fiber-optic illuminator with a 3,200°K lamp. The recordings were made on S-VHS tapes with a Panasonic WV-D5100HS camera with a 100-mm macro lens. Tapes were edited with a Panasonic AG-5700 videotape recorder and an AG-A570 edit control board. To control for differences in swimming rates between recorded males, we used tape segments in which males showed similar levels of activity. We constructed five sets of videotapes, each set consisted of a pair of males, one of which was ornamented (showy), the other one was not (plain). To avoid pseudoreplication, we tested females in groups of five with the same pair of males rather than using one pair of tapes for all females.

Effect of Age on Female Preference

Females that were virgins initially were used to avoid confounding the effects of age with those of mating experience. Each female was presented with video images of two males, at 6 mo ($\bar{X} = 17.63$ mm, $SE = 0.40$ standard length), and then again at 12 mo old ($\bar{X} = 30.28$ mm, $SE = 0.50$ standard length). Jemez females mature much later than females from Trinidadian populations that experience low predation and high adult survivorship. Typically, less than half of the Jemez females mated to males at 3–4 mo old

produced broods, whereas females from Trinidad were fully sexually mature at that age (Reznick et al. 1996). We chose 6-mo-old females because at that age all are mature and can produce a brood. At 12 mo, all Jemez females are still reproductively active. In the laboratory, Jemez females senesce and begin to die at an age of 18–24 mo. Senescence is characterized by smaller brood size or cessation of reproduction. Although we have no information about the age of females in Jemez Springs, gravid females of the size class of our laboratory-reared 12-mo-old females are quite numerous.

Fish were kept in aquaria with a natural gravel substrate, undergravel filters, a water temperature of $28^\circ \pm 2^\circ\text{C}$, and a photoperiod of 16L : 8D. Stock tanks were checked daily for 5 d, and all juvenile fish born each day were removed to the virgin female rearing tank. Thus, females used in our experiment varied in age by no more than 5 d. Males were removed from the rearing tank as soon as they could be sexed. Virgin females were raised in all-female groups in one compartment of a 75-L aquarium. The other compartment, separated from the females with a clear glass partition, contained males. Thus, females could interact visually but not physically with males.

Females used in the mate choice trials were kept in a 75-L aquarium, which was subdivided into eight compartments by opaque Plexiglas partitions. They were individually placed into the compartments 24 h before the start of the experiment and remained there for the duration of the experiment (5 d). On four consecutive days, each female was presented with the same set of videotapes of two males, one of which was ornamented and the other plain. All trials were conducted between 0800 and 1200 hours. After the end of the tests at 6 mo old, females were placed into the two outside compartments of a 75-L aquarium, which had been divided into three compartments with clear glass partitions. The central compartment contained 10 males whose color patterns were representative of the variation in the Jemez population. Thus, females were again in visual, but not physical, contact with males. Two such aquaria were used to house all females. Females remained in these compartments until they reached the age of 12 mo, when they were retested with a set of male images.

Effect of Mating Experience on Female Preference

To determine whether differences in mate preferences between 6- and 12-mo-old females were due to age or lack of sexual experience, we conducted an additional experiment. After testing all 12-mo-old virgin females with the male images, they were placed into a 75-L aquarium with 10 males and allowed to mate. They remained with these males for 2 wk, sufficiently long for all females to become

pregnant. Females were then separated from the males, placed individually into small brood chambers, and reintroduced into the two outside compartments of the three-compartmented aquaria. Thus, they were once again in visual contact with the males that were housed in the central compartment. The females were examined twice each day for the presence of a brood. All 25 females produced broods. Females were retested with male video images 24 h after giving birth, using the same protocol described above. Since female guppies are receptive to males between 24–48 h after giving birth, it is important to test them for visual mate preference within this time frame.

Statistical Analysis

We evaluated, respectively, the effect of age and the effect of mating experience on preference for male color with repeated measures ANOVA. To quantify the response of females to video images of showy males, we subtracted the time a female spent with the plain male from the time she spent with the showy male and divided the difference by the time she spent with both males for each of the four trials. The proportional data were arcsine transformed and analyzed with a three-way repeated measures ANOVA. The main effects of this model were the age treatment (6- and 12-mo-old) or the experience treatment (12-mo virgin and postpartum), female (25) nested within each age or experience treatment, and trial (four trials for each female in each age or experience treatment). Since there were no significant effects of the individual pairs of tapes of males on the response of females across treatments (age: pair, $F = 1.69$, $df = 4, 60$, $P = .15$; age \times pair interaction, $F = 2.20$, $df = 4, 60$, $P = .09$; experience: pair, $F = 1.18$, $df = 4, 60$, $P = .36$; experience \times pair interaction, $F = 1.79$, $df = 4, 60$, $P = .14$), we combined all females within each treatment.

To determine the distribution of female preferences for the two male images, we used a χ^2 analysis to examine the responses of females to the same male images as 6- and 12-mo-old virgins and after they had mated and produced a brood.

We performed two sets of habituation analyses. First, we determined whether females habituated to repeated presentations (four trials) of the same two male images within each treatment (6-mo, 12-mo, postpartum). We summed the time each female spent with both male images for each of the four trials, and analyzed the data with a one-way ANOVA for each treatment. Second, we tested for habituation of females to the video images of males across treatments (age and experience) and the four trials within each treatment. We analyzed the total time females spent with both male images with a three-way repeated measures ANOVA. The main effects were the age or the

experience treatment, female (repeated measure) nested within the age or experience treatment, and trial. The trial effect was tested with the mean squares error term.

Results

Effect of Age and Mating Experience on Female Response to Male Images

Age had a significant effect on female responsiveness to the showy male image ($F = 18.69$, $df = 2, 60$, $P < .0001$). Six-month-old virgin females spent significantly more time viewing the image of the showy male than 12-mo-old virgin females (fig. 1). A greater number of females preferred the showy male at the age of 6 mo than at 12 mo or after mating and producing a brood (6 mo old: $\chi^2 = 14.44$, $df = 1$, $P = .0001$; 12 mo old: $\chi^2 = 1.00$, $df = 1$, $P = .30$; postpartum: $\chi^2 = 0.36$, $df = 1$, $P = .60$; fig. 2). Thus, female preference for showy males decreased with age. Mating experience had no effect on the responses of females to showy males ($F = 0.69$, $df = 1, 48$, $P = .4101$). Twelve-month-old virgin females and postpartum females spent approximately equal amounts of time viewing both showy and plain males (fig. 1).

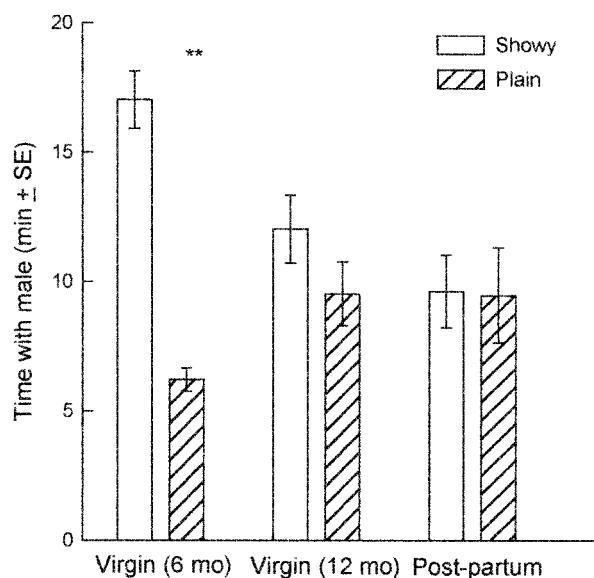


Figure 1: The effect of age (6 and 12 mo) and mating experience (postpartum) on the visual responses ($\bar{X} \pm SE$ min) of female guppies to simultaneous presentations of male video images differing in the area of the body covered with carotenoid pigment. Showy male (open bar), plain male (hatched bar). Asterisks indicate statistically significant difference, $P < .001$. Preference for showy males declined with age but was not affected by mating experience.

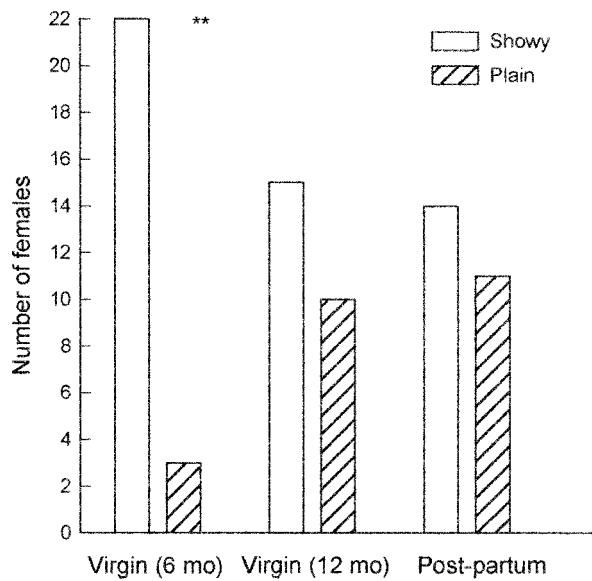


Figure 2: Number of 6-mo-old, 12-mo-old, and postpartum female guppies showing a visual preference for the showy male (open bar) or the plain male (hatched bar). Asterisks indicate statistically significant difference, $P < .001$.

Effect of Age and Mating Experience on the Habituation of Females to Repeated Presentations of the Same Male Images

Female response declined with repeated presentations of the same pair of male images within each of the three treatments, but not in a consistent manner (fig. 3). Six-month-old females and postpartum females did show some habituation to repeated presentations of males (6 mo old: $F = 2.59$, $df = 3, 96$, $P = .0573$; postpartum: $F = 2.59$, $df = 3, 96$, $P = .0572$). In these two treatments, females responded more to the second presentation than to the first, third, or fourth presentation. Since there was no consistent decrease in female response with presentation order, the observed differences probably are not biologically significant. Twelve-month-old females did not habituate to repeated presentations of male images ($F = 1.17$, $df = 3, 96$, $P = .327$). The response of females to the presentation of male images did not decline with age ($F = 1.50$, $df = 1, 48$, $P = .2272$) or with mating experience ($F = 2.97$, $df = 1, 48$, $P = .0915$; fig. 3).

Discussion

In this study, we document age-related changes in female mating preferences and interpret these changes in the con-

text of life-history theory. Since the expression of secondary sexual traits is positively associated with phenotypic and genotypic quality, choosy females enhance their fitness by mating with males with well-developed ornaments (Møller and Alatalo 1999). Changes in the ability of females to discriminate among potential mates should have fitness consequences. Life-history-theory models predict a decline in reproductive value with age and a corresponding increase in reproductive effort (Roff 1992; Stearns 1992). Since selection on traits that enhance fitness declines with age (Williams 1957), younger females should be choosier than older females, and variation in mating preferences is expected to be greater in older females than in younger ones.

Our results clearly show that the observed decline in female preference for the more ornamented male images is due to age rather than sexual experience. Further, they do not support the hypothesis that 12-mo-old females became less selective simply because they had been deprived of mating opportunities. If this were the case, then postpartum females, since they had mated, should once again show a high degree of choosiness as they did as 6-mo-old virgins. This was not the case.

The observed age-related changes in female selectivity also cannot be an artifact of the repeated use of video images, although females did show a slight tendency to habituate to repeated presentations of the same set of male images in the 6-mo-old and postpartum trials.

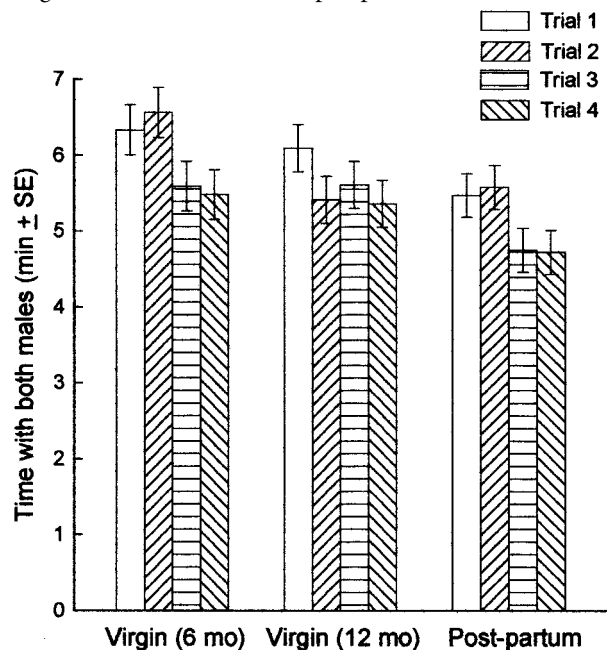


Figure 3: Habituation of female guppies to repeated presentation of the same male images. Time ($\bar{X} \pm SE$ min) 6-mo-old, 12-mo-old, and postpartum females spent viewing both male images in each of four trials.

Effect of Age-Related Physiological Changes

There are few examples of age-related changes in female mate preferences that clearly have a physiological basis. Gray (1999) observed a decline in female mate preferences with age in the cricket (*Acheta domesticus*). He showed that it is female choosiness, rather than the ability to respond to male calls, that declines with age. Juvenile hormone levels affect the sensitivity of auditory neurons in such a way that older females respond to a broader range of stimuli (Henley et al. 1992).

There are at least two possible reasons for the observed reduction of selectivity with age: decreased ability to discriminate due to the deterioration of the visual system (sensory capacity) and decreased choosiness (motivation). Our experiments do not allow us to separate the effects of these two processes, and both of them could be operating. Age-related changes in visual acuity have been shown for vertebrates (Hodos et al. 1991) and specifically for fishes (Müller 1952; Baburina 1968; Douglas 1989; Hawryshyn 1998). Whether the visual system of guppies, especially its sensitivity for longer wavelengths, changes with age has yet to be determined. Several processes are possible: decline in visual acuity, loss of spatial contrast sensitivity (the ability to see pattern in the environment), decline in the sensitivity of individual classes of cone receptors with age, and change in the opacity of the lens or ocular media. On the other hand, older females could have been less motivated to discriminate between the showy and plain males. Even though they spent similar amounts of time as younger females inspecting each male image, older females may have been looking for cues other than red pigmentation—such as courtship displays, for example.

Distinguishing the Effects of Age and Experience

In this study, we were able to analyze the effects of age separately from the effects of experience. Experienced females showed the same lack of preference for showy males as inexperienced females (figs. 1, 2). Thus, age, and not sexual experience, caused the pattern observed in our experiments. A problem in many field studies is that female age and experience are confounded, and, often, changes in behavior or performance are attributed to experience rather than age, per se. Thus, for example, in many mammals and birds with parental care, older females may produce offspring with higher survivorship because they are more experienced (Clutton-Brock 1988; Forslund and Pärt 1995). Similarly, in many fish taxa where males actively care for their offspring, larger, and presumably older, females preferentially mate with larger males, and such males are better parents and are less likely to cannibalize the brood (e.g., sculpins, Downhower and Brown 1980; red-

lipped blennies, Côté and Hunte 1989). However, in many of these examples, female preferences for larger, presumably more experienced males may be constrained by assortative mating of large females with larger males.

Implications for Copying

In studies examining social effects on female choice, it has been suggested that younger females tend to copy the mate choice of older females (Gibson and Hoglund 1992; Dugatkin and Godin 1993). Selection should enhance copying by younger females if young females are under time constraints, if the costs of mate choice are high, or if mating experience enhances the ability of older females to choose mates. Our results suggest that if younger female guppies copied the mate choice of older females, they would not exercise their inherent choosiness and would be more likely to mate with duller, less attractive mates. Thus, young females would potentially pay a fitness cost by producing less fit and/or less attractive offspring. Our results suggest that younger females are more selective and fully capable of selecting high quality mates without copying older, more experienced females. The duration of the receptive period may influence reproductive tactics, especially in females of live-bearing fishes that can store viable sperm to inseminate multiple broods. Female guppies are receptive for only short periods of their 28-d brood cycle (e.g., 24–48 h after parturition; Meffe and Snelson 1989). Even though this may limit opportunity for mating, young females are still highly choosy.

Design of Mate Choice Experiments

Our results also have important implications for the design of mate-choice studies. Potential age-related changes in the sensory or motivational physiology of females, which mediate the response to variation in male signals, imply that female age be considered as a confounding factor and carefully controlled. Age-related physiological changes also may take place in males and affect their signaling ability (Rodd and Sokolowski 1995).

Age-Related Changes and Sexual Selection

Our results document changes in female responsiveness based on one criterion, male ornamentation, specifically the area of carotenoid spots. The intensity and size of carotenoid spots are important criteria for female choice in all populations of guppies examined to date, including laboratory stocks (e.g., Farr 1980; Kodric-Brown 1993), naturalized populations (e.g., Nicoletto 1993; Brooks and Caithness 1995), and native populations in Trinidad (e.g., Endler and Houde 1995). However, our results should not

be taken to imply that older females are incapable of discriminating among males and do not show preferences for particular male traits. Because we tested only the area of carotenoid spots, we cannot rule out mate choice based on other criteria, such as other pigment patterns or courtship displays. Females from the Jemez population do show strong preferences for vigorously displaying males (Nicoletto 1993, 1995). So older females may well select males based primarily on the vigor and duration of courtship displays rather than carotenoid pigments. By deliberately showing images of swimming, not courting males, we controlled for male behavior and focused on the influence of ornamentation. Male courtship displays and the response of females to them as a function of age and experience were not a contributing factor in the age-related changes in female choice documented in these experiments.

Our results have important implications for studies of sexual selection. They suggest that criteria for mate choice may change with female age, thus altering selection for multiple male secondary sexual traits, including male courtship tactics. If older females are less responsive to male morphological traits, such as carotenoid color spots, then males might compensate in their courtship tactics and engage in more vigorous displays. Indeed, male guppies have been reported to increase their courtship displays toward larger, and presumably older, females (Baerends et al. 1955; Houde 1997).

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