THE ROYAL SOCIETY

Loss of preferred mates forces female satin bowerbirds (*Ptilonorhynchus violaceus*) to increase mate searching

J. Albert C. Uy*†, Gail L. Patricelli and Gerald Borgia*

Department of Biology, University of Maryland, College Park, MD 20742, USA

Variation in mate choice among females can have important consequences for the operation of sexual selection, and can result from differences in the way females search for mates. Our previous work indicates that female satin bowerbirds *Ptilonorhynchus violaceus* alter their mate-searching patterns according to long-term experience. Females which mate with very attractive males mate with the same males in the following year, thereby reducing their search. In contrast, females which fail to encounter very attractive males typically reject their previous mates and search for more attractive males in the following year, thereby increasing their search. Here we report results from a natural experiment consistent with these observations. Five males, including the most attractive male of 1997, failed to re-establish display sites in 1998, most probably dying over winter. We monitored the mate-searching behaviour of females which mated with these males in 1997 to determine how the loss of attractive mates affects subsequent mate-searching patterns. Females which lost their mates sampled more males compared with their own search patterns in 1997 and with faithful females in 1998. Results from this natural experiment indicate that the loss of attractive and preferred mates forces females to increase their search and provide evidence that long-term experience with males shapes mate-searching behaviour.

Keywords: mate searching; mate choice; mate sampling; mate fidelity; sexual selection; social learning; satin bowerbirds

1. INTRODUCTION

Females show intraspecific variation in several aspects of their mating behaviour (reviewed by Jennions & Petrie 1997), including their mating preferences (e.g. Johnsen & Zuk 1996), tendencies to copy mate choice (e.g. Dugatkin & Godin 1993), choices of mating sites (e.g. Koga *et al.* 1998) and levels of choosiness (Rosenqvist & Houde 1997). These differences in mating behaviour can have important consequences for the operation of sexual selection and the evolution of elaborate male display (reviewed by Widemo & Sæther 1999). For instance, variation in mate choice among females can be explained by differences in female choosiness, which in turn can be influenced by the presence of predators (e.g. Godin & Briggs 1995; Gong & Gibson 1996). Predation may cause females to lower their threshold for choice resulting in a reduced intensity of sexual selection, and reduced trait elaboration in males. Elucidation of the underlying causes of variation in female mating behaviour provides important insights into the operation of sexual selection.

One other important aspect of mate choice that can show significant variation is the behavioural rules females use when searching for mates; however, empirical tests to explain this variation are lacking (Widemo & Sæther 1999). Differences in mate-searching behaviour can result from variation in experience among females and/or variation in experience during a female's lifetime (Uy *et al.* 2000). Because searching behaviour constrains which

males are chosen as mates, variation in mate-searching behaviour should lead directly to variation in mate choice among females.

Our previous work with satin bowerbirds *Ptilonorhynchus violaceus* indicates that females use information from previous mate-searching bouts to reduce the costs associated with mate searching in subsequent years (Uy *et al.* 2000). Once a female encounters and mates with a very attractive male (a male with high mating success), she reduces searching in the following year by mating with the same male, often without assessing other males. Females which mate with less attractive males typically reject their previous mates and search for more attractive mates in the following year. These observations suggest that variation in mate searching and faithfulness among females may be explained by past experience in locating an attractive male (Uy *et al.* 2000).

The hypothesis that past experience influences female mate-searching patterns can be tested by the experimental removal of attractive males. Specifically, we predict that females which lose their attractive mates and are thus forced to switch mates will increase their searching behaviour to find suitable replacements. We had planned on initiating a male-removal experiment in 1998, but natural losses occurred in our study population that anticipated this protocol. In this natural experiment, five males, including the most attractive male in 1997, failed to return and establish bowers in 1998, presumably dying over winter. Compared with their mate-searching patterns from the previous year and with faithful females in 1998, females whose mates failed to return increased their mate searching. This natural experiment indicates that females alter their search behaviour in response to information available to them on the location of high-quality mates.

*Authors for correspondence (uy@lifesci.ucsb.edu, borgia@umail.umd.edu).
†Present address: Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA.
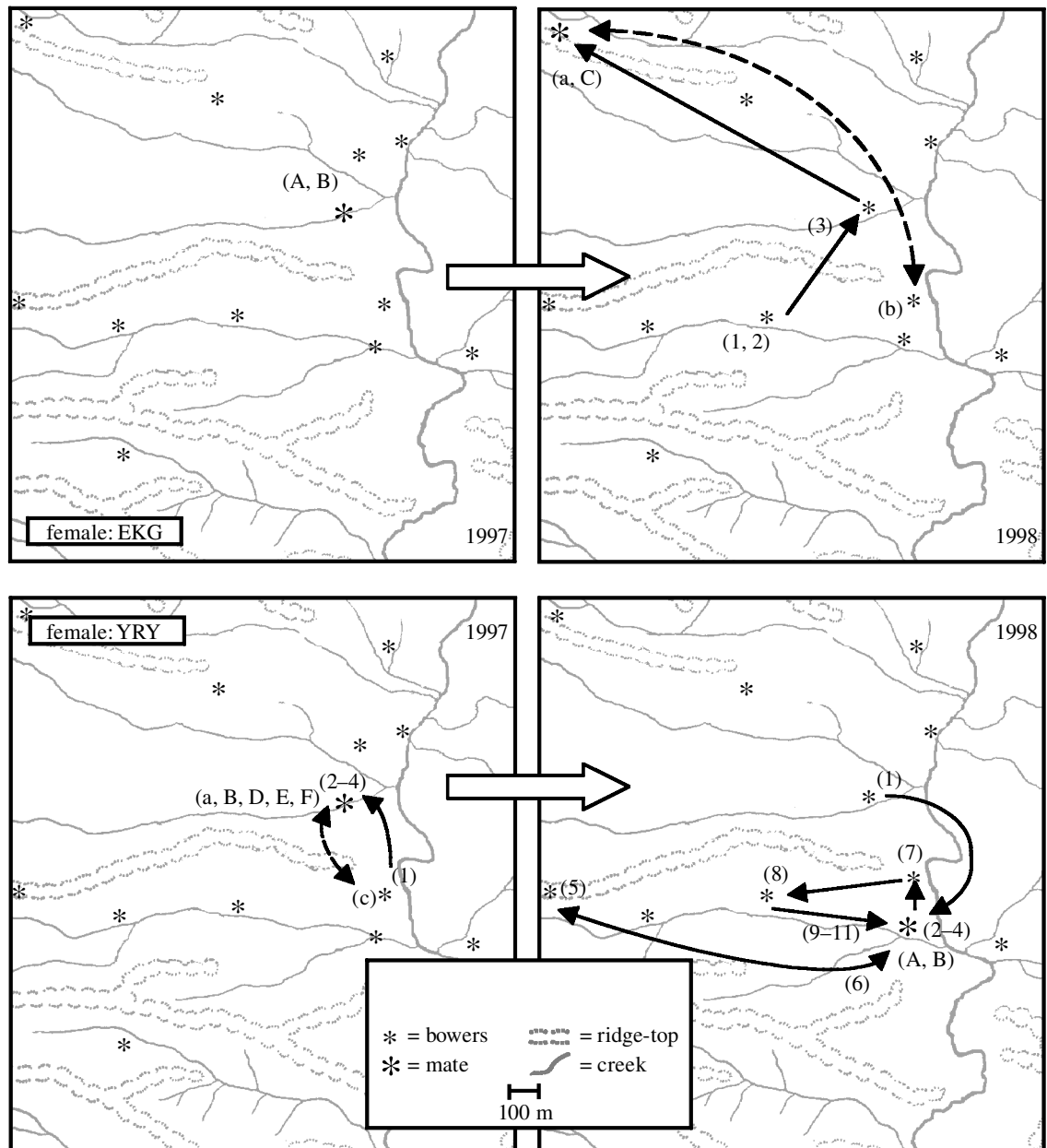
Figure 1. Comparison of search patterns in 1997 (left panels) and 1998 (right panels) for two females which lost their mates in 1998. Both females were faithful to their mates across the 1996 and 1997 mating seasons. Female satin bowerbirds initiate two distinct sampling bouts, separated by a period of nest building (Uy *et al.* 2000). Numbers indicate courtship visits initiated before nest building, with solid arrows representing female movement between bowers. Letters indicate courtships initiated after nest building, with lower-case letters representing failed courtships and upper-case letters representing successful courtships (matings). Broken arrows indicate female movement for courtships (or matings) after nest building.

2. METHODS

(a) *Satin bowerbird mating system*

Satin bowerbirds provide an excellent model system for studies of mate searching for several reasons. First, females are the only choosy sex, and polygynous males provide no parental care to their young (Vellenga 1971; Borgia 1985*a*); therefore, the confounding effects of mutual mate choice do not exist. Second, each display site or bower is owned by a single male and, unlike in lekking species, these display sites are well separated (> 100 m apart) (Borgia 1985*b*) (figure 1) so that females must assess males individually. Third, 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. Fourth, males use the same bower-sites in successive years and male bower display is highly repeatable across years (Borgia 1993), providing females with information useful for relocating previously sampled males and past mates.

(b) *Monitoring mate-searching behaviour*

Our study site was located in Wallaby Creek (Tooloom National Park), New South Wales, Australia (see Borgia 1985*a*). Satin bowerbirds feed in flocks and readily enter baited traps before the mating season; thus, individuals could be captured and banded without interfering with their mating behaviour. Individuals were fitted with unique, three-colour plastic band combinations on each leg that allowed us to

identify females on videotapes of their behaviour at bowers (Uy *et al.* 2000).

Automatic Hi-8^{TM} video cameras that record time and date were used to monitor all the bowers in our study population in 1997 (from 9 November to 20 December) and 1998 (from 28 October to 20 December). Thirty-four and 32 adjacent bowers were monitored in 1997 and 1998, respectively. Video cameras were triggered when motion sensors were activated by movement on the bower (see Borgia 1995), allowing for continuous and simultaneous observation of all behaviours at bowers at our study site. In 1996, 29 bowers were monitored with lower-resolution video cameras that allowed for the accurate identification of females during extended courtships, such as those that led to matings, but not shorter courtships that typically result in rejection of males. Thus, we could identify which males were chosen as mates, but could not accurately reconstruct female mate-searching patterns for the 1996 mating season. Bower positions were mapped using transect and Global Positioning System readings (figure 1). Weekly counts ($n = 5$) of number of decorations for each bower were used to estimate repeatability of bower display for the 1997 and 1998 mating seasons.

Detailed mate-searching patterns of females were reconstructed using the band identification of individuals on the time- and date-stamped video footage. Mate-searching patterns were mapped for each female to determine which males were sampled, number of courtships initiated, and the physical area traversed to search for mates (figure 1). Mate sampling sequences for 68 (see Uy *et al.* 2000) and 78 females were reconstructed in the 1997 and 1998 mating seasons, respectively. To avoid underestimating female sampling ranges, the five females in 1997 and the seven females in 1998 which sampled only a single male (and mated with him) at the edge of Wallaby Creek were excluded from our analyses (see Uy *et al.* 2000). Excluding these females, the mate-searching patterns of 95 different females were reconstructed, with 43 followed in 1997 and 1998.

(c) *Classifying females*

Females were classified as faithful if they mated with the same male for two consecutive years and unfaithful if they rejected previous mates which currently held bower-territories. Females which chose new mates, which include the unfaithful females and those which lost their mates, were grouped generally as switcher females. Females which mated with their previous mates, as well as with an additional male, were excluded from our analyses because classifying these females as faithful or switcher is problematic (see Uy *et al.* 2000). Our results are not altered qualitatively by excluding these females.

For the 1998 mating season, 11 females were faithful, 12 were unfaithful and 12 lost their mates (and found new mates in 1998). Eight females mated with their previous mates in addition to another male, and were excluded. Twenty out of the 35 females which mated with one male in 1998 were also observed to mate in 1996, allowing us to classify them as faithful or switcher females in 1997. Eight out of the 20 females were faithful in 1997, ten switched mates, and two mated with the same male in addition to another bower-holder. Hence, 18 females could be assigned unambiguously into one of four possible classifications: (i) faithful in 1997 and 1998, (ii) switcher in 1997 and 1998, (iii) faithful in 1997 but switcher in 1998, or (iv) switcher in 1997 but faithful in 1998 (table 1).

Table 1. *Classification of females based on their tendency to mate with the same male across years*

(Females that mate with the same male for two consecutive mating seasons are classified as faithful. Females that switch mates, including those whose mates failed to return in 1998 and those that chose new mates even though their previous mates returned, are classified generally as switcher females.)

1996–1997	1997–1998	*n*
faithful	faithful	2
faithful	switcher	6
switcher	switcher	8
switcher	faithful	2

(d) *Natural experiment*

Five males did not return to establish bowers in 1998, providing a natural experiment that anticipated our experimental protocol. These males include (i) the highest-ranking or most attractive male from 1997 which mated with 22 different females, (ii) an average-ranking male (ranked eighth out of 34 males) which mated with six different females, and (iii) three low-ranking males, two of which mated with no females and one with a single female. Hence, these deaths affected 29 females whose mates failed to return in the following year. In 1998, 12 out of these 29 females returned to Wallaby Creek and were monitored as they searched for alternative mates. In 1997, ten out of these 12 mated with the highest-ranking male, while the remaining two mated with the average-ranking male. The single female which mated with the low-ranking male did not return in 1998. To test the hypothesis that the loss of high-ranking, attractive mates leads to increased mate searching, we compared the mate-searching patterns of these ten females in 1998 with (i) their search patterns in 1997, and (ii) the search patterns of faithful and unfaithful females in 1998.

All means are expressed as $\overline{X}^* \pm$ s.e. We used permutation randomization tests (e.g. two-sample or paired-comparison tests), and Monte Carlo simulations involving 50 000 iterations to test for significance of hypotheses (Manly 1991). All randomization tests and Monte Carlo simulations were programmed using QBasic 4.0 (Microsoft Corporation, Redmond, WA, USA), and all tests of significance of hypotheses are two-tailed.

3. RESULTS

(a) *Causes of variation in mate-searching behaviour: observations*

To determine if remaining faithful allows females to reduce searching in the following year, we can compare the search patterns of faithful females across several mating seasons. Although mate-choice information from 1996 to 1998 is known for 18 females, classifying them as faithful or switcher from 1996 to 1998 (see table 1) separates them into four categories with sample sizes too small for a robust paired-comparison test. Alternatively, search patterns of faithful females can be contrasted with search patterns of females which switched mates. In 1998, we found that the 11 faithful females sampled fewer males (2.36 ± 0.28) than the 22 females which switched mates (3.32 ± 0.27; two-sample randomization test, $p = 0.022$). This is consistent with results from our previous work that followed 31 females across the 1996 and 1997 mating seasons (Uy *et al.* 2000).
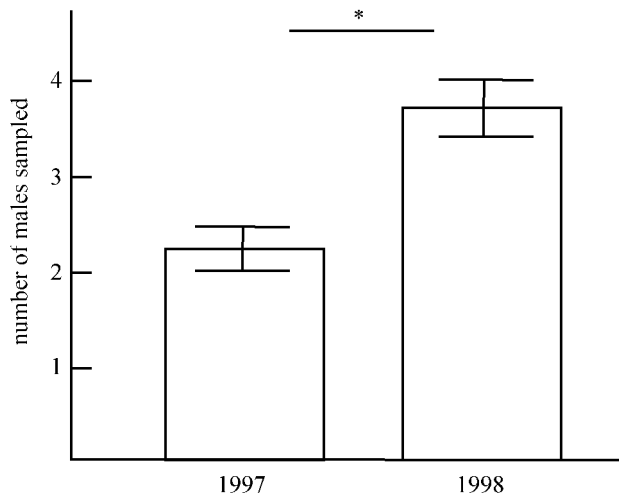
Figure 2. Differences in the number of males sampled between the 1997 and 1998 mating seasons for females whose mates failed to re-establish display sites in 1998 ($^*p = 0.003$, paired-comparison randomization test, $n = 10$).
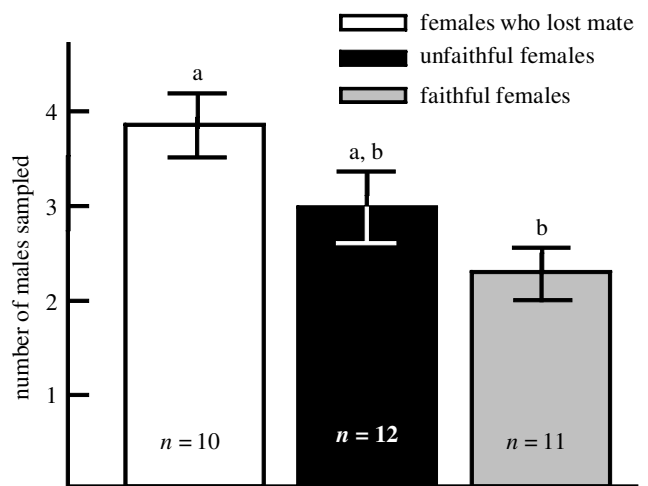

Figure 3. Differences in the number of males sampled among females which lost their very attractive mates (open box), unfaithful (black box) and faithful females (grey box) in 1998. Different letters indicate difference at the $p < 0.01$ level (two-sample randomization test).

(b) *Causes of variation in mate-searching behaviour: natural experiment*

Out of the 12 females whose mates failed to return in 1998, two mated with the new males which established bowers at the display sites of their previous mates ('site-faithful females'), while ten mated with males at new bower-sites. Of the two site-faithful females, one sampled two and the other only one male prior to mating. These limited search patterns are consistent with those of faithful females observed in 1997 (Uy *et al.* 2000) (figure 1) and in our current study in 1998.

The remaining ten females, in contrast, increased their mate searching relative to their own search patterns in 1997. In 1997 these ten females sampled an average of 2.20 ± 0.25 males, while in 1998 they sampled an average of 3.80 ± 0.33 males, indicating that the loss of mates prompted these females to increase their search (figures 1 and 2). The observed increase in number of males sampled across mating seasons could be explained alternatively by an overall increase in searching in 1998. We found, however, that the mean number of males sampled in 1997 (2.65 ± 0.18, $n = 63$) did not differ from 1998 (2.62 ± 0.15, $n = 71$; two-sample randomization test, $p = 0.884$). Number of courtship visits initiated by these females did not differ between the 1997 (6.80 ± 1.52) and 1998 (6.60 ± 0.93) mating seasons (paired-comparison randomization test, $n = 10$, $p = 0.781$).

We can also determine how the loss of attractive mates affects mate-searching behaviour by comparing the mate-searching patterns of the ten females which lost their mates with those of the 11 faithful and 12 unfaithful females of 1998. Females which lost their mates in 1998 sampled more males (3.80 ± 0.33) than faithful females (2.36 ± 0.28) (figure 3). Number of courtships initiated by females which lost their mates (7.80 ± 1.06) did not, however, differ from the number of courtships initiated by faithful females (7.55 ± 1.00; two-sample randomization test, $p = 0.85$). Females which lost their mates tended to sample more males than unfaithful females (2.92 ± 0.38; two-sample randomization test, $p = 0.12$, figure 3), but did

not initiate more courtship visits than unfaithful females (7.50 ± 0.95; two-sample randomization test, $p = 0.85$).

In 1998, faithful and switcher females differed in the number of males sampled, but not in the total number of courtships initiated. This suggests that faithful females initiate more repeat visits with the same male, while switcher females sample more males with fewer repeat visits. Indeed the proportion of the total courtship visits allocated to sampling chosen males differed between faithful and switcher females (two-sample randomization test, $p = 0.034$), with faithful females allocating $74.4 \pm 5.7\%$ and switcher females allocating only $55.7 \pm 4.4\%$ of their total courtship visits to males eventually chosen as mates. Similar results are found if switcher females are further classified into unfaithful females and females which lost their mates, and then compared with faithful females (two-sample randomization test, $p < 0.05$): unfaithful females allocated $54.5 \pm 6.5\%$ and females which lost their mates allocated $57.2 \pm 6.1\%$ of their total courtships resampling their mates.

Another possible explanation for the high rate of resampling of mates by faithful females is that they are guarding preferred males by preventing other females from gaining access to high-quality males (Petrie *et al.* 1992). This model is not supported, however, in that male attractiveness does not correlate with the number of courtship visits males received from each female in 1997 (randomization regression test, $r = 0.09$, $n = 63$, $p = 0.99$) and 1998 (randomization regression test, $r = 0.041$, $n = 71$, $p = 0.73$).

Alternatively, the observed high rate of resampling by faithful females in 1998 may be due to low repeatability of bower display (e.g. Luttbeg 1996) caused by the destruction of bowers and stealing of decorations by competing males (Borgia 1985*b*). Bower-holders initiated an average of 5.57 ± 1.10 bower destruction/stealing bouts in 1997 compared with 13.32 ± 1.94 destruction/stealing bouts in 1998, indicating an increase in aggressive male–male interactions among males in 1998 (paired-comparison randomization test, $n = 28$ bower-holders present in

1997 and 1998, $p = 0.001$). Repeated-measures analyses indicate significant differences in the total number of decorations among our weekly counts for each bower-holder in 1998 ($F_{4,108} = 3.38$, $n = 32$, $p = 0.012$), but not in 1997 ($F_{4,120} = 0.69$, $n = 33$, $p = 0.60$). These observations suggest that the increase in the number of aggressive male–male interactions might have led to the decrease in repeatability of bower display throughout the 1998 mating season. Lower repeatability, in turn, might have caused females to resample at a higher rate in 1998, and, indeed we find that faithful females in 1998 resampled their mates (5.72 ± 0.93, $n = 11$) more often than faithful females (3.20 ± 0.59, $n = 15$) in 1997 (two-sample randomization test, $p = 0.023$).

(c) *The role of bower-sites in mate choice*

We tested whether faithful females use bower-sites as a cue for mate choice by determining how many females mated with the new owner of the bower-sites previously owned by their mates. Eight out of the 12 females which lost their mates sampled the new owners at sites where they mated in the previous year; however, only two mated with these males. Among females followed across the 1997 and 1998 mating seasons (excluding the 12 females which lost their mates) 87% (26 out of 30) returned to sample their previous mates in 1998, and these females sampled an average of 2.77 ± 0.20 males. Therefore, 87% of the 12 females which lost their mates (about ten females) should return to sample their previous mates, and of these ten, 36% are predicted to mate at the same bower-site by chance. The observed frequency of 'site-faithful' females (two out of ten) does not deviate from this null model (Monte Carlo simulations, $p = 0.892$), failing to support the hypothesis that bower-sites play a direct role in mate choice.

4. DISCUSSION

(a) *Causes of variation in mate-searching behaviour*

Our previous work indicates that females alter their search patterns according to the quality and availability of their last mate. Females previously mated to very attractive males search little and mate with the same male in the following year. Females mated to less attractive males, search more and replace them with more attractive mates in the following year (Uy *et al.* 2000).

Failure of five males, including the most attractive male of 1997, to re-establish bowers in 1998 forced several females to find new mates, and this provided us with a natural experiment that tests for the effects of experience on mate-searching tactics. We predicted that females which lose these attractive, preferred mates should increase their search in the following year because they could not use past experience to reduce mate searching. Consistent with this prediction, females which lost their mates increased sampling from 1997 to 1998 (figures 1 and 2), and in 1998 showed higher sampling of males than the faithful females that were able to relocate their mates from the year before (figure 3).

We found that faithful and switcher females differed in the number of males they sampled but not in the number of courtships they initiated. Faithful and switcher females did, however, differ in how they allocated their courtship

visits: faithful females resampled their mates more often than unfaithful females. We tested the hypothesis that high rates of resampling of males may be due to faithful females mate-guarding attractive mates to prevent others from gaining access to them (Petrie *et al.* 1992). We failed to find a relationship between number of repeat courtships and the attractiveness of mates as would be expected by this hypothesis. This hypothesis seems unlikely to apply to satin bowerbirds because (i) the observed levels of repeated resampling appear insufficient to allow effective mate guarding of males (males are available through the day instead of a few hours as on leks), (ii) it is unusual for multiple females to be present at a bower at the same time, and (iii) possible benefits are small relative to the costs of guarding.

Alternatively, high rates of resampling by faithful females in 1998 may increase the accuracy of trait assessment if display trait repeatability is low (see Luttbeg 1996). Competing bower-holders persistently destroy and steal from neighbouring bowers and this may affect the repeatability of bower display. There was over a twofold increase in the mean number of destruction and stealing events in 1998 when compared with 1997, and this may explain the lower repeatability of decoration display in 1998 than in 1997. This low repeatability, in turn, may require females to increase resampling in order to gain a more accurate assessment of the quality of decoration display, a component of male display important in mate choice (Borgia 1985a). Indeed we find that faithful females in 1998 resampled their mates more often than the faithful females of 1997. These results are consistent with the hypothesis that increases in resampling by faithful females are driven by the need to assess accurately displays with relatively low repeatability.

If resampling can increase the accuracy of display assessment, why do switcher females limit their repeat visits? We found that extensive sampling increases the probability of force-copulation attempts from marauding males (Uy *et al.* 2000). This and other factors such as the timing of egg laying may constrain females in the total number of courtship visits they should initiate. These constraints may cause females to allocate their visits to maximize the trade-off between gains from visiting multiple males versus increased accuracy of assessment of single males.

Finally, the lack of difference in the number of courtships initiated by faithful and switcher females may result from a threshold number needed to stimulate females into ovulating (see Bradbury & Vehrencamp 1998). This possibility, however, is unlikely because some females experience only one or two courtships before mating (Uy *et al.* 2000).

(b) *Bower-site as a cue in mate choice*

Female tendency to remain faithful may be based on the bower-holder and his display or simply his bower-site. In many lekking species, male–male competition determines male position in leks, and females use the resulting spatial arrangement as a cue for mate choice (reviewed by Höglund & Alatalo 1995). Because male bowerbirds persistently destroy and steal from neighbouring bowers (Borgia 1985b), bower location may indicate male ability to defend preferred sites, and females may then use bower

location as a mate choice cue. Female tendency to return to the bowers of previous mates suggests an important role for bower-sites in determining which males are sampled for courtship (see also Uy *et al.* 2000). However, only two out of the 12 females which lost their mates in 1998 mated at the bower-sites of their previous mates, and this observed distribution can be explained by chance. These results do not support the hypothesis that bower-sites play an important role in mate choice, and suggest that females are probably assessing and remembering individual males and their display.

(c) *Consequences for mate choice*

Studies in mate choice typically assert that variation in mate choice arises from assessment errors (see Widemo & Sæther 1999). More recently, there has been growing evidence that variation in mate choice is not due to assessment errors, but actual differences in several components of the mate choice process such as female preferences, levels of choosiness or tendencies to mate choice copy (reviewed by Jennions & Petrie 1997; Widemo & Sæther 1999). Although assessment error probably plays a role in accounting for some of the variation in mate choice, our work indicates that variation in mate choice can also be explained by differences in mate-searching behaviour among females, which in turn is caused by differences in long-term experience with males.

The observed variation in mate choice should have important consequences for the operation of sexual selection. For instance, theoretical models indicate that the absence of unanimity in mate choice among females reduces the intensity of sexual selection and so the rate of evolution or elaboration of male display (e.g. Lande 1981; Kirkpatrick 1982; Seger 1985). Variation in mate-searching behaviour that leads to variation in mate choice should thus have important implications for the evolution and maintenance of elaborate display in this species.

Recent studies have begun to elucidate the causes of variation in mate choice among females. The effects of long-term experience and variation in mate-searching behaviour on mate choice, however, are often neglected (Widemo & Sæther 1999; Uy *et al.* 2000). Our results indicate that variation in mate searching among females can be explained by differences in long-term experience with males, and that these differences, in turn, affect the outcome of mate choice. Therefore, our work emphasizes the need to explicitly address the underlying causes of differences in female mating behaviour to gain a more comprehensive understanding of the mate choice process.

REFERENCES

Borgia, G. 1985*a* Bower quality, number of decorations and mating success of male satin bowerbirds (*Ptilonorhynchus violaceus*): an experimental analysis. *Anim. Behav.* **33**, 266–271.

Borgia, G. 1985*b* Bower destruction and sexual competition in the satin bowerbird (*Ptilonorhynchus violaceus*). *Behav. Ecol. Sociobiol.* **18**, 91–100.

Borgia, G. 1993 Cost of display in the non-resource-based mating system of the satin bowerbird. *Am. Nat.* **141**, 729–743.

Borgia, G. 1995 Complex male display and female choice in the spotted bowerbird: specialized functions for different bower decorations. *Anim. Behav.* **49**, 1291–1301.

Bradbury, J. W. & Vehrencamp, S. L. 1998 *Principles of animal communication*. Sunderland, MA: Sinauer Associates.

Dugatkin, L. A. & Godin, J. G. J. 1993 Female mate copying in the guppy (*Poecilia reticulata*) age dependent effects. *Behav. Ecol.* **4**, 289–292.

Godin, J. J. & Briggs, S. 1995 Female mate choice under predation risks in the guppy. *Anim. Behav.* **51**, 117–130.

Gong, A. & Gibson, R. M. 1996 Reversal of female preferences under predation risk in the guppy. *Anim. Behav.* **52**, 1007–1015.

Höglund, J. & Alatalo, R. V. 1995 *Leks*. Princeton University Press.

Jennions, M. D. & Petrie, M. 1997 Variation in mate choice and mating preferences: a review of cause and consequences. *Biol. Rev.* **72**, 283–327.

Johnsen, T. S. & Zuk, M. 1996 Repeatability of mate choice in female red jungle fowl. *Behav. Ecol.* **7**, 243–246.

Kirkpatrick, M. 1982 Sexual selection and the evolution of female choice. *Evolution* **36**, 1–12.

Koga, T., Backwell, P. R. Y., Jennions, M. D. & Christy, J. H. 1998 Elevated predation risk changes mating behaviour and courtship in a fiddler crab. *Proc. R. Soc. Lond.* B **265**, 1385–1390.

Lande, R. 1981 Models of speciation by sexual selection on polygenic traits. *Proc. Natl Acad. Sci. USA* **78**, 3721–3725.

Luttbeg, B. 1996 A comparative Bayes tactic for mate assessment and choice. *Behav. Ecol.* **7**, 451–460.

Manly, F. J. 1991 *Randomization and Monte Carlo methods in biology*. New York: Chapman & Hall.

Petrie, M., Hall, M., Halliday, T., Budgey, H. & Pierpoint, C. 1992 Multiple mating in a lekking bird: why do peahens mate with more than one male and with the same male more than once? *Behav. Ecol. Sociobiol.* **31**, 349–358.

Rosenqvist, G. & Houde, A. 1997 Prior exposure to male phenotypes influences mate choice in the guppy, *Poecilia reticulata*. *Behav. Ecol.* **8**, 194–198.

Seger, J. 1985 Unifying genetic models for the evolution of female choice. *Evolution* **39**, 1185–1193.

Uy, J. A. C., Patricelli, G. L. & Borgia, G. 2000 Dynamic mate-searching tactic allows female satin bowerbirds to reduce searching. *Proc. R. Soc. Lond.* B **267**, 251–256.

Vellenga, R. 1970 Behaviour of the male satin bower-bird at the bower. *Aust. Bird Band.* **1**, 3–11.

Widemo, F. & Sæther, S. A. 1999 Beauty is in the eye of the beholder: causes and consequences of variation in female preferences. *Trends Ecol. Evol.* **4**, 26–31.