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The importance of novelty: Male–female interactions among blue-black grassquits in captivity

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ABSTRACT

Mate choice is a primary mechanism driving the evolution of sexually selected traits such as elaborate displays and ornaments. In a majority of taxa studied to date, females are seen to actively sample and evaluate multiple males, presumably to optimize mating opportunities. During this process females may encounter males both familiar and novel, a distinction that might influence how mate choice proceeds. Using a socially monogamous passerine, the blue-black grassquit (*Volatinia jacarina*), we studied how females respond to novel versus familiar ("paired") males, and how encounters with novel males influence subsequent interactions with their paired males. Additionally, we measured the hormonal response of males after visualizing their paired females interacting with novel males. We found that females were attentive to novel males irrespective of these males' phenotypic attributes, suggesting that in these interactions novelty is highly relevant. After exposure to novel males, females tended to respond aggressively towards their paired males; by contrast, the behaviour of males towards their paired females did not change. Moreover, we did not detect any hormonal responses of males to viewing their paired females interacting with novel males. Together these results suggest that the distinction between familiarity and novelty may hold special relevance for females in mate choice, a finding that bears upon our understanding of the evolution of extra-pair paternity and reproductive behaviour.

1. Introduction

Mate choice is often considered the principal mechanism of sexual selection, driving the evolution of elaborate mating ornaments and displays (Andersson, 1994; Andersson and Simmons, 2006; Kokko et al., 2006). Yet, for most species we know surprisingly little about the mechanisms that underlie mate choice. Basic information is often still required regarding, for example, which ornaments, colour patterns and behaviours are being assessed, what kinds of information these traits encode, and what benefits animals derive by choosing specific mates. Some long-standing questions about mate choice also concern the strategies females use in mate sampling. As females sample multiple males, how do they compare them and how do they decide which male is the optimal partner (e.g., Beckers and Wagner, 2011)? In this regard, studies in diverse taxa suggest that females sampling mates exhibit some preference for novelty over familiarity (fruitflies: Ödeen and Moray, 2008; crickets: Gershman, 2008; pseudoscorpions: Zeh et al., 1998; and guppies: Hughes et al., 1999). In a recent study on bearded reedlings (*Panurus biarmicus*), for instance, females showed interest in novel males that was independent of their social partners' attractiveness (Hoi and Griggio, 2012). Attending to novel males may enable females to access a wider sample of potential mates. Accordingly, in the presence of unpaired same-sex conspecifics, males may be prompted to increase contact with their mates (e.g., for mate guarding), and perhaps incidentally provide females with indirect benefits (e.g., in parental care).

One way to gain insights into mechanisms of mate sampling is through laboratory studies, which allow precise control of the variables that are presumed to influence mate choice. In birds, studies with captive populations have emphasized the function in mate choice of both visual and acoustic signals, often showing that females prefer males with elaborate sexual traits (Burley et al., 1982; Hill, 1990; but see Widemo and Saether, 1999 and Griggio and Hoi, 2010 for alternative examples). Female house sparrows (*Passer domesticus*), to illustrate, prefer to associate with males with larger melanin-based ornaments (Møller, 1988) and

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larger white wing bars (Moreno-Rueda and Hoi, 2011); female common pheasants (*Phasianus colchicus*) prefer males with longer tails (Mateos and Carranza, 1995); and female swamp sparrows (*Melospiza georgiana*) give more copulation solicitation displays in response to playback of songs of high vocal performance (Ballentine et al., 2004). By contrast, the relative roles of familiarity versus novelty in mate sampling by captive birds has been relatively overlooked.

In passerine birds, we might predict females to be partial to novel males, given high natural rates of extra-pair paternity (EPP) (Griffith et al., 2002). This is because females are thought to derive greater benefits from mating with multiple partners than from mating repeatedly with the same partner (Jennions and Petrie, 2000; Griffith et al., 2002; Eakley and Houde, 2004; Neudorf, 2004; Macedo et al., 2008). The benefits of extra-pair mating for females can be either indirect or direct. Indirect benefits are usually genetic and have been the focus of multiple studies (Kempenaers et al., 1992; Stapleton et al., 2007, but see Ferreti et al., 2011; Lee, 2012). Direct benefits, on the other hand, are not as clearly detected nor easily interpreted, but have been demonstrated in a few studies (Gray, 1997; Townsend et al., 2010). To gain the benefits of extra-pair mating, females must spend time and energy searching for and evaluating extra-pair mates, and may put at risk their social partners' investment in parental care (Petrie and Kempenaers, 1998). The distinction between novel and familiar males may ultimately influence how females balance the costs and benefits of mate selection.

Male behaviour also likely influences female mate selection. Given the high costs associated with loss of paternity, males already paired with females are expected to discourage those females from seeking extra-pair copulations. Male tactics towards this end may include mate guarding (Beecher and Beecher, 1979), decreasing paternal investment in nests with extra-pair young (Weatherhead et al., 1994; Gowaty, 1995), and retaliating aggressively against females that stray (Westneat and Stewart, 2003). In the latter case, aggression and forced copulations have been described for contexts where males are unsure about female fidelity (Johnstone and Keller, 2000; Valera et al., 2003).

Mechanistically, male mating tactics and aggression are regulated in part by steroids, namely testosterone (T) and corticosterone (CORT). Varying circulating levels in these steroids influence male social behaviours including mate guarding, male–male interactions, and responses to territorial challenges, and can also modulate the expression of subsequent behaviours (Wingfield et al., 1990; Oliveira, 2004; Soma, 2006). For example, short exposure to simulated territorial intrusions conducted with the song sparrow, *Melospiza melodia*, led to increased T plasma levels 10 min after the event, and T levels remained elevated for up to 1 h afterwards (Wingfield and Wada, 1989). However, because maintaining high T levels generates various physiological costs, the challenge hypothesis predicts that T levels should be elevated only when needed (Wingfield et al., 1990). CORT is released by the adrenal gland, and plasma concentration in birds typically increases significantly after about 3 min in response to stress (Wingfield and Silverin, 1986; Romero and Romero, 2002). While much is known about how these steroids vary with male–male interactions, less is known about how they might regulate male responses to female behaviour.

Here we studied, in a captive population of blue-black grassquits (*Volatinia jacarina*), female responses to novel versus familiar ("paired") males, as well as male behavioural and physiological responses when their paired females were exposed to novel males. With this study we seek to clarify the factors that influence female readiness to copulate with extra-pair partners, how female behaviour may affect the dynamics of a pair, and how males might respond to females that interact with novel males. First, we asked whether "paired" females show any interest in novel males. Despite their socially monogamous mating system, female blue-black grassquits in nature show high rates of extra-pair mating (Carvalho et al., 2006; Manica et al., unpublished data), which suggests that females in captivity might likewise show an interest in novel males. Second, we asked whether any interest females do show in novel males is influenced by the novel males' body condition and plumage traits, both absolutely and relative to traits of her paired male. We expected females to exhibit interest especially when a novel male was phenotypically superior to the social mate. Third, we assessed social pairs' behaviour following the experimental procedure, when male and female pairs were reunited, after females had been exposed to novel males. We expected that interactions of paired females with novel males would elicit reactions from socially paired males, both physiologically (e.g., increases in T and CORT) and behaviourally (e.g., increased aggression directed towards the paired female).

2. Methods

2.1. Study organism

The blue-black grassquit is a socially monogamous, intratropical migratory passerine. Field observations indicate that breeding territories are tightly clustered in a *lek*-like spatial pattern (Webber, 1985; Almeida and Macedo, 2001). Before the breeding season males moult and acquire an iridescent, structurally coloured blue-black plumage, with peak reflectance in short wavelengths (Maia et al., 2009). Throughout the breeding season, males produce characteristic courtship displays, in which they leap upwards, reveal white wing patches while flapping their wings, and emit short vocalizations (Alderton, 1963; Almeida and Macedo, 2001). In addition to these displays, male reproductive effort includes nest construction and provisioning of young (Alderton, 1963; Almeida and Macedo, 2001). Blue-black grassquits have one of the highest levels of extra-pair fertilization rates in passerine birds, of approximately 50% of nestlings in over 60% of sampled nests (Carvalho et al., 2006). A laboratory study showed that social context relative to group composition (i.e. number of males interacting in a group) affected male testosterone plasma concentration and behaviour (Lacava et al., 2011).

2.2. Study subjects

A total of 120 individuals (60 males and 60 females) were mist-netted within the Campus of the University of Brasilia (15°46′ S, 47°52′ W) in December of 2004/2005 and January of 2005/2006, which is at their peak breeding time. Until the end of June 2005, males and females were kept as separate groups and in visually isolated compartments of an outdoor aviary (3.0 m × 3.0 m × 2.0 m) that was exposed to natural conditions of lighting and temperature. At this time (5 months before experiments began in each year), males and females were paired randomly ($N = 60$ pairs) and placed in individual cages (0.70 m × 0.50 m × 0.40 m) within the outdoors aviary. Cages were visually but not acoustically isolated. Cages were set up side by side with visual barriers between them. Experimental trials were conducted from December to February in 2005/2006 and 2006/2007, months that coincide with the grassquits' breeding season in central Brazil. During the pre-experimental and paired phase, paired males were observed to produce display leaps and vocalizations, and to copulate, indicating that courtship and reproductive activities were developing normally. The additional captured males ($N = 11$: 2005/2006 = 5; 2006/2007 = 6) and females ($N = 6$) were maintained in same-sex shared cages (1.5 m × 3.0 m × 2.0 m), to be presented to paired males and females as "novel" stimuli (see below). All birds were