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Dynamic mate-searching tactic allows female satin bowerbirds *Ptilonorhynchus violaceus* to reduce searching

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Females can maximize the benefits of mate choice by finding high-quality mates while using search tactics that limit the costs of searching for mates. Mate-searching models indicate that specific search tactics would best optimize this trade-off under different conditions. These models do not, however, consider that females may use information from previous years to improve mate searching and reduce search costs in subsequent years. We followed female satin bowerbirds *Ptilonorhynchus violaceus* during mate searching and reconstructed their search patterns. We found that females who chose very attractive males typically mated with the same male in the following year, resulting in these females sampling fewer males than those who switched mates. In contrast, females who mated with less attractive males typically rejected their previous mates and searched longer for more attractive mates in the following mating season. A potential cost to mate searching is suggested by the observed increase in the likelihood of force-copulation attempts from marauding males with increased searching. Our results suggest that by using past experiences to adjust their search tactics, females may obtain high-quality mates while limiting search costs. These results emphasize the need to consider historical effects in studies of sexual selection, especially for long-lived species with stable display sites.

Keywords: mate choice; mate sampling; mate searching; mate fidelity; satin bowerbirds

1. INTRODUCTION

Most studies of mate choice focus on determining which traits females prefer, often showing that elaborate display traits function as mate-choice signals and females receive benefits from choosing among males (reviewed in Andersson 1994). Far fewer studies consider how females sample and gather information about potential mates (Gibson & Langen 1996; Houde 1997). The way females search for mates will influence which they ultimately choose as mates; thus, determining how females assess males and what factors affect mate searching is necessary for a comprehensive understanding of mate choice.

In searching for mates, females are predicted to optimize the benefits of choice by balancing search costs against their ability to find high-quality mates (Parker 1983; Real 1990). Mate-searching models indicate that different search tactics perform best under specific conditions (Janetos 1980; Real 1990; Luttbeg 1996). For instance, when sampling costs are low, females should sample several males directly and then return to mate with the best of those sampled (e.g. 'best-of-*n* tactic'; Janetos 1980). If, however, costs of mate searching are high, using a pre-existing internal standard to assess potential mates is more efficient because this allows females to avoid additional sampling when a high-quality male is encountered early in the sampling sequence (e.g. 'threshold rule'; Real 1990). Two important limitations of these models, however, are the assumptions that (i) females use a single, static search tactic, and (ii) mate searching begins anew with each mating season. In long-lived animals mate searching may be a cumulative process, with matings from previous years affecting future mate-searching behaviour. Females who mate with high-quality males may reduce search costs in subsequent years by returning to mate with the same males, while naive females or those who fail to encounter high-quality males may need to search longer the following year to find more suitable mates. Thus, by using a dynamic search tactic that is adjusted according to past experiences, females can reduce searching and mate with high-quality males.

There is growing evidence that females alter their mating behaviour in response to external factors (reviewed in Jennions & Petrie 1997). For instance, laboratory studies in guppies *Poecilia reticulata* show that females adjust their choosiness according to the presence of predators (Godin & Briggs 1996; Houde 1997) and recent exposure to males of varying quality (Rosenqvist & Houde 1997). These studies indicate that the level of choosiness can be influenced by immediate experiences; however, it is unclear whether these manipulations affect mate searching.

Field studies similarly suggest that mate searching is labile, as it is affected by experience (Trail & Adams 1989), condition (Rintamäki *et al.* 1995), temporal constraints (Blackwell & Passmore 1996), and the presence of predators (Koga *et al.* 1998). Trail & Adams (1989) observed that female cock-of-the-rocks *Rupicola rupicola* who were faithful across years sampled fewer males than those who switched mates; however, the factors that influence mate fidelity and the extent to which faithful females can limit their searching are unknown. Further, all of these field studies involve leks in which male aggregations allow females to simultaneously assess several potential mates (see Höglund & Alatalo 1995), making it difficult to identify which individuals

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were sampled and thus to define accurately female search patterns.

Satin bowerbirds *Ptilonorhynchus violaceus* provide an excellent model system for studies of mate searching because each bower or display site is owned by a single male and is separated from other bowers (>100 m) (Borgia 1985*b*). Therefore, unlike lekking species, female bowerbirds must assess each male individually, allowing us to identify unambiguously which males are sampled. Courtships and matings occur at bowers (Borgia 1985*a*) where mate-searching behaviour of banded females can be monitored continuously throughout the mating season using video cameras. Bower-holders use the same bower-sites in successive years (Borgia 1993); therefore, females can use information from previous years to relocate past mates and previously sampled males. Because females are predominantly the choosy sex, copulations represent unconstrained mating decisions by females. Lastly, females arrive at bowers individually; thus, there is little opportunity for females to copy another female's mate choice (J. A. C. Uy, G. L. Patricelli and G. Borgia, unpublished observations). We monitored the mate-searching behaviour and/or mate choice of female satin bowerbirds in 1996 and 1997. Our results suggest that females enhance the trade-off between the benefits and costs of mate choice by adjusting their mate-searching tactics based on past experiences with mates.

2. METHODS

In 1995, we resumed monitoring the satin bowerbird population in Wallaby Creek (Tooloom National Park), NSW, Australia, previously studied by G. Borgia (see Borgia 1985*a*, 1993). Individual birds were fitted with unique, three-colour plastic band combinations on each leg, and categorized into sex and age groups by their plumage, morphology and size (Vellenga 1970). Individuals were captured using baited traps or mist nets prior to the mating season when banding would not interfere with mate-searching behaviour.

From 9 November to 20 December 1997, automatic Hi-8 video cameras that record time and date were used to monitor all 34 adjacent bowers covering an area of *ca.* 4 km^2. Video cameras were triggered when movement on the bower activated motion sensors, allowing for continuous and simultaneous observations of all behaviours at bowers throughout the mating season (see Borgia 1995). Typically, females initiated short courtship visits (174.53 ± 10.29 s) to several bowers early in the mating season and returned later for extended courtships (541.42 ± 36.78 s) that lead to matings. In 1996, 29 bowers at Wallaby Creek were monitored with low-resolution cameras that allowed for the accurate identification of banded females only during the extended courtships and matings. Thus, we were able to determine which males were chosen for mates, but could not identify many females during the short courtship visits to bowers. The use of high-resolution (Hi-8) cameras in 1997 resolved this problem.

Detailed mate sampling patterns of 68 females in 1997 were reconstructed using the band identification of individuals on the time- and date-stamped video footage. The sampling ranges of females visiting bowers at the edge of our population may have extended beyond the set of bowers we monitored. Several lines of evidence, however, argue that our observations are near complete. First, the bowers we monitored at Wallaby Creek form a coherent group. In 1997, 259 out of the 268 (97%) decoration stealing and bower destruction interactions (see Borgia 1985*b*) between mature males were carried out by monitored bower-holders. Second, female sampling ranges fit well within the range of the bowers we monitored. There was no difference in the number of males visited by females who exclusively sampled males at the core (2.47 ± 0.24 males) and those whose sampling range included males at the edge of our population (2.57 ± 0.25 males) (two-sample randomization test; $p = 1.00$). Additionally, females followed with radio-telemetry remained in the study site for the entire duration of the mating season. To ensure that sampling ranges were not underestimated, however, the five females who visited only a single male at the edge of our population were excluded from our analyses. Our results are not altered qualitatively by the exclusion of these females.

Thirty-six out of the 63 females we followed in 1997 were observed to mate in 1996; thus, we were able to determine if females remate with the same male for two consecutive years and how this can affect mate-searching behaviour. For this analysis, all bower-holders chosen by females as mates in 1996 were present and held bowers in 1997. Five females who mated with more than one male, however, were excluded from this analysis because females who mated with more than one male sampled more males than those who chose only one (J. A. C. Uy, G. L. Patricelli and G. Borgia, unpublished observations).

To estimate an index of the attractiveness of a male chosen by a given female, we used the male's total mating success (number of different mates) minus the mating of the focal female. Male attractiveness was estimated for the 1996 and 1997 mating seasons. The six males that accounted for 53% of all the observed matings were grouped as the most attractive males of the population. We used all 63 females to explore the relationship between increased searching and the probability of being disrupted by marauding males (see § 3(b)).

All means are expressed as $x \pm$ s.e. We used Monte Carlo simulations and permutation randomization tests involving 50 000 iterations to test for significance of hypotheses (Manly 1991). All randomization tests and Monte Carlo simulations were programmed using QBasic$^{\mathrm{TM}}$ 4.0 (Microsoft Corporation, Redmond, WA). Logistic regression was used to determine the relationship between increased searching (e.g. number of courtships visits, days spent searching and males sampled) and the likelihood of disruptions by marauding males. All tests of significance of hypotheses are two-tailed unless otherwise noted.

3. RESULTS

(a) *Variation in sampling patterns and past experience effects*

Much of the variation among females in the number of males sampled, the number of courtships visits and the number of days spent searching for mates (figure 1) can be explained by differences in past experiences with males. Past experience can influence female decisions on which males to visit for courtship and/or to mate with in subsequent mating seasons.

Twenty-nine out of the 36 females (81%) who were observed to mate in 1996 and 1997 returned to sample their mates from the previous mating season. Although the number of males within a female's home range is about five (J. A. C. Uy and G. Borgia, unpublished observations), these 36 females visited only 2.86 ± 0.25 males on average. Thus, if female home ranges constrain

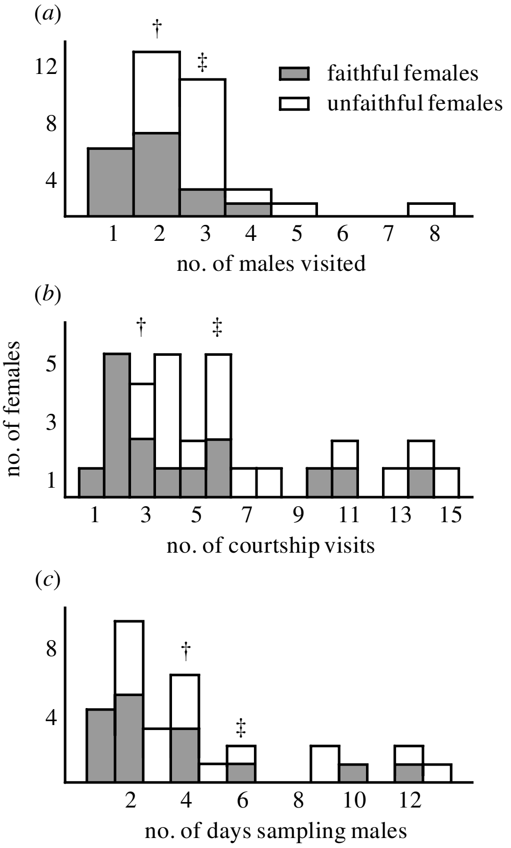

Figure 1. Distribution of (*a*) number of different males visited, (*b*) number of courtship visits, and (*c*) number of days spent sampling in 1997 for the 31 females monitored for two mating seasons († mean for faithful females; ‡ mean for unfaithful females).

mate searching, the probability that a female would encounter her previous mate by chance is about 0.6. The observation that 29 out of 36 females returned to previous mates for courtship the following year indicates that females do not sample males within their home ranges randomly (Monte Carlo simulation; $p < 0.008$).

Although females typically sampled their previous mates, only 15 out of 36 (42%) mated with the same male in 1997 and 1996 (faithful females). Sixteen females switched mates in 1997 (unfaithful females). The remaining five females mated with their previous mates in addition to a second male and were excluded from our analyses to avoid the ambiguity of having more than one mate (see § 2). Faithful females sampled fewer males (1.93 ± 0.23) in 1997 than unfaithful females (3.19 ± 0.38) (figure 2*a*). Further, faithful females mated with more attractive males (12.00 ± 1.92) in 1996 than unfaithful females (7.94 ± 1.08) (figure 2*b*). Since male attractiveness seems to affect female faithfulness, these results suggest that unfaithful females may be switching to find better mates. Thus, females who switch mates are predicted to select more attractive males in the following year, and indeed we found support for this prediction (figure 3). In fact, the attractiveness of mates of faithful (12.00 ± 1.92) and unfaithful (11.81 ±1.99) females in 1997 did not differ (two-sample randomization test; $p = 0.948$). Thus, in a single year, females who initially chose less attractive mates improved their mate choice to the level of faithful females.

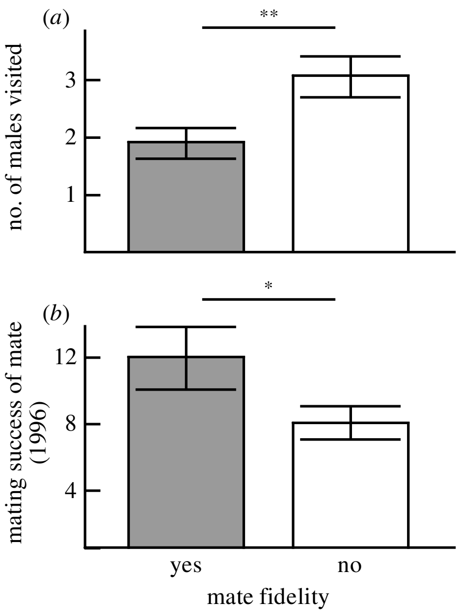

Figure 2. Differences in the (*a*) number of males visited, and (*b*) attractiveness of mates in 1996 between females who remained faithful (grey bar; $n = 15$) and those who switched mates (open bar; $n = 16$) across years (1996–1997) (two-sample randomization test; $^{**}p = 0.005$, $^{*}p = 0.021$).

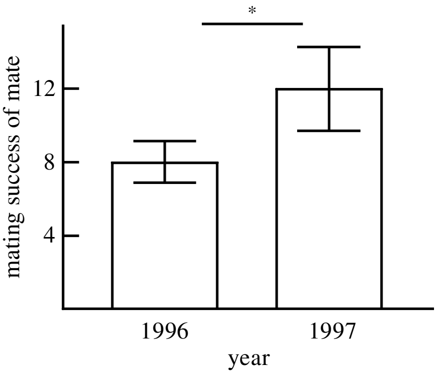

Figure 3. Differences in the attractiveness of mates between 1996 and 1997 for the 16 females who switched mates (one-tailed, paired comparison randomization test; $^{*}p = 0.047$).

Of the five females who visited only one male in 1997 (figure 1*a*), all five mated with the same male in 1996 and 1997. The probability that a female who visits only one male would show mate fidelity is the proportion of all females who were faithful (15 out of 31; 0.48). The observed association between female mate fidelity and single visits was highly significant (Monte Carlo simulation; $p = 0.02$). In addition, the five females who visited only one male mated exclusively with one of the six most attractive bower-holders, who together accounted for 53% of all the copulations in 1997. This observation suggests a significant tendency for females who visited only one male to mate with one of the most attractive bower-holders exclusively (Monte Carlo simulation; $p = 0.043$).

(b) *Potential costs of mate searching*

Courtship disruptions occur when marauding males attempt to force-copulate females during courtships and

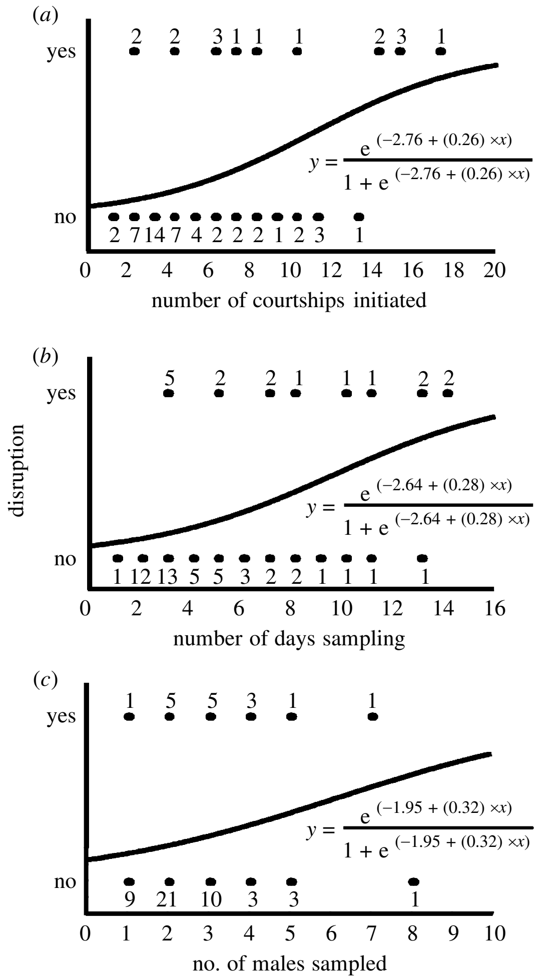

Figure 4. Logistic regression surface of the likelihood of disruptions occurring with increased (*a*) number of courtship visits, (*b*) number of days spent searching, and (*c*) number of males sampled. Numbers next to data points indicate the number of observations ($n = 63$ females).

this could be a cost of mate searching. In 1997, marauding males disrupted 31 out of the 915 (3.4%) unsuccessful courtships and 15 out of the 229 (6.5%) matings. Juvenile males who do not hold bowers performed 96.8% of these disruptions. Sixteen out of 63 (25.4%) females were disrupted at least once during mate sampling. Logistic regression analyses indicate that the probability of females being disrupted by marauding males increased with increased number of courtship visits ($\chi^2 = 12.68$, d.f. = 1, $p = 0.001$; figure 4*a*) and number of days spent searching for mates ($\chi^2 = 10.80$, d.f. = 1, $p = 0.001$; figure 4*b*). Similarly, an increase in number of males sampled increased the probability of disruption ($\chi^2 = 2.51$, d.f. = 1, $p = 0.113$; figure 4*c*). These observations suggest that females who searched longer were more susceptible to force-copulation attempts from marauding males.

Alternatively, because unfaithful females searched longer and typically sampled less attractive males, the positive association between number of courtship visits and the probability of disruptions occurring may be due to higher rates of disruptions at bowers of less attractive males. Attractive males were involved in a disproportionate number of courtship visits, and taking this into account we found that the probability of disruptions occurring for a given visit is not influenced by the attractiveness of the bower-holder (Monte Carlo simulation; $p = 0.998$). Thus, the observed positive relationship between number of courtship visits and probability of disruption is not explained by unfaithful females sampling unattractive males.

4. DISCUSSION

(a) *Dynamic mate searching*

Mate-searching models indicate that the trade-off between the benefits and costs of mate choice will dictate how females should search for mates, but assume that females would use a single search tactic (Parker 1983; Real 1990; Luttbeg 1996). These models do not consider the possibility that the accumulation of experience throughout an individual's lifetime could influence the suitability of each tactic. The results reported here suggest that female mate sampling behaviour is dynamic: females alter their search tactics using previous experiences to relocate attractive males thereby reducing search costs.

Females use information from previous mating bouts to alter their search patterns in at least two ways. First, rather than sampling males arbitrarily, females can use information from previous years in determining which males to resample or omit in the following year, thereby increasing the efficiency of mate searching. Our observation that females usually returned to sample their mates from the previous year supports this hypothesis. Second, females use information on male attractiveness retained from previous years in deciding on how many males to sample and in choosing mates. Females who were faithful sampled fewer males than those who switched mates, with one-third of faithful females returning to copulate with a previous mate without sampling other males.

If remaining faithful allows for the reduction of mate searching, why did over half of the females switch mates the following year? Our observations indicate that females who mated with very attractive males in 1996 typically mated with the same male in 1997, while those who mated with less attractive males rejected their previous mates and switched to more attractive males in the following year. Females who switched mates may have combined the information on male attractiveness accumulated from prior mating seasons and from the current sampling bout to reject their previous mates. Searching for more attractive males may have led to the observed higher rate of sampling for these females. Faithful females, in contrast, may have more experience; thus, they may have better estimates of the population's distribution of male quality and have encountered males that are attractive relative to these estimates. For these females, extensive sampling in subsequent years may become less profitable. At the extreme end of faithful females are those who remated with the same male without further sampling. These females exclusively chose one of the most attractive males of the population, suggesting that once females encounter very attractive males they can remate without additional sampling to limit search costs. Females of monogamous and resource-based polygynous species commonly remain faithful and this has been related to past breeding success, the quality of the resources provided by mates and/or advantages to quick pair formation (see Black 1996; Weatherhead 1999). In polygynous species with no male parental care, however, there has been no previous evidence that male attractiveness, which probably reflects his quality, influences mate fidelity. This is significant because for non-resource-based polygynous species, it is less clear how females decide whether to remate with or reject previous mates.

(b) *Potential costs of mate searching*

What are the search costs that drive females to reduce searching? Search costs may include direct costs such as energetic expenditure and indirect costs such as delayed clutch initiation or force-copulations from low-quality males (see Reynolds & Gross 1990). We found a positive association between increased searching and the occurrence of force-copulation attempts by marauding males. Evidence of active choice in our study suggests that females may gain benefits from mate choice. Thus, females can incur costs from force-copulation attempts by receiving unwanted matings and sperm from lower-quality males (Borgia 1995). Moreover, females can sustain injuries from these disruptions since attempts to force-copulate are violent and often involve several males attempting to mount a female (J. A. C. Uy, G. L. Patricelli and G. Borgia, personal observations). The costs associated with these violent disruptions should favour the evolution of search tactics that reduce the probability of force-copulation attempts. Using information from previous mating seasons and remaining faithful to attractive males may allow females to effectively reduce their exposure to marauding males without compromising their ability to find attractive mates.

(c) *Conditions for the evolution of dynamic mate searching*

Retaining and using information from previous years would be most effective if three conditions are met: (i) individuals are long lived, (ii) display sites are stable, and (iii) male display is repeatable across years. There is no published information on the repeatability of cock-of-the-rock display. In satin bowerbirds, however, male display such as bower architecture and quantity of decorations is highly repeatable across mating seasons (Borgia 1993; J. A. C. Uy, G. L. Patricelli and G. Borgia, unpublished observations). Both satin bowerbirds (Borgia 1993) and cock-of-the-rocks (Trail & Adams 1989) are long lived and return to the same display sites for multiple years, and in these species past experiences with individual males appear to influence subsequent mate-searching behaviour. Faithful female cock-of-the-rocks sampled fewer males than those who switched mates; however, the factors that influence mate fidelity remain unknown (Trail & Adams 1989), and it remains difficult to determine how much information females gain from observing adjacent males. Twenty out of 88 (22.7%) observed matings involved females who mated with the first male sampled, but whether these were faithful females was not reported. The use of information from previous mating seasons may allow cock-of-the-rock females to find attractive mates despite sampling fewer males (as few as one), and that female tendency to remain faithful may be affected by the attractiveness of their previous mates.

For species with stable display sites but higher mortality rates, long-term experience with individuals would be less important. In the black grouse roughly half of adult males return the following year (Johnsgard 1983, pp. 71–77) and so only a small proportion of females can remate with their previous mates (Rintamäki *et al.* 1995). Since there is a low return rate for males, females may instead use signals that are not specific to individuals yet are still reliable indicators of male quality, such as position on leks (see Höglund & Alatalo 1995).

For species with low return rates and unstable display sites, such as the ephemeral leks of buff-breasted sandpipers *Tryngites subrufollicus* (Lanctot & Weatherhead 1997) and leks on ice-covered lakes of certain black grouse populations (Hovi *et al.* 1995), information from previous mating seasons would be of little value. Therefore, mate choice decisions from previous years should have little effect on subsequent search behaviour in these species. Studies in sexual selection rarely consider the effects of individual past history on mate choice. Our study shows that, in long-lived species with stable display sites, these effects can have significant consequences on mate searching and choice.

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