Reversible frequency-dependent switches in male mate choice

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Current sexual-selection theories predict that mating should occur preferentially with the highest-quality partner, and assume that for distinguishing among potential mates the choosy sex applies an internal representation of the characteristics of the desired mate, i.e. a template. Binary choice experiments were performed to test male mate choice between two different female colour morphs in the damselfly *Ischnura elegans*. Choice experiments were conducted before and after an habituation period, during which males were exposed to only one female colour morph. Given the choice between the two female morphs, males did exhibit a choice for the most recently experienced female morph. This is the first evidence for a reversible switch in mate choice in a frequency-dependent way. In contrast with previous studies on mate choice, template formation in male *I. elegans* seems not to be based on quality. Switching mate choice in a frequency-dependent manner, choosing the most common morph, probably allows males to minimize their search efforts and to maximize fitness.

Keywords: mate choice; frequency dependence; habituation; colour polymorphism; Odonata

1. INTRODUCTION

During the last decades, the study of mate choice has been one of the major endeavours of behavioural ecology and researchers have been successful in identifying the mechanisms of mate choice in many species. Mate choice is defined as any behaviour by an individual that restricts its set of potential mates (Halliday 1983; Wiley & Poston 1996; Widemo & Sæther 1999). A key factor in mate choice is the internal representation of the characteristics of the desired mate, i.e. the template, which can be genetically determined or learnt (Krebs & Davies 1996; Owens & Rowe 1999; Widemo & Sæther 1999). Matings will occur when the phenotype of the potential mate bears sufficient resemblance to the template. Traditionally, models on mate choice and sexual selection assume that these characteristics are a reflection of mate quality. Moreover, mate choice is assumed to be fixed within an individual and should not change based on recent experience with potential mates (reviewed by Kirkpatrick & Ryan 1991; Andersson 1994; Krebs & Davies 1996; but see Hughes *et al.* 1999; Westneat *et al.* 2000).

An ideal system in which to study template formation is offered by the widespread phenomenon of discrete polymorphisms (Falconer & McKay 1996). The advantage of such a system is the simplicity of studying template formation and its determination due to the discrete differences among morphs. We focused on a species with a colour polymorphism limited to the female sex. Female-limited colour polymorphisms are encountered in various hummingbirds (see Bleiweiss (1992) and references therein), some Lepidoptera (Cook *et al.* 1994), a marine copepod (Fava 1986) and several Odonata (e.g. Corbet 1999). Recently, we have shown that males of the polymorphic damselfly *Ischnura elegans* (Coenagrionidae: Odonata) do not mate randomly with respect to female

colour morph (Van Gossum *et al.* 1999a). In the latter study, binary choice experiments performed in populations with different female morph frequencies showed that males mated with the most common female morph in the population (Van Gossum *et al.* 1999a). By experimentally switching the frequency of the female morphs we tested whether this choice is fixed or plastic and can be changed in a reversible way.

2. METHODS

(a) Subjects and study site

In total, three adult female colour morphs coexist in populations of *I. elegans*: infuscans and infuscans-obsolata, both gynochrome females, and typica, the androchrome female (e.g. Askew 1988). While androchrome females resemble the males completely, gynochrome females do not (Parr 1965). As shown recently, males cannot discriminate between the gynochrome females, probably because both morphs differ only slightly (Cordero *et al.* 1998; Van Gossum *et al.* 1999a). Differences between gynochrome female morphs are restricted to the absence of black humeral stripes on the thorax of infuscans-obsolata, while the pale parts of the thorax also differ slightly in colour. Therefore, we treated the gynochrome female morphs together in this study. Mate choice was first examined in a field population in Niel, northern Belgium. After this choice experiment, animals were transported to a study site at the campus of the University of Antwerp, northern Belgium, called 'Biotuin'. Outdoor insectaries (3 m × 3 m × 2.5 m) (for more details, see Van Gossum *et al.* 1999b) were used to house the animals and to perform further experiments.

(b) Mate choice experiment

First, male mate choice was tested directly after capture in the field population in Niel with a binary choice experiment (21 June 1999; figure 1, BC1) (see also Van Gossum *et al.* 1999a). One female of each colour morph was placed in a small cage (30 cm × 30 cm × 30 cm) before a single male was introduced.

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Figure 1. Male (M) mate choice for female morphs (A, androchrome; G, gynochrome) in binary choice experiments (BC). BC1 before and BC2, BC3 following habituation periods in insectaries during which males were exposed to the morph that was previously not chosen. *p*-values refer to binomial tests.

The trial was stopped when a male had chosen or after 120 s (see also Van Gossum *et al.* 1999a). Most males approached a female within the first 30 s. For each trial, a new male and new females were placed in the cage. Females quite often prevented males from mating by spreading their wings and curling their abdomen (see also Van Gossum *et al.* 1999a). Therefore, we interpreted a male's attempt to grasp a female at the prothorax as an indication of choice. Claspings a female at the prothorax is the stage before the actual formation of the mating association (e.g. Miller 1987). After the trial, males that did try to grasp a female were transported to 'Biotuin' and were placed in an insectary with 20 females of the non-preferred morph from the same study population. Those females were not used in the first binary choice experiment and remained in the assigned insectary during the further experiments (figure 1, BC2 and BC3). During the habituation period, individuals were free to interact for two days. Pairs were seen mating and females ovipositing. A second binary choice experiment (figure 1, BC2) was then conducted by placing the males again in the small cages with freshly captured females of both colour morphs from the study population. Afterwards, the males were returned to insectaries containing the non-preferred female morph (based on this second binary choice experiment) for a second habituation period. Finally the binary choice experiment was repeated for a third time in an identical way (figure 1, BC3). Outcomes of binary choice experiments were analysed by performing binomial tests.

3. RESULTS

After two days in the insectary with only gynochrome females, males chose to mate with gynochrome females in the majority of the binary choice trials (figure 1, BC2, upper part). Out of the 12 males tested, four did not choose or failed to react to females, whereas seven chose to mate with a gynochrome female and one chose to mate

with an androchrome female. After two days of exposure to only androchrome females the reverse was observed (figure 1, BC2, lower part). Out of the 29 males tested, five failed to react to females, whereas 22 chose to mate with an androchrome female and two chose to mate with a gynochrome female.

Also in the final binary choice experiment, males chose to mate with gynochrome females in the majority of the cases after two days in the insectary with only gynochrome females (figure 1, BC3, upper part). Out of the 23 males (adding the 22 males that reversed preference after two days with the one that did not prefer androchrome females after two days of experience with only this morph) tested, four failed to react to females, whereas 18 chose to mate with a gynochrome female and one chose to mate with an androchrome female. Analogously, after two days of exposure to only androchrome females the reverse was observed (figure 1, BC3, lower part). Out of the nine males tested (adding the seven males that reversed choice with the two that did not reverse their choice and continued to prefer gynochrome females), two failed to react to females, whereas six chose to mate with an androchrome female and one chose to mate with a gynochrome female.

4. DISCUSSION

We provide for the first time, to our knowledge, evidence for a reversible switch in male mate choice in a frequency-dependent way. Indeed, the findings of our experiments indicate that if female morph frequency in the population changes, males can respond to this switch and adjust their mate choice as a function of female morph frequency.

Our results suggest that template formation in male *I. elegans* is based on discrete differences between colour morphs (possibly body coloration). Until now, clear evidence is lacking for a possible correlation between colour morph and fitness advantages (e.g. Fincke 1994; Cordero *et al.* 1998). Since we used the same females during both habituation periods, such a correlation between colour morph and quality, even if present, cannot have determined male choice. Therefore, the discrete characteristics applied for template formation in the study species do not support current models on mate choice because it contradicts the idea that templates are adjusted as a function of mate quality.

Frequency-dependent choice, evidently, does not exclude the potential use of additional cues to decrease the potential set of partners. Differential cues which are used hierarchically to narrow down the search at each stage are probably universal (e.g. Jennions & Petrie 1997). Therefore, we do not intend to exclude mate choice on female quality after the choice for a certain female colour morph. This mechanism also does not exclude the possibility of female mate choice among males (see Fincke 1997).

The system of switching between female colour morphs is in many ways identical to a predator foraging on polymorphic prey species or different types of prey, whereby the consumer concentrates on the most profitable prey (e.g. Begon *et al.* 1995, pp. 302–304). Analogously, a male's ability to attune its mate-recognition template to the most abundant morph is likely to be advantageous in terms of

reduced search time. Especially because the frequency of female colour morphs often varies rapidly (spatial and temporal) within natural populations (Fincke 1994; Cordero *et al.* 1998; Sirot 1999). We argue that this reversible switch in mate choice may be widespread in polymorphic species, especially in those that practise a scramble competition polygyny where females are not concentrated in monopolizable patches (Andersson 1994). Evidently, this mechanism of mate choice may have great implications on an individual's realized fitness. In scrambling species, males compete by trying to reach and successfully mate with receptive females before their rivals do. The most persistent and perceptive searchers enjoy highest mating success. A plastic, frequency-dependent mate recognition template allows males to adapt to the most common morph in the population, thus minimizing their search efforts and maximizing mating success.

The mechanisms creating maintenance of different colour morphs within populations are still debated. Traditionally, negative frequency-dependent selection has been invoked to explain maintenance of different colour morphs (e.g. Allen 1988; Hughes *et al.* 1999; but see Endler 1988; Partridge 1988). Interestingly, our study shows that positive frequency-dependent selection is also compatible with morph coexistence. At the moment, however, we cannot rule out the possibility that other negative frequency-dependent processes (such as predation) actually drive the coexistence of female morphs. Further experimental and theoretical work is needed to determine whether the observed positive frequency-dependent mate choice is neutral, favouring or dis-favouring colour morph coexistence.

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