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Female preference for blue in Japan blue guppies (Poecilia reticulata)

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Abstract

Guppies (*Poecilia reticulata*) are widely used as a model species in mate choice studies. Although native to South America, guppies have been introduced to natural water bodies in disparate regions of the globe. Here, for the first time, we examine guppies from one such introduced population in Japan where males have evolved a predominantly blue color pattern. Previous studies of wild-type guppies have shown blue to play a relatively minor role in the mate choice decisions of females compared to other traits, such as orange, and the importance of blue is not universally supported by all studies. The Japanese population therefore presents an ideal opportunity to re-examine the potential significance of blue as a mate choice cue in guppies. Mate choice experiments, in which female Japan blue guppies were given a choice between pairs of males that differed in their area of blue coloration but were matched for other traits, revealed that females prefer males with proportionately larger amounts of blue in their color patterns. We discuss possible factors, including sexual and ecological selection, which may have led to the evolution of unusually large areas of blue at the expense of other colors in Japan blue guppies. However, further studies are needed to distinguish between these scenarios.

Introduction

Guppies (*Poecilia reticulata*) are small and brightly colored fish native to South America and islands of the Caribbean. The color patterns of wild-type males are highly polymorphic and vary widely among populations, but generally consist of a combination of carotenoid (red, orange, and yellow) and melanin (black) pigments, that absorb certain wavelengths of light, and iridescent (blue, green, violet, and white) structural colors that scatter and reflect certain wavelengths (Bagnara et al. 2007; Price et al. 2008). These elements differ in size, position, shape, and intensity (Houde 1997). Numerous studies have demonstrated the significance of male color patterns to female mating preferences in both natural (Houde 1987; Houde and Endler 1990; Kodric-Brown 1993; Evans et al. 2004) and introduced (Brooks and Caithness 1995; Brooks and Endler 2001; Karino and Shinjo 2004) populations of guppies. In particular, these studies have provided overwhelming evidence in support of the role of size and saturation of carotenoid patches as major targets of mate choice (e.g., Houde 1987; Kodric-Brown 1989; Long and Houde 1989; Houde and Endler 1990), although the relative strength of this preference for orange does vary extensively among individuals (Kodric-Brown and Nicoletto 1996) and populations

(Houde and Endler 1990; Endler and Houde 1995; Kemp et al. 2009). In addition to color, females may also evaluate other cues when selecting a mate, such as display rate (Farr 1980; Bischoff et al. 1985; Kodric-Brown 1993; Kodric-Brown and Nicoletto 1996), body size (Reynolds and Gross 1992; Karino and Matsunaga 2002), caudal fin size (Bischoff et al. 1985), dorsal fin size (Karino et al. 2011), gonopodium length (Brooks and Caithness 1995), and social cues (Godin et al. 2005). However, reported female preferences for individual size components may instead reflect an overall preference for a larger combined body and fin surface area (lateral projection area) (MacLaren and Fontaine 2012).

Besides orange, the relative importance of other components of the color pattern, such as melanin and iridescent colors, remains less certain, but they may be the focus of female mate choice decisions in at least some populations (Endler 1983; Kodric-Brown 1985, 1993; Kodric-Brown and Johnson 2002; Kemp et al. 2009). It is likely that the various elements that comprise the complex color patterns of male guppies work together to enhance attractiveness. For example, it is suggested that carotenoid and iridescent colors both function in female mate choice (Endler 1983; Kodric-Brown 1985) but assume different roles during courtship, with carotenoids attracting females from a distance and iridescent colors functioning more in the close-range assessment of displaying males (Endler 1983). Because iridescent colors change according to the direction of ambient light and viewing angle, animals are able to direct their visual signals towards an intended receiver, making them ideally suited to close-range communication (Doucet and Meadows 2009). However, because iridescent colors are extremely conspicuous at close ranges, they are generally reduced in guppy populations with high levels of predation (Endler 1978, 1980, 1983).

Iridescent (structural) coloration may serve multiple functions in the mate choice displays of animals. Many recent studies have demonstrated a link between male condition and iridescent color in a variety of taxa, including butterflies (Kemp et al. 2006; Kemp and Rutowski 2007), damselflies (Fitzstephens and Getty 2000), spiders (Lim and Li 2007), and birds (Doucet 2002; McGraw et al. 2002; Møller and Petrie 2002; Doucet and Montgomerie 2003; Hill et al. 2005). This provides strong evidence that iridescence serves as an honest signal of male quality. Furthermore, iridescence may play a role in signal amplification by enhancing the appearance and conspicuousness of other visual elements in the display (Doucet and Meadows 2009). This is achieved because iridescent colors tend to be brighter and more saturated than pigment-based colors, thus providing high contrasts with other color components and/or the background. The amount of iridescence has been shown to increase with age in guppies (Miller and Brooks 2005), in which case females choosing mates on the basis of iridescence may be selecting for older males with demonstrated survivorship.

Japan blue guppies represent a feral population of wild-type guppies introduced to a river in the Kanagawa prefecture of Japan. Since their discovery in the late 1980s, they have been widely used in artificial breeding for the aquarium trade due to their unusual coloration. Male Japan blue guppies are predominantly blue in color, especially towards the posterior half of the body. Orange and black spots are also present in the color pattern, but these are

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relatively small in size and number, and may even be absent in some individuals. This population thus provides an ideal opportunity to examine the role of blue in female mating preferences. Despite their uniqueness, there have been no previous mate choice studies conducted on Japan blue guppies, and the factors that have contributed to this deviation in color pattern remain unknown. The increased proportion of blue area at the expense of other colors could be due to founder effects, genetic drift, different ecological pressures, sexual selection, or a combination of the above.

Here, we provide an initial examination of female mating preferences in Japan blue guppies, to establish whether females favor males with greater amounts of blue in their color pattern.

Materials and methods
Study animals
All fish used in the experiment were laboratory-reared offspring (F1 or F2) of wild-caught parents that had been obtained from a local supplier. As the fish matured, males and females were separated to ensure that females were virgins, and therefore sexually responsive, when tested. Fish were housed communally in same-sex groups in aquaria measuring 900 mm× 350 mm, with a water level of 300 mm. Each aquarium contained a corner water filter, water heater, and gravel substratum, and was fitted with a Sun-Glo fluorescent tube to simulate the energy spectrum of sunlight. Fish were maintained on a 12-h light–dark cycle with a combination of natural and artificial lighting. The temperature was maintained at 24–26 °C.

The guppies were fed flake food three times daily. Measuring male characters prior to the start of the female choice experiments, each male was photographed on both left and right sides using a digital camera (Canon 600D). Males were placed individually into a small glass container that restricted movement in order to allow photographs to be taken more easily. A section of ruler was included for scale. Males were positioned near a window so that the side being photographed was lit by natural lighting. The room also contained an overhead fluorescent bulb. Photographs were taken side-on at a distance of approximately 100 mm. These conditions were kept constant for all images taken. From these photographs, NIH Image J software (http://rsb.info. nih.gov/ij) was used to obtain measurements of total body area, area of blue coloration, body length, caudal fin length, number and area of orange spots, and number and area of black spots. Boundaries defining color areas were judged by eye. Color measurements were averaged between left and right sides, and relative area was calculated as the total area of color divided by the total body area. Based on the proportional amount of blue coloration, males were separated into two groups of equal number, representing males with relatively "more" (Group A) and relatively "less" (Group B) blue color relative to the median score. Males were subsequently housed individually in 5-l containers for the remainder of the experiment to allow for easy individual identification and to ensure that the males' recent social experience was similar.

Measuring female preference

The experimental aquarium (900 mm×350 mm, with a water level of 300 mm) was maintained as per the stock aquaria (see above), but was divided into three equal compartments, separated by clear glass partitions. The central compartment was further subdivided into three equal sections, demarcated on the outside of the aquarium for ease of recording the position of the female. Three sides of the aquarium were covered with tan paper to obtain a uniform background.

Female choice was tested by placing a female in the central compartment of the aquarium and giving her 20 min to acclimatize. After the acclimation period, two males (one from Group A and one from Group B) were randomly selected from each group and placed in the two end compartments of the aquarium. The trial was then recorded on a digital camcorder (Sony Handycam DCR – TRV608E). From the video recordings, the amount of time (s) spent by the female in each of the three demarcated areas was calculated to determine female preference for each male. Time spent in the proximity of a male has been demonstrated to be a reliable measure of female choice in guppies and other poeciliid fish (e.g., Bischoff et al. 1985; Kodric-Brown 1989, 1993; Walling et al. 2010). While males were reused in more than one experimental trial, the same combination of males was not repeated. Females ($n = 20$) were only used once. In order to control for potential bias towards one side of the tank, males from each group were alternately assigned to the left or right compartment in successive trials. Fish were fed 30 min before observations and each trial lasted 15 min.

Statistical analysis

Data was first tested for normality using Shapiro–Wilk tests, and where data did not conform to a normal distribution, data was log-transformed. Student's t tests were used to confirm that males in Groups A and B differed significantly in the amount of blue color, and to establish whether they also differed in any of the other measured characters, which may have influenced female preference. Pearson correlations were used to test for a relationship between the amounts of blue, orange, and black, body lengths and caudal fin length in males. A paired t test (time as the dependent variable, group as the independent variable) was used to test for a difference in the amount of time that females spent near each of the two groups of males. To test whether any other male traits may have influenced female preference, a general linear model (GLM) was conducted, with the difference in the amount of time the female spent in the two choice sections as the dependent variable and differences in orange area, black area, body length, and caudal fin length between paired stimulus males as co-variates. All statistical analyses were carried out using IBM SPSS Statistics 20.0.0 (IBM2011).

Results

Males placed in Group A (more blue) had significantly larger amounts of blue in their color patterns than males in Group B (less blue). The two groups did not differ significantly in any other measured character (Table 1). A comparison of traits for the two groups is shown in Table 1. Correlations of male characters revealed that blue area was positively correlated

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with caudal fin length only ($r = 0.537$, $P = 0.048$). Body length and caudal fin length were also significantly correlated with each other ($r=0.582$, $P=0.029$). All other correlations between measured male characters were non-significant. Because of the observed correlation between blue area and caudal fin length, an ANCOVA was performed with blue area as the dependent variable, group as the fixed factor, and caudal fin length as the co-variate. This served to confirm whether blue was the only trait that differed significantly between males of the two groups. Results of this ANCOVA showed that blue differed significantly between the groups ($F_{1,37} = 90.716$, $P<0.001$), but caudal fin length did not ($F_{1,37} = 0.063$, $P=0.803$).

Results from the female choice trials showed that females spent significantly more time with males from Group A (more blue) than they did with males from Group B (less blue) ($t_{19} = 2.587$, $P=0.014$) The amount of time females spent in each of the three sections of the choice tank is shown in Fig. 1. The results of the GLM showed that none of the other measured male characters significantly influenced female preference (black: $F_{1,15} = 0.856$, $P=0.369$; orange: $F_{1,15} = 0.213$, $P=0.651$; caudal fin: $F_{1,15} = 1.338$, $P=0.265$; standard length: $F_{1,15} = 0.359$, $P=0.558$).

Discussion

This study provides evidence on the critical role of blue coloration as a mate choice cue in Japan blue guppies. Our results show that males with a greater amount of blue in their color pattern were more attractive to females than males with less blue, as measured by the amount of time females spent close to them. Other measured male traits were not correlated with the amount of blue, with the exception of caudal fin length. However, males from the two groups did not differ significantly in caudal fin length, which suggests that females have a preference for blue that is independent of caudal fin length. The significance of blue in the color pattern of males of this population is underlined by the observation that blue has become exaggerated at the expense of other pattern elements. Black and orange account for a relatively small proportion of total body area, and cover less than one-sixth the area covered by blue (median values shown in Table 1). Although color patters vary significantly among populations, wild-type guppies typically have a far greater proportion of the body covered by orange and black spots than the values observed in this population (Alexander and Breden 2004; Kemp et al. 2008). It is intriguing that a male ornament of such importance to female choice in other populations (orange pigment) has become reduced to such an extent that it either covers a very small area of the body or is completely absent in the color pattern of individual males.

The exaggerated expression of blue and the corresponding female preference for this trait in the study population may be due to a number of non-mutually exclusive factors, including founder effects, female preferences, or ecological differences. Genetic founder effects in the introduced population could be responsible for the observed disparity between this population and others. If founding males had an unusually high expression of the trait and/or founding females had an unusually strong preference for the trait, this

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could be sufficient to drive the evolution of the trait, assuming genetic linkage between trait and preference (Houde 1994).

Table 1 Median values and standard errors of the median of male characters in Group A and Group B, and results of *t* tests comparing males from each group; blue area is the only character that is significantly different between the two groups

Male character	Group A Median ± SE$_m$	Group B Median ± SE$_m$	Significance *t*	*P*
Blue area (%)	39.81±1.52	30.14±1.14	6.397	<0.001
Black area (%)	2.23±1.31	1.37±0.47	1.938	NS
Orange area (%)	3.35±1.09	3.19±0.97	0.533	NS
Caudal fin length (mm)	8.15±1.89	5.72±0.86	2.051	NS
Standard length (mm)	16.79±0.46	17.04±1.00	0.542	NS

Fig. 1 Average amount of time (mean and standard deviation) spent by females with males of Group A (more blue), Group B (less blue) and in the neutral (no choice) zone
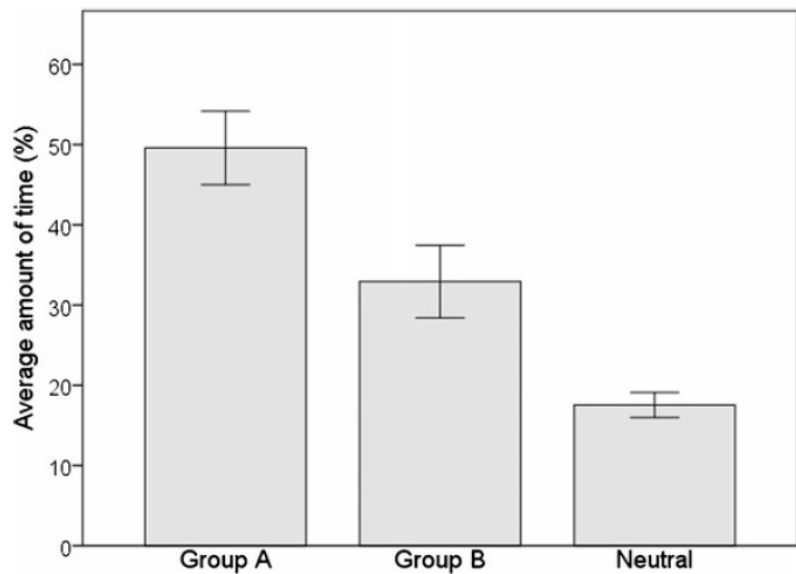
Alternatively, evolving female preferences may be responsible for the altered phenotype of Japan blue males. Sexual selection is known to be a strong driving force of male trait divergence (e.g., Uy and Borgia 2000; Maan and Seehausen 2011). If female Japan blue guppies developed a strong preference for blue coloration, this could explain both the high phenotypic expression of blue in males and the reduced expression of other, less preferred colors, which compete for space on the body surface.

A further possibility is that there has been selective pressure for an increase in blue in order to aid conspicuousness in the surrounding natural environment. Differences in the ecological environment of an organism can promote divergence and may ultimately lead to reproductive isolation (Rosenblum and Harmon 2010; Sobel et al. 2010; Riesch et al. 2011). In animals that rely on signaling systems for mate choice cues, any alteration of the environment under which signaling occurs can critically influence both the nature and perception of signals. Divergence in both mating signals and preferences as a result of ecological differences is referred to as sensory drive (Endler 1992, 1993), a process whereby male traits evolve to exploit the sensory capabilities of females, of which mating

preferences are a by-product (Endler and Basolo 1998; Tobias et al. 2010; Egger et al. 2011). Colors that function as visual mate choice cues will have the greatest impact when they achieve maximum contrast with the background. According to the sensory bias hypothesis, signals that transmit more effectively in a particular environment are favored by selection (Endler 1992). That the evolution of visual signals may be strongly dependent on ambient lighting conditions is supported by empirical studies (e.g., Douglas et al. 2007; Doucet et al. 2007). Under such a scenario, blue coloration would be selected for if it is more conspicuous to females than other colors under local lighting conditions (Endler and Basolo 1998). Previous studies on fish have shown that clearer water with a higher transmission of short (blue) wavelengths is associated with the appearance of red color morphs, while heavily stained water with a lower transmission of short wave-lengths is associated with an increase in blue color morphs (Reimchen 1989; Fuller 2002). Furthermore, female guppies living in environments with a higher transmission of shorter wavelengths of light have a greater preference for males with blue and silver iridescent colors (Endler and Houde 1995). Light intensity does not only affect the physical appearance of males, but also their behavior. Males guppies exposed to lower levels of light are shown to increase their rates of display (Endler 1987; Archard et al. 2009) and to display at a closer range to the female (Long and Rosenqvist 1998). Further investigation is warranted in order to assess the natural conditions under which Japan blue guppies evolved, and to determine whether this has impacted the physical appearance as well as the behavior of the fish.

Not only lighting conditions but also other ecological factors may impose selective pressures on color pattern. Differences in predation pressure have been shown to cause a corresponding change in male coloration in guppies (Endler 1978). Males from high predation populations have fewer color spots, particularly blue and iridescent ones, and there is a closer match between spot size and gravel size in these populations (Endler 1980). Transplant experiments have also demonstrated that changes in predation pressure can cause guppy populations to evolve extremely rapidly (Magurran 1998), thus allowing populations to diverge in color pattern over relatively short time periods.

In conclusion, the results presented here indicate that the predominantly blue color pattern of male Japan blue guppies may have arisen as a result of female preferences. This is the first study to examine female preferences in this unusual feral population, and more studies are needed to further investigate the roles of mate choice as well as other factors in the evolution of these guppies.

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