A Comparative Bayes tactic for mate assessment and choice

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Models of mate choice tactics have assumed that females randomly encounter males when collecting information and the information is perfect. Empirical observations of four bird species show that females selectively visit males and repeat visits to males before mating. This suggests that the assumptions of previous models have been too restrictive. An alternative model of information gathering and mate choice, which relaxes the assumptions of random encounters and perfect information, is presented. In this Comparative Bayes model, the decision of when and from whom to collect information is made using Bayesian estimates of each male's quality. Predictions from the model are that: (1) the occurrence of mate assessment will increase as initial uncertainty about the quality of males increases, as the cost of gathering information decreases, and as the signal perceived by the female becomes a better representation of males' actual qualities; (2) the occurrence of repeat visits to males will be highest when signals from males are of medium reliability; and (3) the decision of which male to assess will depend on the estimated qualities of males, prior certainty about each male's quality, the reliability of each male's signal, and the costs of assessment. Simulations compare the fitness outcomes of the Comparative Bayes tactic to other mate choice tactics. The fitness from the Comparative Bayes tactic is significantly higher than from the fixed threshold tactic and than from the best-of-n tactic when the cost of assessment is low. Key words: assessment, mate choice, value of information. [Behav Ecol 7:451–460 (1996)]

How females assess males affects which mates females choose. Female mate choice has received much interest due to its connection to sexual selection and mating systems. Traditionally, females are assumed to have preferences for male traits, and thus on average females will mate with males that bear those traits (Andersson, 1994). To assume that a female automatically will find a mate that matches her preferences ignores how uncertainty and female assessment behavior impact mate choice outcomes. Uncertainty about the quality of males is shaped by the amount and quality of information available to females, and this shapes their ability to discriminate which males best match their preferences. Female assessment behavior can determine which males are encountered and which male. The thoroughness of assessment and the discrimination abilities of females determine the precision of mate choice, and thus the strength of sexual selection (Seger, 1985) and the evolution of honest communication systems (Johnstone, 1994).

Active mate choice means females must assess male traits and reject some potential mates (Arak 1988; Parker, 1983; Trail and Adams, 1989). Evidence exists that females assess potential mates (Brown, 1981; Dick and Elwood, 1989; Gibson and Bradbury, 1986; Grant and Grant, 1987; Gronell, 1989; Hunte et al., 1985; Pruett-Jones and Pruett-Jones, 1990) and several tactics have been proposed for how females choose mates (Janetos, 1980; Parker, 1983; Real, 1990; Wittenberger, 1983). A female initially is uncertain about the quality of specific males. To reduce her uncertainty and improve her choice she can gather information about male quality, but time, energy, predation, and opportunity costs limit the profitability of the information (Arak, 1988; Pomiankowski, 1987; Thornhill, 1980). The profitability of gathering information will depend on how many males a female assesses (Real, 1990), which males a female assesses, which traits the choice is based upon (Reid and Weatherhead, 1990; Sullivan, 1994), and the method by which males are compared to each other or to a threshold (Janetos, 1980; Parker, 1983; Real, 1990; Wittenberger, 1983).

Proposed mate search tactics can be divided into two general classes: comparison and threshold tactics. With comparison tactics, females assess a male when his quality exceeds that of another male or group of males. Two examples of comparison tactics are the best-of-n tactic, in which a predetermined number of males are assessed and the female returns to mate with the best male (Janetos, 1980; Wittenberger, 1983), and the sequential tactic, in which the female continues to assess males when the quality of the present male exceeds that of the preceding male and returns to mate with the preceding male when it does not (Wittenberger, 1983). With threshold tactics, females accept a mate if his quality exceeds a threshold of acceptance. These thresholds can be fixed before females encounter males (Janetos, 1980; Real, 1990) or adjusted by experience.

The previous models of tactics have made assumptions about the information females receive and how males are encountered. The models assume that a female receives perfect information from males and thus has no uncertainty about the quality of encountered males (Gibson and Höglund, 1992; Sullivan, 1990). For this reason, the best-of-n (Janetos, 1980) and sequential tactic models (Wittenberger, 1983) predict that females will repeat visits to males only to mate. Threshold models predict females will randomly repeat visits with males (Real, 1990). The models have assumed that during assessment females encounter males randomly in regard to male quality. The best-of-n model assumes that females assess different males, but those males are randomly drawn from the population (Janetos, 1980). Threshold models randomly draw males from the population with replacement (Brown, 1981; Real, 1990).

Empirical observations contradict the assumptions of the previous models. The sequences of female movements before mating have been reported for four bird species (great reed warblers: Bensch and Hasselquist, 1992; pied flycatchers: Dale et al., 1990; Hovi and Ratti, 1994; peafowl: Petrie et al., 1991; cock-of-the-rock: Trail and Adams, 1989) and one amphibian species (natterjack toads: Arak, 1988). In all four bird species females made repeated visits to individual males, suggesting...
they receive imperfect information. The majority of pied flycatcher females made repeated visits to males (Hovi and Ratti, 1994), and 8 of 12 females visited at least one male many times in row (Dale et al., 1992). Female cock-of-the-rocks, during four years, apparently made repeated visits to a subset of males (Trail and Adams, 1989). The best-of-n (Janetos, 1980) and the fixed threshold tactics (Real, 1990) could explain repeated visits as females randomly or mistakenly returning to previously encountered males. This is likely not the case for female pied flycatchers who visited the same male multiple times (up to 19) in a row. An adjustable threshold model predicts that a female may repeat visits to males, but consecutive visits to a male are not an effective way to estimate the distribution of male qualities in the population. The assumption that males are randomly encountered during assessment is also contradicted by these observations. Females of the cock-of-the-rock (Trail and Adams, 1989) and the pied flycatcher (Dale et al., 1992) appeared to restrict their mate search to a non-random subset of males and exhibited long strings of consecutive visits to males.

A Comparative Bayes (CB) mate choice tactic is presented as an alternative. The tactic relaxes the assumptions of previous models; females receive imperfect information about males and females are selective about which males they visit. The task for the female is to choose a high-quality male while not paying too high a cost for information. The decisions to assess or mate and with which male are made by following the option with the highest expected fitness. The female estimates the expected fitnesses using estimates of the qualities of individual males. When the female assesses a male, the estimated quality of that male is updated by the information she receives. The CB tactic expands the process of mate choice from the female having control only over the selection of a mate, to the female additionally having control over how many and which males she assesses before mating. The model has been formed around female mate choice, but the assumptions do not exclude it from applying to male mate choice, habitat selection, or any decision in which benefits are not gained during assessment.

**Figure 1**
The fitness function used to translate male quality into female fitness. The parameters K (=10) and γ (=0.5) determine the slope and height of the curve.

**Figure 2**
An example of the female's estimates of male qualities (normal distributions with \( \mu_A = 4 \) and \( \mu_B = 4 \), \( \mu_A = 2 \)). The female's greater certainty (smaller \( P^I \)) in male B's quality decreases the range of anticipated male quality.

**MODEL ASSUMPTIONS**

**Available males**

For the model, I assume that the female knows of a set of potential mates, and she either can recognize individuals or regularly can find the same individual in the same area. Therefore, the model should be applicable to species in which males lek or hold territories.

**Male quality and female fitness**

Male quality is constant over the time scale of the model. The quality of a male may be a function of his genotype, health, level of parasites or disease, parental care he will supply, or the resources he holds. The fitness a female gains when she mates is a concave function of male quality (Figure 1).

I present the methods and results for the female choosing between two males. The general form of the model can handle any number of males, but computation and presentation become difficult as the number of males increases. A version of the model with three males showed that the female's decision to assess or mate with a male depends only on the estimated qualities of the focal male and the best alternative male. Therefore, the results of the two male model are transferable to situations involving more males.

**Prior estimates of the males**

The female is uncertain of the exact value but has an estimate of the quality of each male. This prior estimate is a normal distribution (Figure 2), with the mean, \( \mu \), being the most likely quality and the variance increasing with the range of potential quality (Hunte et al., 1985) and decreasing as her information about the male increases. Presentation of the results will often refer to the mean estimated quality, \( \bar{\mu} \), but it is important to remember that the female's estimate of the male is a distribution. The prior estimate is used to predict the quality of the male and the information that might be received if he were assessed. If the female has no information about an individual male, the prior estimate would be the distribution of male qualities in the population. If the female has encountered a particular male, earlier in the breeding season or in previous seasons, her prior estimate of...
the male could be based on the information received during those encounters.

Cost of assessment

Each assessment of a male is assumed to have a fitness cost [time, energy, or predation risk (Pomiankowski, 1987)] for the female. Males may differ in their cost of assessment because of their spatial or temporal distribution and their ability to ward off predation or interference.

Variance in the information from assessment

The information the female receives by assessing a male is imperfect. The quality perceived by the female in the male’s signal may not match his actual quality for several reasons (Dawkins and Guilford, 1991; Wiley, 1983). The female must perceive and decode a signal from a male to gain information about that male. Any perceptual or decoding mistakes will contribute to increasing the difference between the perceived signal and the actual quality of the male (Johnstone, 1994; Johnstone and Grafen, 1992; Schluter and Price, 1993). Variation in the male’s signal caused by physiological or abiotic factors (Gerhardt, 1991) will also contribute to increasing the difference. While not explicitly incorporated into this model, if the quality of a male changes, the signal perceived by the female may not be a perfect representation of that male’s quality later (Sullivan, 1990). Thus, even if a male honestly advertises his quality, exogenous factors can cause the female to receive imperfect information about his quality (Dawkins and Guilford, 1991).

Dynamics of decision making

Dynamic modeling is used to calculate the expected fitnesses of the behavioral options available to the female. The behavior of the female affects her fitness by influencing what occurs then and her state and behavioral options in the future. For each time period, \( t \), the female is trying to maximize her expected fitness given that her estimate of male A’s quality is centered at \( \mu_A \) and has a variance \( \sigma_A^2 \), and her estimate of male B’s quality is centered at \( \mu_B \) and has a variance \( \sigma_B^2 \) (Figure 2).

\[
V((\mu_A, \sigma_A^2), (\mu_B, \sigma_B^2), t) = \max \{E\{Benefit(\mu)|\mu_A, \sigma_A^2\}; E\{Benefit(\mu)|\mu_B, \sigma_B^2\}\}
\]

(1)

Behavioral decisions should incorporate future effects of the present decision, and this is done by working backward in time (Mangel and Clark, 1988). To work backward requires a terminal fitness function. At the final time period (the last possible chance for a successful mating), \( T \), the female must mate and she chooses her mate to maximize the expected benefit.

\[
V((\mu_A, \sigma_A^2), (\mu_B, \sigma_B^2), T) = \max \{E\{Benefit(\mu)|\mu_A, \sigma_A^2\}; E\{Benefit(\mu)|\mu_B, \sigma_B^2\}\}
\]

(2)

MODEL STEPS

The female has prior estimates of the qualities of each male, in the form of normal distributions with mean \( \bar{\mu} \), and the uncertainty represented by the variance \( \rho^2 \) (Figure 2) (De Groot, 1970). The prior probability density for male quality is then

\[
Pr(\text{quality of male is } \mu) = \frac{1}{\rho \sqrt{2\pi}} \exp \left[ \frac{-(\mu - \bar{\mu})^2}{2\rho^2} \right].
\]

(4)

Step 1: Expected benefit of mating

The female estimates the expected benefit of mating with a male. The benefit received is determined by the quality of the male. I use a concave fitness function, so that the change in benefit gained by the female is greater at low male qualities (Figure 1). This represents a situation in which the female benefits most by avoiding bad males, and there is less difference between average and high quality males. The function applies to species in which females try to avoid males with deleterious traits (Kondrashov, 1988) or males that will abandon or give reduced parental care (Downhower and Brown, 1980; Howard, 1978; Knapp and Kovach, 1991; Petrie, 1983). The benefit of mating with a male of quality, \( \mu \), is

\[
\text{Benefit}(\mu) = K[1 - \exp(-\gamma \mu)] \quad \text{for } 0 < \mu \leq 10
\]

(5)

\[
\text{Benefit}(\mu) = K[1 - \exp(-10\gamma \mu)] \quad \text{for } \mu > 10
\]

\[
\text{Benefit}(\mu) = 0 \quad \text{for } \mu \leq 0
\]

K and \( \gamma \) are constants that determine the shape and height of the curve.

If a female were certain of a male’s quality the expected benefit of mating is a single point on the fitness function. Because the female’s estimate of the male’s quality is a distribution, the expected benefit of mating is a weighted average of the fitness function over the estimate of the male’s quality. The expected benefit of mating with a male given that the prior estimate of his quality has a mean \( \bar{\mu} \) and variance \( \rho^2 \) is
Step 2: Expected information in the signal

The female predicts what information she would receive by assessing a male. The prediction is based on the female's prior estimate of the male. If the actual quality of a male is \( \mu \), the probability the information perceived by the female equals \( x \) is

\[
\Pr[X = x | \text{male quality is } \mu] = \frac{1}{\sigma \sqrt{2\pi}} \exp\left(-\frac{(x - \mu)^2}{2\sigma^2}\right). \tag{7}
\]

Here, \( \sigma^2 \) represents the accuracy of the perceived signal from the male. I assume that for each male the female has an estimate of \( \sigma^2 \) that does not change. If \( \sigma^2 = 0 \), the signal gives perfect information and perfectly represents the male's actual quality. As the variance in the signal increases, a wider range of male qualities could be responsible for the perceived signal and the accuracy of the information is reduced. Because the female does not know the actual quality of the male, the estimate of what signal would be perceived includes the female's uncertainty about the male. The probability that the female perceives a quality level \( x \) from a male with a prior estimate centered at \( \mu \) and variance of \( \rho^2 \) is

\[
\Pr[X = x | \hat{\mu}] = \frac{1}{\rho \sqrt{2\pi} \sigma \sqrt{2\pi}} \exp\left(-\frac{(x - \mu)^2}{2\sigma^2} - \frac{(\mu - \hat{\mu})^2}{2\rho^2}\right) \tag{8}
\]

Step 3: Posterior estimates of the male

The information that the female predicts she would receive is used to update the female's estimate of the quality of the male. In this model, Bayesian updating combines the new information with the female's prior estimate to form a posterior estimate of male quality (Mangel, 1990; Martz and Waller, 1982). For this situation Bayes's theorem is

\[
\Pr(\hat{\mu} = \mu | X = x) = \frac{\Pr(\hat{\mu} = \mu) \Pr(X = x | \hat{\mu} = \mu)}{\Pr(X = x)}
\]

Thus, the probability that the male's actual quality is \( \mu \), given that the quality sampled was \( x \), is the combination of Equations 4 and 7 divided by Equation 8

\[
\Pr(\hat{\mu} = \mu | X = x) = \frac{1}{\rho \sqrt{2\pi} \sigma \sqrt{2\pi}} \exp\left(-\frac{(x - \mu)^2}{2\sigma^2} - \frac{(\mu - \hat{\mu})^2}{2\rho^2}\right) \tag{9}
\]

Equation 9 can be simplified by using the precisions (Martz and Waller, 1982),

\[
\tau = \frac{1}{\sigma^2} \quad \text{and} \quad R = \frac{1}{\rho^2},
\]

in place of variance terms. Then Equation 9 simplifies to

\[
\Pr(\hat{\mu} = \mu | X = x) = \frac{1}{\sqrt{\tau + R} \sqrt{2\pi}} \exp\left(-\frac{1}{2} \frac{1}{\tau + R} (\mu - \frac{xt + \hat{\mu}R}{\tau + R})^2\right). \tag{10}
\]

Equation 10 is a normal distribution, and after the signal \( x \) is received the mean is \( (xt + \hat{\mu}R)/(\tau + R) \) and the variance is \( 1/(\tau + R) \).

If the female samples a male quality, \( x \), and she has an initial mean estimate of the male \( \mu_{\text{old}} \), the new mean estimate of male quality is

\[
\hat{\mu}_{\text{new}} = \frac{xt + \mu_{\text{old}}R}{\tau + R}. \tag{11}
\]

If \( x = \mu_{\text{old}} \), then no revision of the estimate is made (\( \hat{\mu}_{\text{new}} = \mu_{\text{old}} \)). If \( x > \mu_{\text{old}} \), then an upward revision is made (\( \hat{\mu}_{\text{new}} > \mu_{\text{old}} \)), and if \( x < \mu_{\text{old}} \) then a downward revision is made (\( \hat{\mu}_{\text{new}} < \mu_{\text{old}} \)). As \( R \) increases, the accuracy of the initial estimate increases and the new information has a decreased effect on the female's estimate; as \( \tau \) increases, the accuracy of the signal increases and the new information has an increased effect.

Posterior estimates of the male are formed for each level of \( x \) that was predicted in step 2.

The updated variance in the posterior estimate, \( \rho_{\text{new}}^2 \), is

\[
\rho_{\text{new}}^2 = \frac{1}{\tau + R} = \frac{1}{\sigma^2} + \frac{1}{\rho^2} \tag{12}
\]

and must be included in estimates of the benefit of mating. In Bayesian updating, variance in the estimate is reduced by every new piece of information. The magnitude of this reduction depends solely on the variance in the signal, independent of its content.

Step 4: Expected benefit of assessment

The expected benefit of assessment is formed by comparing the expected benefits of mating with the two males, given a level of the signal. For each level of signal a new estimate of the male and a new expected benefit from mating (Equation 6) with the male are produced. The higher of the two expected benefits is multiplied by the probability of that level of signal occurring. This is done across the range of expected signals, and the sum is the expected benefit of assessment.

The net expected benefit of assessment is formed by subtracting the cost of assessment.

Steps 5: The behavioral decision

Steps 1-4 are repeated for each male, giving the female estimates for the net benefits to be gained from each behavioral options. The female follows the behavioral option with the highest expected net benefit.

MODEL RESULTS

Fitness function

The function that converts male quality into female fitness determines the region of estimated male qualities in which the female should gather information (Figure 3). The two males were given identical parameters: variance in the perceived signal, \( \sigma^2 = 1 \); variance in the prior estimate, \( \rho^2 = 2 \);
Variance in the prior estimate ($p^2$)

Increasing the variance in the prior estimate, $p^2$, from 2 to 4 expanded the range of circumstances in which assessment occurred (Figure 4a compared to Figure 3) and only the less familiar male, male B, was assessed. The female's uncertainty about male B was increased representing a situation in which she has encountered male A and has more prior information about him. As the variance in the prior estimate of a male increases, new pieces of information have larger effects on the posterior estimate of that male (Equation 10).

This manipulation of the variance in the prior estimate shows that in some circumstances the female should mate with the male with the lower mean estimated quality (upper right corner, Figure 4a). With a concave fitness function, an increase in the variance of the prior estimate leads to a decrease in the expected benefit of mating with that male. Thus, if both males have similar high mean estimated quality, the female should be risk-averse and mate with the male for which she has a more certain estimate, even if the other male is estimated to be of slightly higher quality.

Variance in the perceived signal ($\sigma^2$)

Decreasing the variance in the perceived signal, $\sigma^2_{\mu}$, from 1 to 0.1, expanded the range of circumstances in which assessment occurred (Figure 4b compared to Figure 3) and only the male with the more reliable signal, male B, was assessed, including cases in which male A had higher mean estimated quality. More accurate signals (smaller $\sigma^2$) have a greater impact on the posterior estimate of a male (see Equation 11).

Cost of assessment

Decreasing the cost of assessing male B from 0.1 to 0.05 expanded the range of circumstances in which assessment occurred (Figure 4c compared to Figure 3) and only male B was assessed.

Comparing the two variances

The previous results showed that increases in $p^2$ or decreases in $\sigma^2$ result in more information gathering. We can compare the strength of their effects by simultaneously changing both. Setting $p^2_{\mu} = \sigma^2_{\mu} = 2$ and $p^2_{\mu} = \sigma^2_{\mu} = 1$ caused only male B to be assessed (Figure 4d). The female benefits more by assessing the male for which she has more uncertainty, even if that male has a signal that is a less accurate representation of his quality. The effect of the variance in the prior estimate, $p^2$, dominates the effect of the signal variance, $\sigma^2$.

COMPARISON OF TACTICS

Methods

A simulation was used to compare the fitness outcomes of the CB, best-of-n, and the fixed threshold tactics. The female is presented with 200 sets of three males. The actual quality of each male is randomly drawn from a uniform distribution from 0 to 10. Her prior estimates for the three males ($\mu = 3$, $p^2 = 2$) are identical. The accuracy of the signal and the cost of assessment are identical for the three males but are varied across trials. One hundred replicates of her selecting a mate are performed for each set of three males. If the female mates, the fitness she receives is the translation of the male's actual quality (Figure 1). If the female assesses a male, the information she receives is drawn from a normal distribution, centered at the male's actual quality with a variance $\sigma^2$, the variance in the male's signal (Equation 8). Net fitness for all three tactics is the fitness received from mating minus the cost of the number of assessments.

The three tactics are independently used to select a mate. For the CB tactic, the female follows the behaviors prescribed by the model. For the best-of-n tactic, the female randomly assesses $n$ males ($n = 1, 2, 3$; avoiding repeated visits) and mates with the male with the highest assessed quality. For the fixed threshold tactic, the female randomly assesses males and
Results

The CB tactic outperformed the fixed threshold tactic in all cases and the best-of-n tactic when the cost of assessment was low (Figure 5). Wilcoxon paired-sample tests were used to compare the average fitnesses from the three tactics between the 200 sets of males. The average fitness from the CB tactic was significantly higher than the average fitness from the fixed threshold tactic in all cases ($p < .001$). The average fitness from the CB tactic was significantly higher than the average fitness from the best-of-n tactic when cost was low ($= 0.01, p < .001$), and there was no significant difference when cost = 0.1.

PATTERNS OF ASSESSMENT

Methods

A simulation was used to illustrate the sequences of mate assessment and choices that are formed by the CB tactic. The female is presented three males and the actual quality of male A is 2, male B is 3, and male C is 4. Her estimates for the three males ($\mu = 3$ and $\sigma^2 = 2$) and the accuracy ($\sigma^2 = 1$) and cost of gathering information ($c = 0.1$) from the males are identical. The information received by the female is randomly drawn from a normal distribution with a mean equal to the male's actual quality and a variance equal to $\sigma^2$. 

Results

As the variance in the perceived signal, $\sigma^2$, was increased the female more often mistakenly chose male A or B (Figure 6). When the signal was very accurate ($\sigma^2 = 0.1$) the female was nearly perfect in her discrimination of which male was best. The number of mistaken choices increased as $\sigma^2$ increased, but even with a very inaccurate signal ($\sigma^2 = 8$) the female selected the best male more than half of the time.

The average net fitness received by the female decreased as the variance in the perceived signal increased (Figure 7a). This occurs because as the variance in the perceived signal increases, the female increases the average number of assessment visits (Figure 7b) increasing the cumulative cost paid, and she makes more mate choice mistakes.

The model predicts that decreasing the variance in the perceived signal, $\sigma^2$, makes assessment advantageous in a wider range of circumstances. However, as $\sigma^2$ increases, the average number of visits rises and then declines (Figure 7b). With little variance in the information, one visit to a male gives a female an accurate posterior estimate of the male. As the vari-

Figure 4
Optimal female behavior for pairs of estimated mean male qualities for the concave fitness function. a) Variance in the prior estimate of male B ($\sigma^2 = 4, \alpha^2 = 1$ and $c = 0.1$) exceeds that for male A ($2, 1, 0.1$). b) Variance in the perceived signal from male B (0.1, 1, 0.1) is less than from male A (2, 1, 0.1). c) Cost of assessment for male B (2, 1, 0.05) is less than for male A (2, 1, 0.1). d) Both variances are less for male B (1, 1, 0.1) than for male A (2, 2, 0.1). In the stippled region the female mates with male B, in the open region the female assesses male B, and in the striped area the female mates with male A.
Figure 5
The average benefits from and proportion of trials won by alternative mate choice tactics. Each comparison represents 200 sets of three males and 100 replications per set. Comparisons were made using levels of $n$ and threshold that gave the greatest level of fitness for the best-of-$n$ and fixed threshold tactics. The solid portions of the pie charts represent the proportion of sets in which the CB tactic had the highest average fitness, open portions the best-of-$n$ tactic, and stippled the fixed threshold tactic. Average benefits from a set were compared to the hundredth and credit for victory was split in cases of ties. The numbers are the average net benefit from the CB, best-of-$n$, and fixed threshold tactics for all 200 sets, respectively. * Wilcoxon paired-sample tests between the CB tactic and each of the alternative tactics: $p < .05$. The best level of $n$ for the best-of-$n$ tactic was 3. The best threshold level was 5 for $c = 0.1$ with $\sigma^2 = 1$, 5 and for $c = 0.01$ with $\sigma^2 = 1$, 6 for $c = 0.1$ with $\sigma^2 = 10$ and for $c = 0.01$ with $\sigma^2 = 5$, and 7 for $c = 0.01$ with $\sigma^2 = 10$.

Figure 6
Mate chosen by the female versus variance in the perceived signal. The open bars are the number of times the female selected the highest quality male (actual quality = 4), the diagonal slashed bars are for the middle quality male (3), and the solid bars are for the lowest quality male (2).

Figure 7
The average net fitness received (a) and the average number of visits to males (b) versus variance in the perceived signal. a) Each point is the average from choices among 200 sets of males. The dashed line represents the average fitness received by randomly selecting a mate. b) The open squares represent the average number of visits to assess males (200 sets of males). Best fit lines for the data are: a) $y = 8.06 - 0.41370 \log x$; $r^2 = 0.963$, $p < .01$; b) $y = 2.669 + 0.067 x - 0.006 x^2$; $r^2 = 0.615$, $p < .01$.

Variance increases it is more frequently beneficial to repeat a visit to a male, raising the average number of visits. Then, as the variance continues to increase, the expected benefit from information continues to decrease because of its inaccuracy, and a smaller estimated difference in male qualities is enough for the female to choose to mate rather than gather more information. The average number of visits by the female is greatest when the signal variance is large enough that a repeat visit is beneficial but small enough that gathering information is beneficial.

The frequency of repeated visits is a function of the two variance terms and the cost of assessment. The occurrence of repeated visits increased with increases in the variance of the prior estimate and the variance in the perceived signal and a decrease in the cost of assessment (Table 1). The prior estimate variance had a larger effect than the perceived signal variance, despite equivalent changes in the variances.

With the parameters $\mu = 3$, $\sigma^2 = 1$, $\sigma^2 = 1$, and $c = 0.1$ the female repeated a visit to a male in 11.8% of trials. Four examples of these sequences are ABCC, ACBBCC, CABB-
A and then mates with male B or C. Information leading to explain previously puzzling behavior. For example, repeat visits by females for information to reduce uncertainty about males; (2) assessment only reduces uncertainty about the counter males and obtain perfect information. The model I present integrates the processes of assessing potential mates, choosing a mate. Note that in the last two sequences she visits male A and then mates with male B or C. Information leading to rejection of a male has value as well as information that leads to acceptance of a male. In every case in which a pied flycatcher female visited more than one male, the visit immediately before mating was to a male other than the accepted mate (Dale et al., 1992). Female pied flycatchers may be receiving information about one male that causes them to return to another male to mate.

**DISCUSSION**

The process of mate choice is the summation of the processes of searching for potential mates, assessing potential mates, and choosing a mate. Previous models of mate choice have focused on the last step. They have tested the performances of rules for choosing a mate. In these models the assessment process is simplified by assuming that females randomly encounter males and obtain perfect information. The model I present integrates the processes of assessing potential mates and choosing a mate.

The CB tactic views the decision to choose a mate as the equivalent of choosing to stop assessing potential mates. The model presents a framework by which females can selectively gather information: (1) females operate with distributions of quality they expect from males; (2) assessment only reduces uncertainty about the quality of males; and (3) by Bayesian updating new information is combined with estimates to form new estimates. This framework results in a model that helps explain previously puzzling behavior. For example, repeat visits to males by females can be understood as females gathering information to reduce uncertainty about males.

### Table 1

The distributions of the number of visits performed prior to mating

<table>
<thead>
<tr>
<th>Number of visits</th>
<th>Base</th>
<th>( \rho^2 = 2 )</th>
<th>( \sigma^2 = 2 )</th>
<th>Cost = 0.05</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>537</td>
<td>395</td>
<td>584</td>
<td>547</td>
</tr>
<tr>
<td>2</td>
<td>468</td>
<td>331</td>
<td>476</td>
<td>318</td>
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<tr>
<td>3</td>
<td>765</td>
<td>999</td>
<td>632</td>
<td>756</td>
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<td>198</td>
<td>184</td>
<td>277</td>
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<tr>
<td>5</td>
<td>68</td>
<td>113</td>
<td>92</td>
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<td>0</td>
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<tr>
<td><strong>Average</strong></td>
<td>2.39</td>
<td>2.69</td>
<td>2.41</td>
<td>3.02</td>
</tr>
<tr>
<td><strong>Revisits</strong></td>
<td>235</td>
<td>335</td>
<td>308</td>
<td>579</td>
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The number of visits includes all but the final visit, in which the female mates but does not gather information. Revisits is the number of trials, out of 2000, in which the female visited at least one of the males more than once. In the base simulation the three males had \( \rho^2=1 \), \( \sigma^2=1 \), and the cost=0.1. The actual qualities of the three males were 2, 3 and 4. In the following simulations the base parameters were used, but one parameter was changed. In the second simulation the prior estimate variance, \( \rho^2 \), was 2 for the males. In the third simulation the signal variance, \( \sigma^2 \), was 2 for the males. In the final simulation the cost of assessment was 0.05 for the males. Comparisons were made between the number of revisits given the base parameters versus the number of revisits for each of the three manipulations. Each manipulation of the base parameters increased the number of revisits that occurred (df = 2); for \( \rho^2 = 2 \) (\( x^2 = 44.8, \ p < .01 \)), for \( \sigma^2 = 2 \) (\( x^2 = 2.50, \ p < .01 \)), and for cost = 0.05 (\( x^2 = 485.4, \ p < .01 \)).

The model has shown that a female should assess a male over other males if her uncertainty about that male is higher, if the information that will be received is anticipated to represent more accurately the quality of the male, or if the cost of assessment is less. These predictions can be tested. Empirical work suggested by these predictions includes the following:

1. **Less certainty about the quality of males will cause females to increase assessment.** If increasing the time of exposure to a male decreases the variance in the female's prior estimate, then the variance can be manipulated by altering the length of exposure. In this case, given a choice, a female is predicted to first assess males to which she has had less exposure. Whether the female assesses or mates with a male, however, will also depend on the cost of assessment. For species in which mating must occur during a period of fertility, the cost of spending time to assess a male may increase as the time available to mate decreases. If a female is introduced to males early in her reproductive cycle, I predict that initially she will spend more time assessing the least familiar male. If the female is introduced to the males late in her reproductive cycle, I predict she will mate with the familiar male if the concave fitness function is in effect. To test these predictions, mate choice studies must measure changes in the cost of assessment and the female's exposure or familiarity with males.

2. **Reducing the variance in the perceived signal causes females to assess males in a wider range of circumstances.** The number of visits by the female, however, will be greatest at intermediate levels of variance. For fish, for example, light wavelengths and levels (Milinski and Bakker, 1990) and the clarity of the water can be manipulated to change the ability of females to assess males. The simulation predicts that increasing the variance in the signal should decrease the number of different males a female visits, but increase the number of repeated visits to males.

3. **As the cost of assessment increases, females will reduce the number of times they visit males, ultimately assessing no males before mating.** If a female collects less information before mating, the probability that she will choose the best male decreases. Fewer female gobids spent a majority of their time near the larger of two males (incorrect mate choice) in the presence of a predator (6 of 14) than in the absence of a predator (12 of 14) (Forsgren, 1992). Two reasons proposed by Forsgren are: (1) the predator distracts the female from making the decision that best matches her criteria, or (2) the predator prevents the female from collecting the information needed to make the correct decision. To distinguish between the two hypotheses, males could be presented to females, without a predator present, such that the females can assess males but not mate with them. After this assessment, the females could then be allowed to choose a mate in the presence or absence of a predator. If a predator distracts the female during her choice, then more incorrect mate choices would be made in the presence of a predator. If the predator is limiting the collection of information, then the number of mistakes would be equal for the two treatments, because assessment occurred without a predator present.

Individuals selectively gathering information compare the expected value of the information to its cost. To make this comparison they need criteria by which to assign value to information. Because the decision to gather information is made before the information is known, the currency is the expected value of the information. Since individuals are maximizing their expected fitness, the value of the information should be a measure of the information's potential to affect their behavior (Mangel, 1990; Stephens, 1989, 1990). However, the potential of information to affect behavior is difficult to calculate. A piece of information may not immediately af-
fect behavior, but it may cause or prevent a change in behavior when combined with other information. Therefore, to calculate the potential would require estimates of all of the pieces of information that could be collected. The large number of combinations of information that could be received will often make this unmanageable. Therefore, an approximation for the potential of information to affect behavior is needed.

I have used the change in expected fitness as my measure of the value of information. The change in expected fitness approximates the potential of information to affect behavior. Expected fitness, in this model, can be changed by the female altering which male she favors or updating her estimate of the male she favors. Altering which male she favors affects her behavior by altering which male is likely to be chosen, and the information causing the alteration is given the value of the change in expected fitness. Updating the estimate of the favored male does not immediately change her behavior, but it may when combined with future information. In addition, information that makes the differences between males clearer should have value, even if it does not immediately change the ranking of males. By using the change in expected fitness as a measure of information's value it is not necessary to anticipate the combinations of future information that may be received, and this makes it more manageable.

A potential drawback of giving value to all changes in expected fitness is that in some circumstances information may change estimates of males (and hence expected fitness) but have little potential to affect behavior. By Jensen's inequality for a concave curve (De Groot, 1970), reducing the variance in the estimate of a male's quality, while holding the mean constant, will raise the expected fitness of mating with that male. The strength of this effect was tested by starting the model with a male of known low quality and a male of estimated high quality. The female did not assess the high-quality male even at low costs. Thus, the drawback of giving value to all changes in expected fitness will not be severe if there are costs to assessing males.

Just as mate choice and mating systems are built upon intersexual and intrasexual interactions, so are the processes females use to assess and choose mates. In general, females will prefer to mate with males about which they have information. If the fitness function is concave, reducing uncertainty about a male will on average increase the expected benefit of mating with that male. Thus, being one of the first males assessed by a female may increase a male's chance of being chosen by the female. Males could compete to attract assessment by females by lowering the cost of assessment or by offering signals that appear to be more reliable. Whether this will benefit a male depends on how females assess males, the actual quality of the male, and the tactics of competing males. Therefore, the process of mate assessment will be shaped by games between females trying to gather information efficiently and males making an optimal effort to attract females.

Females may use the behavior and mate choices of other females as a source for information about males (Gibson and Höglund, 1992; Pruett-Jones, 1992). The information gained in seeing another female courting with a male depends on the assessment tactics used by other females. If females selectively gather information about males based on the cost of assessment, the reliability of the signal, or uncertainty about the male, then courting is not a perfect indication that the female estimates the male to be of higher quality. Therefore, how females can cue off the actions of other females will depend on the processes they use to assess and choose a mate.

How females gather information about males influences mate choice and sexual selection. I have shown that the decision to gather information depends on the expected costs of information the female has about males, the cost of visiting males, and the reliability of the information the female would receive. For this reason, it may be incorrect to assume that proximity to a male is an indication that a female estimates that male to have the highest quality. The female may be less familiar with the male, he may be less costly to visit, or his signal may be more reliable. I have shown that the number of visits to males is shaped by the cost of assessment, and females discriminate more poorly between males as signals become less reliable. The cost and reliability of information influence the process of assessing potential mates, and the process shapes the accuracy of discrimination and the strength of sexual selection.

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REFERENCES


