

Complex Mate Searching in the Satin Bowerbird

Ptilonorhynchus violaceus

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ABSTRACT: Mate-choice studies typically focus on male traits affecting female mating decisions, but few studies seek to identify the behavioral rules females use when searching for mates. Current models suggest that females may either directly compare a set of males ("pooled comparison") or compare each male to an internal standard ("sequential-search rule") when judging the suitability of potential mates. Models also differ in other specific aspects, such as the predicted number of sampling bouts initiated and the tendency of females to return to males after previous visits. We monitored 63 female satin bowerbirds, *Ptilonorhynchus violaceus*, during mate sampling to reconstruct their search patterns. We found that females typically sampled several males and returned to the most attractive male for mating: a behavior consistent with the pooled-comparison tactic. Females, however, varied in the number of males sampled; some visited only one male before mating. We found that this variation can be explained by differences among females in the number of mates, the date mate searching is initiated, and long-term experience with males. Further, females were observed to initiate two distinct sampling bouts, with the rejection of most of their potential mates occurring before the start of the second sampling bout. This suggests that the choices of potential mates are narrowed prior to the second sampling bout and that the later visits may function to reconsider preliminary decisions made during the first sampling bout or to resolve decisions concerning the remaining potential mates. Our results indicate that mate searching is a complex process in which females use multiple sampling bouts to find suitable mates and in which several different factors influence their search behavior.

Keywords: mate searching, mate sampling, mate choice, satin bowerbird, *Ptilonorhynchus violaceus*.

Recent studies indicate that females can gain material (Gwynne 1988), proximate (Borgia 1995*b*), and genetic (e.g., Hasselquist et al. 1994; Wilkinson et al. 1997) benefits from choosing among males. The net benefits of mate choice, however, are reduced by the costs associated with searching for mates. Thus, to maximize the benefits of mate choice, females need to choose among males as well as use a mate-searching tactic that limits search costs (Janetos 1980; Parker 1983). Several theoretical studies address the behavioral search rules females should use to optimize this trade-off (Janetos 1980; Real 1990; Dombrovsky and Perrin 1994; Luttbeg 1996; Wiegmann et al. 1996, 1999); however, empirical tests of these models are still needed (see Gibson and Langen 1996; Houde 1997; Widemo and Sæther 1999).

Janetos (1980) was the first to explicitly explore female mate searching as an adaptive trait by simulating four mate-searching tactics and comparing the fitness advantages of each. Females could employ a random-mating, fixed-threshold, one-step-decision, or best-of-*n* (called "pooled comparison" by Wittenberger [1983]) search tactic. The best-of-*n* tactic involves females sampling and directly comparing a pool of males, then returning to mate with the male of the highest quality. In contrast, the fixed-threshold and the one-step-decision tactics involve females sequentially sampling males and deciding to either reject or accept males as they are encountered. The decision to accept males is based on a fixed internal standard for the fixed-threshold tactic or the expected benefits of continued sampling for the one-step-decision tactic. Janetos (1980) found that the best-of-*n* resulted in the highest fitness for the chooser.

Parker (1983) expanded the ideas presented by Janetos (1980) by considering search-time costs in his models and found that with an increase in benefits (e.g., more variance in male quality) and a decrease in costs, females become choosier. Building on the efforts of Janetos (1980) and Parker (1983), Real (1990) considered direct (e.g., increased risks of predation) and opportunity (e.g., loss of potential mates) costs associated with mate searching. He discovered that, when costs are considered, the best-of-*n*

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no longer results in the highest fitness for the chooser and that a form of the one-step-decision rule, which he calls "sequential search," dominates. The sequential-search tactic is similar to Janetos' (1980) one-step-decision tactic in that females sequentially encounter and compare each male to a standard or threshold that can change in response to the quality of the male being sampled and the estimated probability of finding better males with continued searching. The sequential-search tactic yields a higher fitness return for the chooser because it allows females to avoid further sampling when high-quality males are encountered early in the search sequence. In contrast, since the decision to mate is deferred until several males have been sampled, the best-of- n tactic causes females to bypass high-quality males if the males were visited early during the search, thereby incurring unnecessary search costs.

Both Real's (1990) and Janetos' (1980) models assume that females receive accurate information on male quality and that potential mates are encountered randomly. Lutt-beg (1996) relaxed these two assumptions and compared a Comparative Bayes (CB) tactic of resampling against the best-of- n and threshold tactics. The CB tactic involves females visiting a select pool of males and combining information from the current assessment with prior estimates to create a more accurate assessment of male quality. Multiple visits increase the accuracy of mate choice, but the inherent costs associated with assessments constrain the number of repeat visits. When the cost of searching is low and signals are imprecise indicators of male quality, a CB tactic is more successful than the fixed-threshold and the best-of- n tactics.

The amount of variation among potential mates dictates the benefits of mate choice and, therefore, the extent to which females should invest in mate searching (Parker 1983). Mate-searching models often assume that females have an estimate of the current distribution of male quality before initiating their search (e.g., Janetos 1980; Real 1990; Wiegmann et al. 1999); however, this may not be the case in natural populations. Dombrovsky and Perrin (1994) suggest that without a prior estimate of the distribution of male quality, females initiate two distinct sampling bouts: an early sampling bout to obtain a threshold for mating followed by a second sampling bout to find a suitable mate. Although explicitly applied to the threshold or sequential-search rule, Dombrovsky and Perrin's (1994) model can extend to females using a pooled-comparison tactic in which the first sampling bout determines the quality of available mates, and the second sampling bout is used to choose suitable mates.

Recent studies are beginning to elucidate the factors that shape female choice and the behavioral rules females employ when searching for mates (reviewed by Gibson and Langen [1996] and Widemo and Sæther [1999]). Consis-

tent with predictions of theoretical models, several studies indicate that female choosiness is influenced by the costs of searching (e.g., Dale et al. 1992; Choudhury and Black 1993) and the quality of potential mates (e.g., Collins 1995; Reynolds and Côté 1995; Rosenqvist and Houde 1997). In terms of the actual behavioral rules involved in mate searching, evidence of females employing a threshold rule (e.g., Downhower and Lank 1994; Moore and Moore 1994; Forsgren 1997; Reid and Stamps 1997) or a one-step-decision tactic (e.g., Brown 1981; Bakker and Milinski 1991; Choudhury and Black 1993) typically involves systems in which mate searching can be costly or in which individuals may lack the capacity to recall previously sampled males (but see Zuk et al. 1990), while evidence of females using a form of the pooled-comparison tactic typically involves systems in which females are long lived, have the capacity to recall previously sampled males, or can easily compare potential mates, such as in leks (e.g., Trail and Adams 1989; Petrie et al. 1991; Bensch and Hasselquist 1992; Fiske and Kålås 1994; Rintamäki et al. 1995; Backwell and Passmore 1996; but see Gibson 1996).

Work on mate searching in the field often involves lekking species (e.g., Trail and Adams 1989; Petrie et al. 1991; Fiske and Kålås 1994; Rintamäki et al. 1995; Backwell and Passmore 1996; Gibson 1996). Although these studies provide valuable information on mate searching in natural populations, the confounding elements of lek-mating systems leave some important issues unresolved. For instance, an accurate estimate of the number of males sampled prior to mating may be difficult to obtain because males display in tight aggregations so females can assess neighboring males while they visit individual courts (Borgia 1979; Höglund and Alatalo 1995). Further, because females commonly arrive in groups at leks, some females copy the mate choice of others (reviewed by Gibson and Höglund [1992]).

Satin bowerbirds, *Ptilonorhynchus violaceus*, provide an excellent model system for studies of mate searching for several reasons. First, each individually owned display site is well separated (>100 m apart; Borgia 1985a), causing females to assess males individually and allowing us to unambiguously quantify courtship visits at display sites. Second, females arrive at bowers independently, leaving little opportunity for direct mate copying (J. A. C. Uy, G. L. Patricelli, and G. Borgia, unpublished observations). Third, females are the only choosy sex, and polygynous males provide no parental care to their young (Vellenga 1970; Borgia 1985b); thus, the confounding effects of mutual mate choice do not exist. Finally, courtships and copulations occur at bowers (Borgia 1985b) where mate-searching behavior of banded females can be monitored continuously throughout the mating season with auto-

matic video cameras. This allows for a detailed reconstruction of female search patterns.

The objective of our study is to elucidate the behavioral rules females use when searching for mates. Although several mate-searching tactics have been proposed, all can be classified into two general classes (Wittenberger 1983; Real 1990; Reid and Stamps 1997): females can either directly compare a pool of males (e.g., best-of- n or pooled comparison) or sequentially sample males and compare the suitability of each to an internal standard (e.g., fixed-threshold or sequential sampling). Thus, our first aim is to determine whether female satin bowerbirds employ a pooled-comparison or a sequential-search tactic. Second, we test if female mate searching is simple or relatively complex, such that females initiate multiple sampling bouts and that several factors shape their search behavior.

Methods

Monitoring Mate-Searching Behavior

Our study site was located in Wallaby Creek (Tooloom National Park), New South Wales, Australia (see Borgia 1985*b*). We captured and banded females without interfering with their mate-searching patterns since females fed in flocks and readily entered baited traps before the mating season. Individuals were fitted with a unique three-color plastic band combination on each leg and a numbered Australian Bird and Bat Banding Scheme metal band. Bilateral morphological measurements (e.g., wing chord, tarsus, and tail lengths), weight, plumage description, and ectoparasite counts (see below) were also taken during banding (for details, see Borgia and Collis 1989). Individuals were typically caught and measured only once prior to the onset of the mating season; therefore, we could not test the repeatability of our measurements.

From November 9 through December 20, 1997, Hi-8 video cameras that record time and date were used to monitor 34 adjacent bowers, covering an area of approximately 4 km². Juvenile males owned one of these bowers, and adult males owned the remaining 33. Video cameras at each bower were triggered when motion sensors were activated by movement on the bower (for details, see Borgia 1995*a*). This allowed for continuous and simultaneous observation of all behaviors at all the bowers for the duration of the mating season. A similar video monitoring system was used to observe 29 bowers in 1996. Bower positions were mapped using global positioning system and transect readings. To estimate an index of the attractiveness of a male chosen by a given female, we used the male's total mating success minus the mating of the focal female. Total mating success for each bower holder was quantified as the number of different mates in a single

season. Total number of courtships was likewise quantified for each bower holder.

Mate-searching patterns of 68 females were reconstructed using the band identification of individuals on the time- and date-stamped video footage. Mate-searching patterns were determined for each female by quantifying the number of males sampled, the number of courtships initiated, and the number of days spent searching. In addition, detailed observations (e.g., length of courtship) for each courtship visit were scored from the video footage. A total of 20 nests were found in 1997; however, only three were found at the early stages of nest building. Hence, the timing of nest building can be compared to the timing of mate searching for only three females.

Because females might leave Wallaby Creek to sample males that were not monitored, our reconstruction of mate-searching patterns may be underestimates. Several lines of evidence, however, suggest that our observations are near complete. First, the bowers we monitored at Wallaby Creek formed a coherent group. In 1997, 259 of the 268 (97%) decoration-stealing and bower-destruction interactions (see Borgia 1985*a*) between mature males were initiated by monitored bower holders (Uy et al. 2000). Second, there was no difference in the number of males visited by females who exclusively sampled males at the core (2.47 ± 0.24 males, $n = 38$) and those who sampled males at both the edge and the core of our study population (2.57 ± 0.25 males, $n = 30$; two-sample randomization test, $P = 1.00$; see Uy et al. 2000). Finally, 12 females, who were observed mating in Wallaby Creek, were followed with radiotelemetry and remained in the study site for the entire duration of the mating season (J. A. C. Uy, G. L. Patricelli, and G. Borgia, unpublished data). To insure that sampling patterns were not underestimated, however, the five females who visited (and mated with) only a single male at the edge of our study population were excluded from our analyses. Our results are not altered qualitatively by the exclusion of these females.

Individual condition may influence female search behavior (e.g., Rintamäki et al. 1995). Thirty-two of the 63 females used in our study were captured and measured in 1997, allowing us to estimate female condition. The remaining 31 females were banded in previous years and were not recaptured in 1997. We used three standard measures of female condition. First, condition was estimated by taking the residuals of a regression of individual mass (\log_e) on tarsus length (\log_e), with individuals in poor conditions having negative residuals (Packard and Boardman 1987). There was no significant relationship between date of capture (starting from the first day a female is caught) and female mass (correlation randomization test; $r = -0.244$, $n = 32$, $P = .16$), suggesting that female weight does not change considerably as the mating season

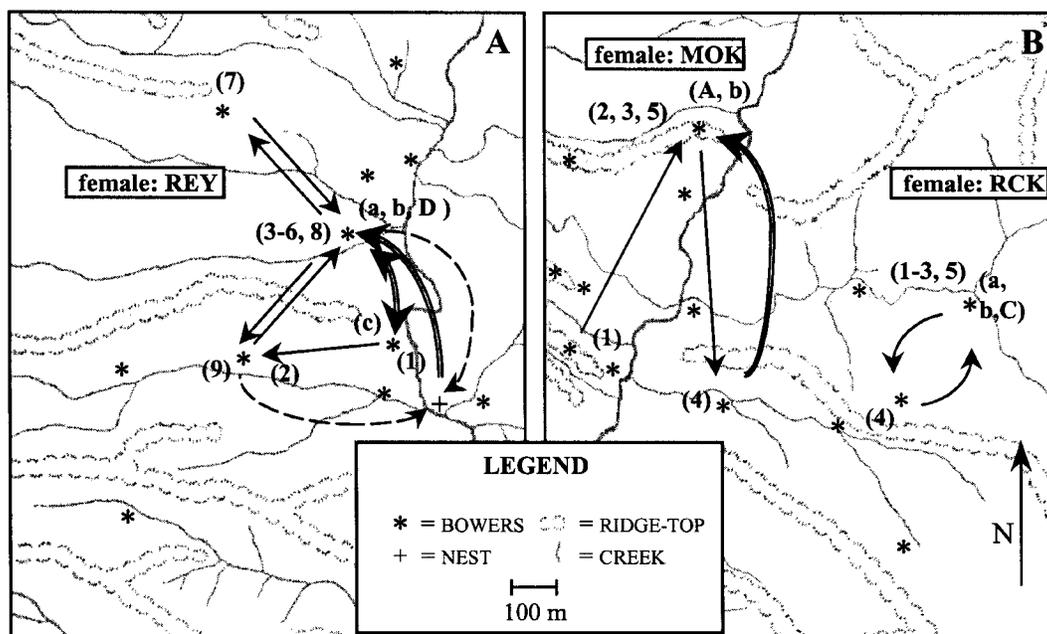


Figure 1: Three examples of female mate-searching patterns. The search pattern of female REY is shown in A, and the search patterns of females MOK and RCK are shown in B. Numbers in parentheses indicate early courtship visits, lowercase letters indicate later courtship visits, and uppercase letters indicate courtships that led to copulations. Numbers and letters are arranged in the sequence of visitation. Arrows with solid lines indicate movement among bowers for early visits, arrows with double solid lines indicate movement among bowers for later courtship visits and matings, and arrows with broken lines indicate movement to and from the nest (nest-building bout).

approaches. Female condition was also estimated using ectoparasite load. Nits of the most common external parasite, the louse (*Myrsidea ptilonorhynchi*), were found almost exclusively around the eyes; therefore, our counts of external parasite load focused on these areas (see Borgia and Collis 1989). Finally, fluctuating asymmetry of tarsi length was used as an index of condition and was quantified as the absolute value of the right-minus-left difference in tarsus lengths (see Palmer and Strobeck 1986). These three indices of female condition were not correlated (highest $r = -0.15$, $n = 32$, $P = .38$), so each measure was evaluated independently.

Statistical Analyses

All means are expressed as $\bar{X} \pm SE$. Permutation randomization tests and Monte Carlo simulations were used to test for significance of hypotheses (Manly 1991). To test for differences between predicted and observed distributions, we used the randomization χ^2 test or Monte Carlo simulations. To test for association between variables and differences between means, we used correlation (Pearson's coefficient) and two-sample (paired) comparison permutation randomization tests, respectively. All randomi-

zation tests involved 50,000 iterations and were programmed using QBasic 4.0 (Microsoft, Redmond, Wash.). All tests of significance of hypotheses are two tailed.

Results

General Mate-Searching Behavior

We followed the timing of mate searching and nesting for the three females whose nests were located before the nests were completed. All three females initiated short courtship visits to several bowers, ceased bower visitations to build their nests, and then resumed sampling by visiting a smaller set of males for extended courtships and matings (fig. 1A). Fifty other females followed in 1997 showed a similar pattern of initiating two distinct sampling bouts separated by a period of no search activity, which was likely allotted for nest building (fig. 1B). We classify the courtship visits prior to the period of no search activity (e.g., nest building) as early courtship visits and those initiated after as later courtship visits.

Fifty-three of the 63 females (84%) we followed initiated early courtship visits (fig. 1). These 53 females visited an average of 2.43 ± 0.19 males for early courtships. Each

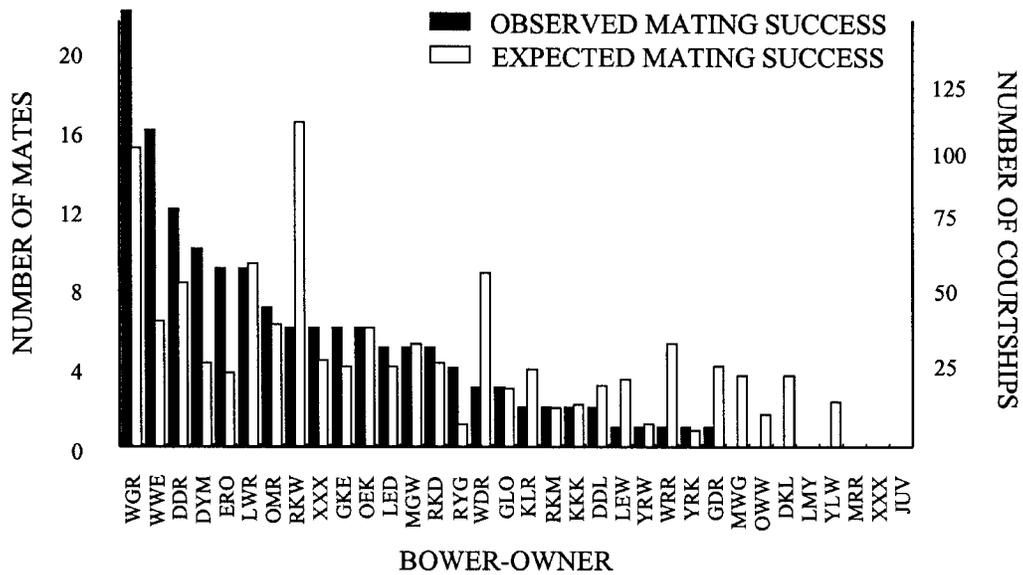


Figure 2: Observed distribution (black bars) of male mating success versus the expected distribution (white bars) if courtship visitations directly translated to matings.

early courtship lasted, on the average, 174.53 ± 10.29 s. Females typically initiated a single (1.17 ± 0.03) courtship visit per day, and this early sampling bout lasted 8.45 ± 1.11 d. During the early courtship visits, females were typically uneasy, observing courtship displays from the area between the bower walls (“avenue”) for only short periods of time and sometimes jumping in and out of the bower avenue. Females ceased sampling for a week ($7.34 \pm$

0.61 d), then resumed their search by sampling a subset of males (1.57 ± 0.07 males; range 1–3) for extended courtships (541.42 ± 36.78 s). Later courtship visits were significantly longer than the early courtship visits (paired-comparison randomization test; $n = 53, P < .001$) and involved females repeatedly sampling (3.35 ± 0.32 times) the same individual prior to mating. Later courtship visits lasted 3.11 ± 0.36 d. During the later courtship visits, females remained in the bower avenue for extended periods of time while observing the male display. Females solicited matings by fluttering their wings and tilting forward to expose their cloaca.

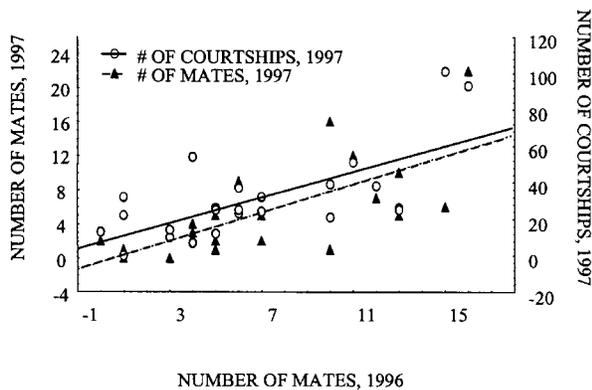


Figure 3: Correlation between the number of mates in 1996 and 1997 (filled triangles, broken line; correlation randomization test: $n = 24, r = 0.70, P < .001$) and between the number of mates in 1996 and the number of courtships received in 1997 (open circles, solid line; correlation randomization test: $n = 24, r = 0.68, P < .001$). Lines are drawn to graphically differentiate the two relationships.

Test of Mate-Searching Models

Active Female Choice. Courtship visits were not distributed randomly among the 34 bowers in Wallaby Creek (randomization χ^2 test; $\chi^2 = 928.58, df = 33, P < .001$). Likewise, matings were not randomly distributed among males (randomization χ^2 test; $\chi^2 = 192.73, df = 33, P < .001$); six bower holders accounted for 53% of the total observed matings. The distribution of matings, however, differed from the distribution of courtships (randomization χ^2 test; $\chi^2 = 74.31, df = 33, P < .01$; fig. 2), consistent with female rejection of some of the bower holders they sampled. Further, male mating success for the 1996 mating season is positively correlated with the total number of courtships visits and male mating success for the following year (fig. 3).

Excluding the 10 females who visited only one male (table 1) and the six females who mated with all the males they visited during the initial and later sampling bouts, 35 out of 47 (75%) females mated with the most attractive male among the bower holders they sampled during the early and later courtship visits. Using the mean number of males visited by these females, one out of three females is expected to mate with the most attractive male just by chance. The observed proportion of matings with the most attractive males exceeds the null model (Monte Carlo simulations; $P < .001$).

Mate-Searching Tactics. Females who employ a sequential-search rule, such as the fixed-threshold or one-step-decision tactics, cease searching once they encounter a male that meets their standard for mating; thus, chosen males are predicted to be first encountered at the end of the sampling sequence. In contrast, the pooled-comparison tactic predicts that the chosen male can be first encountered anytime during the sampling sequence because females defer their decision to mate until they sample and compare several males (see Janetos 1980; Real 1990). We classify the CB tactic (Luttbeg 1996) as a complex form of the pooled-comparison tactic that allows resampling.

Thirteen of the 22 (59%) females who visited two males (excluding four who mated with both males they visited during the early and later sampling bouts) returned to mate with the first male they encountered, indicating that females did not typically mate with males first encountered at the end of the sampling sequence. This observation fails to provide support for a sequential-search tactic (fig. 4A). Among the 14 females that visited three males (excluding one who mated with all three males visited during the early and later sampling bouts), four returned to mate with the first, four returned to mate with the second, and six mated with the last male encountered, again showing that females did not typically mate with males first encountered at the end of the search sequence (fig. 4B). In addition, most females repeatedly visited previously sam-

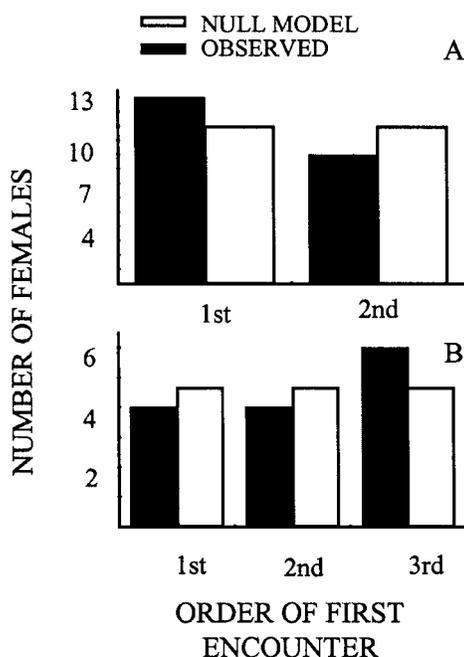


Figure 4: Order of first encounter of the chosen male for females who sampled two (A) and three (B) different males. The null model represents the situation in which females can return to any previously sampled male for mating. Monte Carlo simulations indicate no significant difference between the observed and expected frequency distributions for females who visited two ($P = .84$) and three ($P = .31$) males.

pled males before choosing their mates (table 1; fig. 1), a pattern consistent with a complex form of the pooled-comparison tactic, such as the CB tactic.

The pooled-comparison and sequential-search tactics also make predictions about female tendency to mate with the first male they encounter. The pooled-comparison tactic requires females to directly compare at least two males before choosing a mate, while the sequential-search tactic allows females to mate with the first male they encounter as long as he meets their standard for mating (Janetos 1980; Real 1990). Although most female bowerbirds sampled between two to eight males (table 1), 10 of 63 (16%) sampled only one male before mating and, thus, are seemingly consistent with the sequential-search or threshold rule.

Test of Dombrovsky and Perrin's (1994) Model. In satin bowerbirds, females initiate two distinct sampling bouts that may fit with the pattern suggested by Dombrovsky and Perrin (1994). First, this model predicts an optimal proportion of initial assessment visits given the total number of males sampled (fig. 5). We found that the observed correlation coefficient between number of males sampled

Table 1: Descriptive statistics of mate-sampling behavior ($n = 63$ females)

	Mean \pm SE	Range
Mates	1.27 \pm .06	1–3
Males visited	2.64 \pm .18	1–8
Copulations	1.87 \pm .11	1–4
Total courtship visits initiated	5.84 \pm .52	1–17
Courtship visits with mate	3.42 \pm .33	1–12
Courtship visits with all rejected males	1.84 \pm .27	0–10
Days sampling	5.11 \pm .44	1–14
Period of sampling (d)	14.76 \pm 1.30	1–39
Courtships per day	1.14 \pm .04	1–2

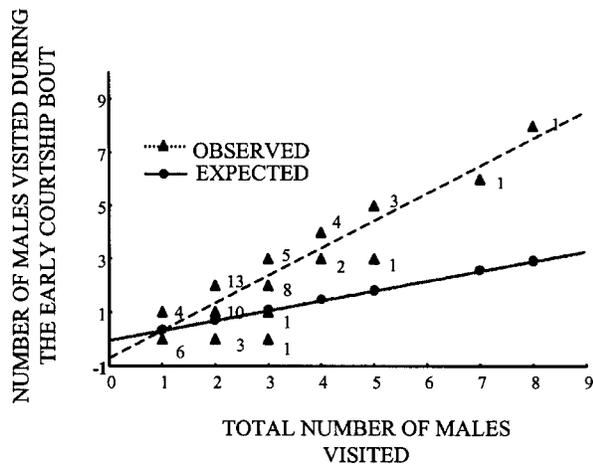


Figure 5: Test of Dombrovsky and Perrin's (1994) model: the relationship between the total number of different males visited and the number of different males visited for the early sampling bout. Lines are drawn to distinguish between the predicted and observed relationships. Triangles and the dashed line represent field observations ($r = 0.89$), while circles and the solid line represent the prediction of their model ($r = 0.37$). Numbers next to the triangles indicate the number of observations represented by each data point. A correlation randomization test indicates that the observed correlation coefficient significantly differs from the predicted coefficient ($n = 63$, $P < .001$).

during the early visit and the total number of males sampled before mating is significantly greater than the predicted coefficient from Dombrovsky and Perrin's (1994) model (fig. 5). Second, Dombrovsky and Perrin (1994) assume that during the second sampling bout, females encounter previously sampled males only by chance. We observed that 40 of the 53 (75.5%) females who visited more than one male in their early sampling bout returned to mate with one of the previously sampled males. Females visited approximately three (2.94 ± 0.18) males, and female home ranges encompassed the bower territory of about five males (J. A. C. Uy, G. L. Patricelli, and G. Borgia, unpublished data); therefore, a conservative estimate of the probability that females would encounter a previously sampled male is three out of five. The observed distribution (40 of 53; 75.5%) is not explained by chance (Monte Carlo simulations; $P = .024$). Finally, Dombrovsky and Perrin's (1994) model predicts that females decide to reject or accept males exclusively during the second sampling bout. Twenty-one of the 53 (40%) females who visited more than one male during the early sampling bout visited (and mated with) only one male during the later sampling bout. Further, the remaining 32 (60%) females visited an average of 2.15 ± 0.08 males for extended courtships; 15 of the 32 (47%) mated with all the males they sampled for extended courtships. Therefore, 36 of these

53 females (68%) showed no discrimination among males in the second sampling bout.

Factors That Influence Search Behavior

Females varied in the number of males they sampled, number of courtship visits they initiated, and number of days they spent sampling males (table 1). This variation may be explained by differences in number of mates, timing of mate searching, quality of mates, and female condition.

Number of Mates. A majority of females (47 of 63; 75%) mated with one male (fig. 6), although they may copulate with the same male several times (table 1). Sixteen of 63 (25%), however, mated with two males, and one mated with three (fig. 6). Females who mated with more than one male copulated more often and visited more males than those who only mated with a single male (table 2).

Females may opt to mate with two different males for several reasons. Males sampled in the second sampling bout may be similar in quality, so the benefits of choosing among them may not offset the costs of further assessment. However, we found that the range in male attractiveness between chosen and rejected males ($n = 17$ females, 10.65 ± 1.49) and between males who were both chosen ($n = 15$ females, 8.80 ± 1.28) did not differ significantly (two-sample randomization test; $P = .364$). Alternatively, disruptions by marauding males during copulations may drive females to seek additional copulations and mates. Of the 17 females who mated with more than one male (fig. 6), only two were disrupted during their first copulation. Because six of the 63 females we followed were disrupted during copulation, we expect that about two (1.62) of the 17 females who mated with more than one male should be disrupted just by chance. The observed relationship

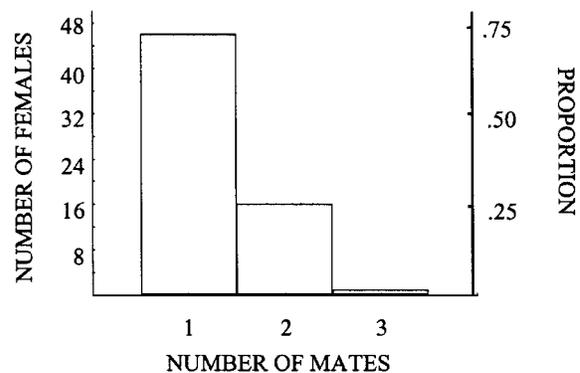


Figure 6: Distribution of number of different mates for the 63 females followed in 1997.

Table 2: Contrasting females who mated with one and more than one different males

	1 mate (<i>n</i> = 46)	>1 mate (<i>n</i> = 17)	<i>P</i>
No. of males sampled	2.39 ± .20	3.29 ± .34	.027
No. of courtship visits	5.46 ± .57	6.88 ± 1.15	.011
No. of days sampling	4.84 ± .46	5.82 ± 1.01	.275
No. of copulations	1.65 ± .12	2.47 ± .19	.003

Note: Two-sample randomization test. Values indicate mean ± SE.

between disruption during copulation and females mating with more than one male can be explained by chance (Monte Carlo simulations; $P = .45$).

Timing of Mate Searching. Female satin bowerbirds differed in the date they initiated mate searching (the date females were first observed to sample a bower): some started as early as the first week of November and some as late as the first week of December. Starting date of mate searching was associated negatively with the number of days spent sampling (correlation randomization test; $r = -0.35$, $n = 63$, $P < .01$; fig. 7A), number of courtship visits initiated (correlation randomization test; $r = -0.342$, $n = 63$, $P < .01$; fig. 7B), and number of males visited (correlation randomization test; $r = -0.357$, $n = 63$, $P < .01$; fig. 7C). We found that females who mated with the same male for two consecutive mating seasons (faithful females) sampled fewer males than those who switched mates across years (unfaithful females; Uy et al. 2000). Thus, the observed negative relationship between date of initiating mate searching and level of mate searching may be due to faithful females initiating their search later in the mating season. Faithful females ($n = 15$) started their search 5.2 ± 1.51 d after the first observed female visitation at a bower, while unfaithful females ($n = 16$) initiated their search 2.5 ± 0.52 d after. A two-sample randomization test shows no significant difference in the date mate searching is initiated between faithful and unfaithful females ($P = .16$).

Sampling Activity and Quality of Mates. The number of courtships initiated (correlation randomization test; $r = -0.03$, $n = 63$, $P = .841$) and the number of days spent searching for a mate (correlation randomization test; $r = 0.02$, $n = 63$, $P = .91$) did not correlate significantly with the attractiveness of the chosen male. Unexpectedly, there was a negative trend between the number of males sampled and the attractiveness of the chosen male (correlation randomization test; $r = -0.242$, $n = 63$, $P = .053$). Females who find highly attractive males remain faithful and often forgo sampling other males in the following year (Uy et al. 2000). Thus, these faithful females

may account for the negative trend between number of males sampled and the attractiveness of the chosen male. When females who did not visit more than one male are excluded from our analysis, we no longer observe this trend (correlation randomization test; $r = -0.16$, $n = 53$, $P = .844$).

Female Condition. Residuals from a regression of weight (\log_e) on tarsus length (\log_e ; $F_{1,30} = 7.77$, $r = 0.46$, $P < .01$) were taken to estimate individual condition. No significant relationship was observed between this measure of condition and the number of males visited (correlation randomization test; $n = 32$, $r = 0.07$, $P = .67$). Asymmetry of tarsi (correlation randomization test; $n = 32$, $r = 0.073$, $P = .79$) and ectoparasite load (correlation randomization test; $n = 32$, $r = -0.237$, $P = .192$), likewise, are not correlated significantly with the number of

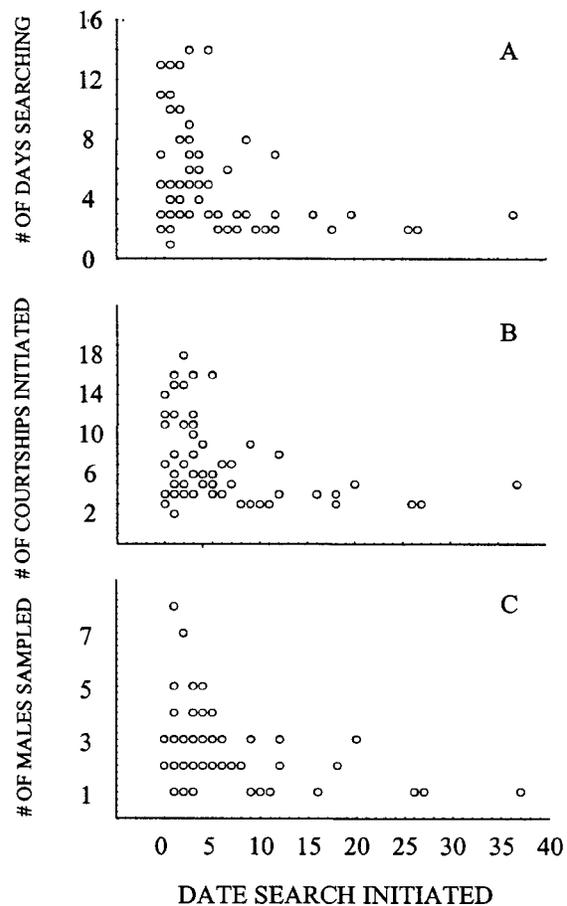


Figure 7: Correlation between the date mate searching is initiated and (A) the number of days spent searching, (B) the number of courtships initiated, and (C) the number of males sampled.

males visited. Similar nonsignificant results are found between these three measures of condition, and total number of courtship visits and days spent searching.

Discussion

Test of Mate-Searching Models

Evidence of Active Choice. Skew in mating success among males may be explained by females passively attracted to males with the most intense signals rather than actively choosing among potential mates (e.g., Arak 1983). We observed, however, that female bowerbirds typically chose the most attractive male of the subset of males they sampled for courtship and that females initiated multiple sampling bouts and resampled potential mates before mating. Also, the distribution of courtship visits males received differs from their mating success (fig. 2). These observations, along with previous work showing that bower display affects male mating success (Borgia 1985*b*), provide direct evidence of active female choice in satin bowerbirds.

Courtship visits among bower holders were not distributed randomly: six of the 33 adult bower holders received a majority of the total courtship visits in 1997 (fig. 2). This indicates that females chose a subset of males for courtship. Several lines of evidence suggest that the nonrandom distribution of courtship visits among males can be partially explained by females using information from previous mating seasons to determine which males to sample for courtship. Females returned to sample their mates from the previous year, and remaining faithful allowed females to reduce their mate searching (Uy et al. 2000, 2001). Further, male mating success in 1996 positively correlated with the total number of courtship visits a male received in 1997 (fig. 3).

Alternatively, as observed in several lekking species (Trail and Adams 1989; Rintamäki et al. 1995; Gibson 1996), assessment of males above display sites may allow females to determine which males to visit for courtship, and this may explain the nonrandom distribution of courtship visits. Our video cameras only monitored behavior on bowers; thus, we are unable to directly test this possibility. However, several lines of evidence suggest the primary importance of bower visitation in mate assessment. In spotted bowerbirds, *Chlamydera maculata*, the presence of large piles of bones in open areas near bowers appear to attract females for courtship (Borgia 1995*a*). No similar long-range signal, apart from male vocalizations, is apparent in satin bowerbirds. Also, results from a natural experiment show that females are forced to increase the number of males or bowers they sample when attractive mates fail to reestablish display sites in the following year (Uy et al. 2001). Even if off-bower assessment occurs, these

observations indicate the significance of bower visitation in mate assessment. A third alternative that may explain the nonrandom distribution of courtship visits among males is that dominant males may hold bower territories in areas of high female traffic (Bradbury and Gibson 1983). We currently do not have data to address this possibility.

Mate-Searching Tactics. Females who employ a sequential-search tactic should first encounter their mates at the end of their sampling sequence because mate searching ceases once an acceptable male is found (Real 1990). In contrast, females who use a pooled-comparison tactic can first encounter their mates anytime during their search sequence because the decision to reject or accept a male is deferred until several males are sampled, and females can return to any previously sampled male for mating (Janetos 1980; Wittenberger 1983; Luttbeg 1996). We observed that chosen males were not typically first encountered at the end of the sampling sequence (fig. 4), and a majority of females sampled several males before returning to the most attractive male for mating (fig. 1), providing consistent support for the pooled-comparison tactic. Moreover, most females repeatedly sampled several males before mating (table 1; fig. 1), a pattern consistent with a complex form of the pooled-comparison tactic such as the CB tactic (Luttbeg 1996). The CB tactic is most effective if there is error associated with mate assessment, and the cost of assessment is relatively low. Because male-male interactions occur regularly and influence the quality of bower display (e.g., bower structure and number of decorations; Borgia 1985*a*) and females use bower display in assessing potential mates (Borgia 1985*b*), repeat visits and Bayesian updating may allow for more accurate assessments of display quality (see also Uy et al. 2001).

However, 10 of the 63 females we followed restricted their sampling to only one male before mating and are thus inconsistent with the pooled-comparison tactic that requires direct comparison of at least two males (Janetos 1980; Real 1990). These 10 females are more consistent with the sequential-search tactic that allows females to mate with the first male they encounter because the suitability of potential mates is assessed relative to an internal standard or threshold. This interpretation only holds, however, if experience from previous mating seasons does not influence current mate choice. We observed that females returned to sample their previous mates in the following year, and those who mated with the same male for two consecutive years (faithful females) sampled fewer males than those who switched mates (Uy et al. 2000, 2001). In fact, of the females who sampled only one male and whose mate choice is known for two consecutive years, all were faithful. Thus, rather than using a threshold for mating, females who sampled only one male may have used in-

formation from previous mating seasons to relocate attractive mates.

Mate Sampling in Two Bouts. Parker's (1983) model indicates that the benefit of additional sampling is directly proportional to the current distribution of male quality (see also Wiegmann et al. 1999). When variation in male quality is high, the probability that additional visits will result in finding better mates is higher than if the variation among males is low. Dombrovsky and Perrin (1994) found that without prior estimates of the distribution of male quality, females initiate early visits to gain a standard for mating (e.g., threshold), followed by later visits to choose a mate. Analogously, females who employ a pooled-comparison tactic initiate an early sampling bout to establish the current distribution of male quality (e.g., to set n , the number of males to sample), followed by the second bout to choose a mate.

Female bowerbirds initiated two distinct sampling bouts. This pattern may fit with Dombrovsky and Perrin's (1994) model. However, we failed to find support for any of their model's predictions. First, this model predicts that females should allocate about one-third (0.37) of all of their visits to sampling males during the early or initial sampling bout. We found that the actual number of males sampled during the early visits exceeds their prediction, with a correlation coefficient of near one (fig. 5). A correlation coefficient of one would indicate that the sampling of all different males occurred during the early visitation bout. Second, nearly one-half (40%) of the females sampled only one male during the later sampling bout, and about one-half of the remaining females who sampled more than one male for later courtships mated with all the males they visited. Therefore, 68% of females who initiated an early and a later sampling bout appear to show no discrimination among the males they sampled during the later courtships. For females who only sampled one male during the later sampling bout, the decision to reject males was likely made before initiating the later bout. Females who visited more than one male during the later sampling bout and mated with all of them either did not discriminate in the second bout or actively chose to mate with all the males (often two males). These observations suggest that the sampling of different males mostly occurred during the early sampling bout and that the pool of potential mates was narrowed considerably prior to initiating the later sampling bout. Finally, Dombrovsky and Perrin (1994) assume that females reencounter males first sampled in the early sampling bout only by chance. In contrast, we found that females consistently returned to mate with a male who was first encountered during the early courtship visits and that most of the rejection of males occurred prior to the later courtship visits. If there

are costs associated with sampling and females have the capacity to remember individuals, it is reasonable to expect that females would use the information obtained from the early visits when choosing suitable mates.

Females can incur significant costs from mate searching if prolonged searches result in poor timing of mating (Trail and Adams 1989; Rintamäki et al. 1995; Backwell and Passmore 1996). Reducing the time for mate sampling, however, may constrain female ability to find high-quality mates. By sampling several males early in the mating season, the set of potential mates is narrowed considerably before female bowerbirds initiate nest building and during the period when they are under the most time pressure to make mating decisions. Initiating multiple sampling bouts may be a tactic to reduce the constraints on female ability to find high-quality mates.

Females who initiated extensive searches were more likely to receive force-copulation attempts from marauding males (Uy et al. 2000). Evidence of active choice suggests that females gain benefits from mate choice; hence, unwanted matings may be costly to females. The majority of sampling of different males occurred during the early sampling bout, and courtships during this bout were short, with females often hopping in and out of the bower avenue. Short courtships and skittish behavior likely reduce the probability of successful force-copulation attempts from marauding males and low-quality bower holders. Once the set of potential mates has been narrowed, the risk of receiving unwanted matings from low-quality bower holders is reduced, and females can focus on initiating longer courtship visits with higher-quality males.

Variation in Mate-Searching Behavior

In general, mate-searching models predict that the probability of encountering high-quality mates increases with increased searching (Janetos 1980; Real 1990; Luttbeg 1996), and several studies provide support for this prediction (e.g., Dale and Slagsvold 1996; Sikkel 1998). Our observations, however, indicate that females who searched longer did not necessarily find more attractive mates. If there are costs associated with mate searching in satin bowerbirds (Uy et al. 2000), why do females vary in the extent of their mate searching?

Several factors may explain the observed differences in female search patterns. Female condition may influence the extent to which she could invest in mate searching. However, we found that female condition does not correlate significantly with female search activity, suggesting that mate searching is not energetically costly. This finding makes intuitive sense because mate searching in satin bowerbirds involves the initiation of a single courtship visit

per day for several days. This leaves adequate time for females to forage between courtship visitations.

We observed at least three factors that may explain why females varied in their search behavior. First, we observed a negative relationship between the timing of mate searching and the extent to which females searched. Previous studies in monogamous or pair-bonded species show that females who initiated their search later in the mating season were less choosy because of the costs associated with the loss in mating opportunities (Dale et al. 1992; Choudhury and Black 1993; but see Hovi and Rätti 1994). In satin bowerbirds, females may time their mating with the emergence of cicada (J. A. C. Uy, G. L. Patricelli, and G. Borgia, personal observations), the primary food source for nestlings (Donaghey 1981). Thus, delays in mating may result in failing to synchronize nesting with the peak abundance of food. This may explain why females who initiated their search later in the mating season searched less.

Second, females who mated with more than one male sampled more males and copulated more often than those who mated with only one male (table 2). Our results indicate that disruptions from marauding males during copulation and differences in attractiveness among males sampled for later courtships do not explain the female tendency to mate with more than one male. Two alternatives that we were unable to test directly may explain this behavior. First, postcopulatory sexual selection may explain why some females mate with multiple males (reviewed by Eberhard [1996] and Birkhead and Møller [1998]). However, because 75% of the females we monitored mated with only one male, it is unlikely that sperm competition or postcopulatory female choice is a general mate choice strategy in bowerbirds. Second, males that copulate multiple times within a short time span may experience sperm depletion (e.g., Birkhead and Fletcher 1995; Westneat et al. 1998), so some females may opt to mate with more than one male to insure fertilization. This hypothesis may explain female tendency to recopulate with the same individual several times, but it cannot explain female tendency to mate with more than one male. Although the reasons that some female bowerbirds mated with multiple males still remain unclear, our observations suggest that mating with additional mates may explain why some females searched longer.

Finally, female experience from previous mating seasons influenced their subsequent mate-searching behavior. We found that male mating success from the previous year correlates with male mating success and number of courtships visits received in the following year (fig. 3). Further, females typically resampled their mates from the previous year, and remaining faithful allowed females to reduce searching in the subsequent year, to the extent that some faithful females remated without sampling other males (Uy

et al. 2000). These observations indicate that long-term experience shapes female search tactics and can explain much of the variation in their search behavior (see also Uy et al. 2001).

Our work shows that female mate searching in satin bowerbirds is a complex process. Females initiate multiple sampling bouts to find suitable mates, and a suite of factors shape their search tactics. This complex pattern of mate searching may be more common than previously appreciated, especially in long-lived species, and future work should explicitly consider this complexity.

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