ANIMAL BEHAVIOUR, 1999, **58**, 907–916
Article No. anbe.1999.1225, available online at http://www.idealibrary.com on IDEAL

Familiarity leads to female mate preference for novel males in the guppy, *Poecilia reticulata*

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(Received 11 December 1998; initial acceptance 6 April 1999; final acceptance 17 June 1999; MS. number: A8148R)

Guppies are a model vertebrate for studies of sexual selection and life history evolution. None the less, there have been few investigations of the factors responsible for maintaining extreme within-population genetic variation in male coloration. In a laboratory study, we tested the hypothesis that frequency-dependent mate choice contributes to the maintenance of this variation. We attempted to avoid biases inherent in earlier studies of the 'rare male effect' by familiarizing females to males bearing a particular colour pattern and later presenting them with alternate male types, in equal numbers. Females were significantly more likely to mate with males having novel colour patterns than with males having a colour pattern with which they were familiar. This result is consistent with the hypothesis that mate choice is frequency dependent. Other factors such as male and female size were unrelated to mate preference. Implications of the results for theories of sexual selection and the maintenance of variation are discussed.

Understanding the causes and consequences of genetic variation is one of the key challenges of modern population biology (Lewontin 1974; Kimura 1983; Gillespie 1991). Behavioural mechanisms can play a role in maintaining genetic variation in traits related to survival and reproduction and are therefore an important, but often overlooked, source of variation in organismal fitness. In the simplest scenario, genetic variation within a population is maintained by a balance (equilibrium) between the input of new variation by mutation and elimination of (mostly deleterious) mutations by natural selection. However, population genetic models indicate that some forms of natural selection can actively maintain variation at higher levels than are expected under the simple scenario (reviewed in Charlesworth 1987; Barton & Turelli 1989). Heterozygote advantage, environmental heterogeneity (in which the relative fitnesses of alternative alleles changes in different environments), and frequency-dependent fitness (in which the relative fitnesses of alternative alleles depends upon their frequency within the population) are all forms of selection that can maintain genetic variation at higher levels than expected under mutation alone. Behavioural mechanisms can lead to the maintenance of variation by one of these forms of selection: for example, a mating preference for rare or novel mates is a form of frequency dependence that can maintain multiple genotypes within a population (Farr 1977, 1980b; Lank et al. 1995).

In guppies, extreme within-population variation for male coloration has been noted (e.g. Haskins et al. 1961; Endler 1978). Mature males display colour patterns characterized by irregular areas of structural (blue, green and purple areas) and pigment-based (yellow, orange, red and black) colours. These colours can appear on the body, caudal fin, or dorsal fin and vary in position and size. This variation has a genetic basis (Winge 1922, 1927; Winge & Ditlevsen 1947; Haskins et al. 1961). It is apparently under selection, as it is associated with variation in mating success (Farr 1980a; Endler 1983; Houde 1988), female mate preference (Kodric-Brown 1985; Breden & Stoner 1987; Houde 1987; Stoner & Breden 1988; Reynolds & Gross 1992; Brooks & Caithness 1995; Endler & Houde 1995) and predation risk (Endler 1978, 1980, 1983). Despite abundant variation in male coloration and strong evidence for selection operating on it, there have been few direct tests of the selective forces that can maintain it (Farr 1977; Endler 1980).

Frequency-dependent selection, in which rare phenotypes are favoured over common ones, is a form of

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