

Condition-dependent mate choice: A stochastic dynamic programming approach



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ABSTRACT

We study how changing female condition during the mating season and condition-dependent search costs impact female mate choice, and what strategies a female could employ in choosing mates to maximize her own fitness. We address this problem via a stochastic dynamic programming model of mate choice. In the model, a female encounters males sequentially and must choose whether to mate or continue searching. As the female searches, her own condition changes stochastically, and she incurs condition-dependent search costs. The female attempts to maximize the quality of the offspring, which is a function of the female's condition at mating and the quality of the male with whom she mates. The mating strategy that maximizes the female's net expected reward is a quality threshold. We compare the optimal policy with other well-known mate choice strategies, and we use simulations to examine how well the optimal policy fares under imperfect information.

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1. Introduction

How females choose their mates has long been a central question in the study of sexual selection. Ultimately, females seek to mate with a high quality male, where quality is measured either in terms of direct benefits to the female, good genes, or attractive offspring (Kirkpatrick, 1987). However, the proximate mechanism of female mate choice, i.e., how an individual female actually goes about choosing a mate, has received much less attention (Gibson and Langen, 1996). When choosing a mate, a female must balance her ultimate desire for a male in good condition with the proximate concerns of search costs, male availability, and her own condition. We develop a model of female mate choice that considers the tradeoff between offspring quality and search costs. In our model, we consider female condition as a stochastically changing variable, and search costs as a function of female condition. We find that the optimal strategy is a condition-dependent threshold for male quality, and that it outperforms previously identified strategies, e.g., best-of- n , Janetos (1980), under changing conditions.

Previous models of mate choice decisions typically tried to determine policies that would maximize the quality of a female's

eventual mate. Such models have generally resulted in strategies that can be divided into three categories: best-of- n , threshold, and comparative Bayes. Note that throughout this paper, we use the term 'policy' to refer to a specific decision rule used to determine mate choice (the definition of a policy will be formalized in Section 2), while 'strategy' refers more broadly to a type of policy. The best-of- n strategy states that females should assess a fixed number (n) of males and then return to and choose the option with the highest quality; the optimal value of n depends on assessment costs and the variance of male quality (Janetos, 1980), and such a strategy assumes the ability to return to a previously encountered male. A threshold strategy states that females set a quality threshold and mate with the first male they encounter who exceeds the threshold. As with the parameter n in the best-of- n strategy, the optimal threshold depends on the mean and variance of the distribution of male traits (Real, 1990). Comparative Bayes is a dynamic search algorithm that involves sampling males and learning about the distribution of male traits to develop a threshold that improves with each observation (Luttbeg, 1996).

Earlier models of mate choice generally neglect to account for female condition as a factor. While some models include search costs (Real, 1990; Luttbeg, 1996; Collins et al., 2006), these are assumed to be fixed; all females experience the same search costs, which are intended to capture both direct costs (such as risk of predation and expended energy) and opportunity costs (Real, 1990), and these search costs do not change over time. However, there

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is ample empirical evidence that female search costs are a function of female condition; in general, poor condition females suffer higher search costs (Alatalo et al., 1988; Milinski and Bakker, 1992; Woodgate et al., 2010). Cotton et al. (2006) highlighted the role of condition dependent search costs in mate choice, emphasizing that female preferences can change plastically in response to condition. Previous models also assumed that a female's offspring quality was solely dependent on the quality of her mate (Janetos, 1980; Real, 1990; Collins et al., 2006), when it is actually a function of the quality of both parents (Eshel and Hamilton, 1984). By overlooking female condition and variability in search costs, prior models of optimal mate choice failed to explore an interesting problem.

In this article, we develop a mathematical model that describes condition-dependent mate choice and explicitly models dynamically changing female condition and condition-dependent search costs. The specific model we use is a Markov decision process (MDP), which we solve using a dynamic programming approach. While our paper is the first to apply dynamic programming techniques to the problem of mate choice with changing female condition, the use of dynamic programming in models of sexual selection is well established. Dynamic programming is often applied to optimization models in behavioral ecology (Mangel and Clark, 1988). Using techniques similar to those employed in our model, Yoshimura et al. (2013) used Markov decision processes to examine decision making in uncertain environments, although they focused on growth rates. Within the field of sexual selection, dynamic programming has been used for several purposes, including modeling intrasexual conflict and identifying the conditions under which sexual conflict may occur (Parker, 1978), determining the optimal behavior to employ when sequentially searching for mates (Mazalov et al., 1996), and studying seasonal mate choice (Crowley et al., 1991). While the works by Mazalov et al. and Crowley et al. consider a topic similar to our own, our paper is unique in combining a sequential mate search with variability in female condition.

Our model considers females with variable condition that can change stochastically throughout the course of the mating season. They encounter males sequentially, and attempt to select the male that will maximize their net reward, which is equal to the quality of their offspring minus search costs. We consider the reward to be offspring quality, rather than mate quality, and thus we calculate it as a function of the quality of both parents. In the remaining sections of this article, we describe the model and solve it to obtain the optimal mate choice policy for this scenario. We find that a condition-dependent threshold policy is optimal, and confirm that the optimal policy outperforms the oft-cited best-of- n strategy under changing conditions. We also test the robustness of the optimal policy against limited information about male quality, and confirm that even with limited information, a condition-dependent threshold policy maximizes expected net reward.

2. Methods

We model the process by which a particular female searches for a mate. We assume that the female's condition may have a range of possible values and that she encounters males of varying quality. More formally, let $S = \{1, 2, \dots, N_S\}$ be the set of values for the female's condition and $Q = \{1, 2, \dots, N_Q\}$ be the set of values for the quality of encountered males. Let $f(q)$ be the probability that a randomly-encountered male has quality q and define $F(q) = \sum_{q' \leq q} f(q')$, that is, F is the probability that a randomly encountered male has quality at most q . For a given female of condition s and male of quality q , denote the expected condition of their offspring by $G(s, q)$, and assume that better condition (of the female) and better quality (of the mate) both lead to better offspring; that is, G is non-decreasing in both s and q . For any fixed s , we can also map offspring condition back to mate quality:

let $q_{\min}(s, g)$ be the minimal mate quality yielding an offspring of condition at least g when the female is in condition s . Specifically,

$$q_{\min}(s, g) = \begin{cases} \min\{q \in Q : G(s, q) \geq g\}, & g \leq G(s, N_Q) \\ N_Q + 1, & g > G(s, N_Q). \end{cases}$$

Note that we use the dummy condition $N_Q + 1$, which is not an element of Q , so that $q_{\min}(s, g)$ will be defined for any non-negative offspring condition g . In other words, if the desired offspring condition is too high, no male with quality in Q will be sufficient. Our model does not require any additional assumptions about the function $G(s, q)$; in our experiments, we will employ a concave function for $G(s, q)$, based on empirical evidence (Luttbeg, 1996).

We assume that the female's condition evolves according to a Markov chain. This means that the female's condition at the next decision point depends on her past history only through her present condition, and is independent of everything else in the problem. Therefore, we can represent the changing condition by a probability transition matrix $P = [p_{st}]$, where p_{st} , for $s, t \in S$, is the probability that the condition will be t when next encountering a potential mate, if the condition is currently s and the female continues to search. By assuming that the condition evolves according to a Markov chain, we can formulate the mate choice problem as a Markov decision process. A Markov decision process (MDP) is a type of dynamic program where costs, rewards, and state transitions are affected by decisions. In this case, the future net expected reward will depend on the decision to mate or continue searching. If the individual decides to mate, then the reward $G(s, q)$ is earned. If the individual decides to continue searching, she pays a state-dependent search cost $c(s)$ and then experiences a state transition according to P (she cannot subsequently return to the previously-encountered male). Both rewards and costs are allowed to be state-dependent in the MDP formulation.

Markov decision process formulation. A complete MDP formulation includes states, actions, and rewards. The state space is $S \times Q$; that is, all combinations of female condition and male quality. The action set A consists of two actions, mate or continue; we denote this by $A = \{M, C\}$. A non-randomized stationary policy for a MDP is a function that maps each state to one of the actions, independent of the prior states visited. For the type of MDP we consider, there must be a non-randomized stationary policy that is optimal (Puterman, 2005), and so we restrict ourselves to policies of this type. Let π denote any non-randomized stationary policy; that is, $\pi : (S \times Q) \rightarrow A$.

Let $V^\pi(s, q)$ be the net expected reward (i.e., offspring reward minus search costs) earned under policy π if the current state is (s, q) . Then $V^\pi(\cdot)$ must satisfy

$$V^\pi(s, q) = \begin{cases} G(s, q), & \text{if } \pi(s, q) = M, \\ -c(s) + \sum_{t \in S} \sum_{r \in Q} p_{st} f(r) V^\pi(t, r) & \text{if } \pi(s, q) = C. \end{cases} \quad (1)$$

In other words, if policy π prescribes mating in state (s, q) , then the offspring condition $G(s, q)$ is earned. Otherwise, cost $c(s)$ is incurred and we move to a new state; the future expected net reward is calculated according to the probability of transitioning to all future states (t, r) . Our objective is to find a policy π that maximizes $V^\pi(s, q)$ for all $s \in S, q \in Q$. That is, regardless of the starting state, the sequence of actions prescribed by π will lead to the largest possible expected reward. We use the notation $V(s, q)$ to denote the maximum net expected reward when starting in state (s, q) , and note that $V(\cdot)$ must satisfy

$$V(s, q) = \max \left\{ G(s, q), -c(s) + \sum_{t \in S} \sum_{r \in Q} p_{st} f(r) V(t, r) \right\}, \quad \forall s \in S, q \in Q. \quad (2)$$

The set of equations given in (2) are known as Bellman's equations. For more details on the derivation and use of Bellman's equations for stochastic dynamic programs, we refer the interested reader to Ross (1983) and Puterman (2005). We can simplify (2) by defining $V(t) = \sum_{r \in Q} f(r)V(t, r)$ for all s . The function $V(t)$ is the net expected reward earned starting in condition s if the optimal policy is followed for any encountered mate. Then

$$V(s, q) = \max \left\{ G(s, q), -c(s) + \sum_{t \in S} p_{st} V(t) \right\}, \quad \forall s \in S, q \in Q. \quad (3)$$

We will use this simplified version of Bellman's equations throughout the rest of the paper.

Using the formulation that we have defined above, we can show that for each female condition, the optimal policy is a threshold policy in terms of the male quality; i.e., for each $s \in S$ there exists q^* such that the optimal action is to mate if and only if $q \geq q^*$.

To see why this is the case, consider a finite-horizon version of this problem where $V_M(s, q)$ is the maximum net expected reward earned starting in state (s, q) if the female has M remaining opportunities to mate should she continue searching (i.e., not including the current male). In this formulation, if the female does not mate at the last decision point (when $M = 0$), the search ends and a reward of zero is earned. The function $G(s, q)$ is non-negative, and hence the female will always mate when $M = 0$. Then $V_M(s, q)$ must satisfy

$$V_M(s, q) = \max \left\{ G(s, q), -c(s) + \sum_{t \in S} p_{st} V_{M-1}(t) \right\}, \quad \forall s \in S, q \in Q, \quad (4)$$

with the convention that $V_M(t) = \sum_{q \in Q} f(q)V_M(t, q)$ for all $M \geq 0$ and $V_{-1}(s) = 0$. Note that the difference between (3) and (4) is that the solution to (4), i.e., the maximum net expected reward with a finite number of decision points remaining, can be calculated recursively, by first calculating $V_0(s, q)$, then calculating $V_1(s, q)$, etc., while in (3), both the left-hand and right-hand sides depend on the function $V(\cdot)$, so such a calculation is not possible.

From the above analysis, the optimal action to take when M decision points are remaining is to mate if and only if $G(s, q) \geq -c(s) + \sum_{t \in S} p_{st} V_{M-1}(t)$, or in other words, if and only if

$$q \geq q_{\min} \left(s, -c(s) + \sum_{t \in S} p_{st} V_{M-1}(t) \right). \quad (5)$$

The right hand side of (5) does not depend on the optimal action taken at decision point M , so the policy, to mate if and only if (5) holds, is a condition-dependent threshold policy where the action depends on the quality of the encountered mate.

We can use the finite-horizon analysis to make a conclusion about the structure of the infinite-horizon problem. In particular, according to a theorem given in Chapter 2.3 of Ross (1983), $V_M(s, q) \rightarrow V(s, q)$ uniformly as $M \rightarrow \infty$. Thus, $V(s, q)$ will have the same structure and the optimal policy will still be a condition-dependent threshold even when there are infinitely many future decision points.

An important point is that while the optimal policy for this problem is a threshold policy in the male quality, the threshold is dynamic; that is, it changes according to the female's condition, taking into account the probability of transitions from one condition to another.

Recall that π maps each combination of female condition and male mate quality to an action (mate or continue), i.e., $\pi : (S \times Q) \rightarrow A$. However, we have now established that the optimal policy can be expressed in a simpler form, $\theta : S \rightarrow Q \cup \{N_Q + 1\}$.

That is, the optimal policy θ maps each condition $s \in S$ to a single quality $\theta(s) \in Q$ or to the dummy quality $N_Q + 1$ (the latter in the case where the optimal action is always to continue when the female is in condition s), such that a female in condition s will mate if and only if the encountered male's quality is at least $\theta(s)$. It is not possible to write the function θ in closed form. However, we can approximate the optimal infinite-horizon policy to any desired level of precision using the value iteration algorithm. For more details about the value iteration algorithm, we refer the reader to Puterman (2005). Here, we simply state how we can apply the algorithm to this problem. Recall that we can calculate $V_M(s, q)$ exactly using recursion. We calculate $V_M(s, q)$ using (5) for $M = 1, 2, \dots$, stopping when $\|V_M(s, q) - V_{M-1}(s, q)\| < \epsilon$ for small $\epsilon > 0$. We then use the computed value of $V_M(s, q)$ to solve (2) and determine the values of θ . The resulting thresholds θ give the female a net expected reward that differs from the maximum net expected reward by at most ϵ .

We derive lower bounds for the optimal mating thresholds by examining a one-step version of the mate choice problem. The one-step version of the mate choice problem assumes that if the female continues searching, she will always mate at the next decision point. That is, the reward earned by the one-step mate choice is $V_1(s, q)$. Let g_s denote the net expected reward from mating with a randomly selected male, if the female is in state s , and note that $g_s = \sum_{q \in Q} f(q)G(s, q)$. Therefore, if the female continues searching with one decision point remaining, she will earn a future expected reward of $\sum_{t \in S} p_{st} g_t$. On the other hand, she always has the option to stop and mate with the current male. Hence, the female's optimal net expected reward is $V_1(s, q) = \max \{ G(s, q), -c(s) + \sum_{t \in S} p_{st} g_t \}$. According to (3), $\theta(s) = q_{\min} \left(s, -c(s) + \sum_{t \in S} p_{st} V(t) \right)$. Additionally, $V(t) \geq g_t$ for all $t \in S$, because $V(t)$ is the reward earned by following the optimal policy in state t while g_t is the reward earned by following the always-mate policy in state t . Then because $q_{\min}(s, g)$ is non-decreasing in g , we can conclude that

$$\theta(s) \geq q_{\min} \left(s, -c(s) + \sum_{t \in S} p_{st} g_t \right). \quad (6)$$

The above equation states that the mating threshold obtained from the one-step version of the mate-choice problem is a lower bound on the optimal mating threshold. While this result does not completely characterize the optimal policy, it does show that if the male quality is below the threshold resulting from the one-step problem, the female should definitely choose to continue searching. Moreover, when conditions (such as high search costs) make the threshold very low (i.e., the female will mate with almost any male), then the one-step threshold turns out to be a good approximation of the optimal threshold.

Evaluating best-of- n with changing conditions. In the literature, best-of- n strategies have been widely cited as a simple heuristic for mate choice. A best-of- n strategy involves evaluating n males and then returning to mate with the best male encountered (Janetos, 1980). Although subsequent theoretical and empirical work has called this into question (Gibson and Langen, 1996; Jennions and Petrie, 1997), it is still used as a baseline comparison strategy in theoretical models (Real, 1990; Luttbeg, 1996; Collins et al., 2006). To better understand the behavior of the two policies developed in this article (the optimal threshold and the one-step threshold), we must be able to compare their net expected rewards to the net expected reward for best-of- n under the same regime of search costs and dynamic conditions.

To derive the net expected reward for a female in condition s utilizing the best-of- n strategy, we calculate the expected reward for mating using this strategy, which we denote by R_n , and then subtract the cost, denoted by D_n , of sampling n males and

returning to the highest quality male encountered. We calculate the expected reward for a female using best-of- n by averaging twice, first over the female's final condition t after n steps and then over the highest mate quality q encountered. To compute the probability of each possible final condition, we begin by noting that the k -step probability transition matrix for female condition is P^k (that is, matrix P multiplied by itself k times). Let p_{st}^k denote the (s, t) th element of matrix P^k ; this quantity is the probability of transitioning to state t over k steps when starting in state s . To compute the probability that the highest-quality male encountered is of quality q , first note that each encounter is assumed to be independent. Hence, $F(q)^n - F(q-1)^n$ is the probability that all n males encountered had quality at most q , but not all of them had quality at most $q-1$. Hence, the expected reward for the best-of- n strategy for a female beginning in state s is

$$E[R_n|s] = \sum_{t \in S} p_{st}^n \sum_{q \in Q} [F(q)^n - F(q-1)^n] G(t, q).$$

The expected cost of using the best-of- n strategy is calculated similarly, by averaging over the possible states at each of the n time steps; as a result, $E[D_n|s] = \sum_{k=0}^n \sum_{t \in S} p_{st}^k c(t)$. Here, we do not need to average over qualities because search costs do not depend on mate quality. Thus, the net expected reward for a female in state s using best-of- n is $E[R_n|s] - E[D_n|s]$, the expected reward of mating minus the expected search cost of employing a best-of- n strategy.

Policy comparison. To test how well the optimal policy (found via the value iteration algorithm) performs, we performed a numerical study to calculate the expected reward under the optimal threshold, the one-step threshold, and the traditional best-of- n model. As a baseline, we also calculated the net expected reward for random mating (i.e., the always-mate policy that selects the first encountered male), g_t . We considered three probability transition schemes: (1) a random walk, where condition is equally likely to increase or decrease; (2) a biased random walk, where condition is more likely to decrease than increase over time to approximate aging; and (3) uniformly random transitions, where an individual is equally likely to transition to any possible condition. (1) is most closely equivalent to a female searching for a mate in a fairly constant environment with some natural stochastic variation (changes in resource abundance, disease or injury), whereas (2) approximates age related decreases in fecundity, or the passage of an optimal breeding period (e.g. moving from a season where food and shelter is abundant to another where resources become more scarce); (3) represents a totally random scenario, such as might be experienced by small organisms with very little control over their surroundings, such as reef fish that could be carried by waves, or insects blown about by wind. In both (1) and (2), an individual was most likely to stay in the same state, so that large condition changes would require the passage of time. We considered low, intermediate, and high nominal search costs; intermediate search costs were 10 times as large as low, and high search costs were 100 times as large as low. In all scenarios, search costs increased as condition decreased, and we used a concave reward function (see Appendix A for the full set of parameters used in the numerical study).

The net expected rewards for the optimal threshold policy, the one-step threshold policy, random mating, and best-of- n were computed for all combinations of the parameters described above, and plotted in Fig. 1. When presenting the net expected reward for best-of- n strategies, we assume that the female uses the value of n with the highest expected reward, given her transition scheme, costs, and initial state. If a fixed n were used for each state in lieu of the optimal value, then the resulting net expected reward would be lower. In all scenarios, the numerical results confirm that the optimal condition-dependent threshold policy performs best. When search costs are high, the one-step policy is a close approximation of the optimal policy. The optimal policy outperforms best-of- n in

every scenario except the biased random walk with medium costs, where they are approximately the same. Best-of- n performs particularly poorly with high search costs. It is also important to note that although the expected reward increases for all strategies with improving initial female condition, the differences between the strategies decrease with increasing initial female condition. The latter observation suggests that the choice of mating strategy is more important for low-condition females than for high-condition females.

Mate quality thresholds, i.e., the minimum male condition required for the female to choose to mate, are plotted in Fig. 2. As one might expect, higher costs and less predictable or worsening future condition lead to lower thresholds. Consistent with (6), the one-step thresholds are a lower bound on the optimal thresholds. When females can expect that there is a good chance their condition will increase in time, low condition females have higher thresholds than high condition females (see, e.g., low costs and random transitions), because they can benefit from waiting for their own condition to improve. When costs are high and females are likely to decrease in condition over time (see, e.g., biased random walk and high cost), low condition females have lower thresholds than high condition females, because the potential benefit from waiting to find a better mate is offset by the likelihood that their own condition will decrease and in the meantime they will accrue high search costs. These results are consistent with empirical evidence of condition-dependent variability in female preferences (Cotton et al., 2006).

Incomplete information. In a real system, it is unlikely that a female can accurately assess the true state of a potential male. Instead, she is likely to have a general idea of a male's condition, which may be more or less accurate depending on the honesty of the signals he is using to advertise to potential mates. To assess whether our optimal threshold policy would be viable in such a scenario, we tested its performance under varying degrees of uncertainty about a male's true condition and compared the average reward values to those obtained through mating randomly.

We used an individual based model to simulate mate choice and rewards for females employing either random mating or an optimal threshold. Male traits and female condition were assigned according to a discretized normal distribution with 24 bins, and changed via a biased random walk. We examined three levels of imperfect information, approximated by decreasing granularity: high (12 visible states), medium (6 visible states), and low (3 visible states). We compared these results to those derived from mating with perfect information, i.e., where females could observe all 24 male states. In each case, the female perceives the quality of the male to be the weighted average of all males in the same perceived state. For each level of information, we repeated the simulations with low, medium, and high search costs.

In the simulation, each female sampled males until she found a male whose perceived quality exceeded her condition-dependent threshold value. Each female's net fitness was calculated as $G(s, w) - C_{\text{total}}$, where w was the mate's actual quality and C_{total} her accumulated search cost. As a baseline, we also simulated best-of- n mate choice for each level of information, using the optimal value of n for each female given her starting condition. In these simulations, females sampled n males, and returned to the highest (perceived) quality male they encountered. As a control, we calculated the net expected reward for random mating. Complete details on the simulation are described in Appendix A.

In all simulations, the optimal policy outperformed both random mating and best-of- n mate choice (see Fig. 3). The best-of- n strategy performed surprisingly poorly, but this can be explained because we are looking at the average reward over a population of females; recall that in Fig. 1, we saw that best-of- n performed much worse than the optimal policy for lower condition females. In

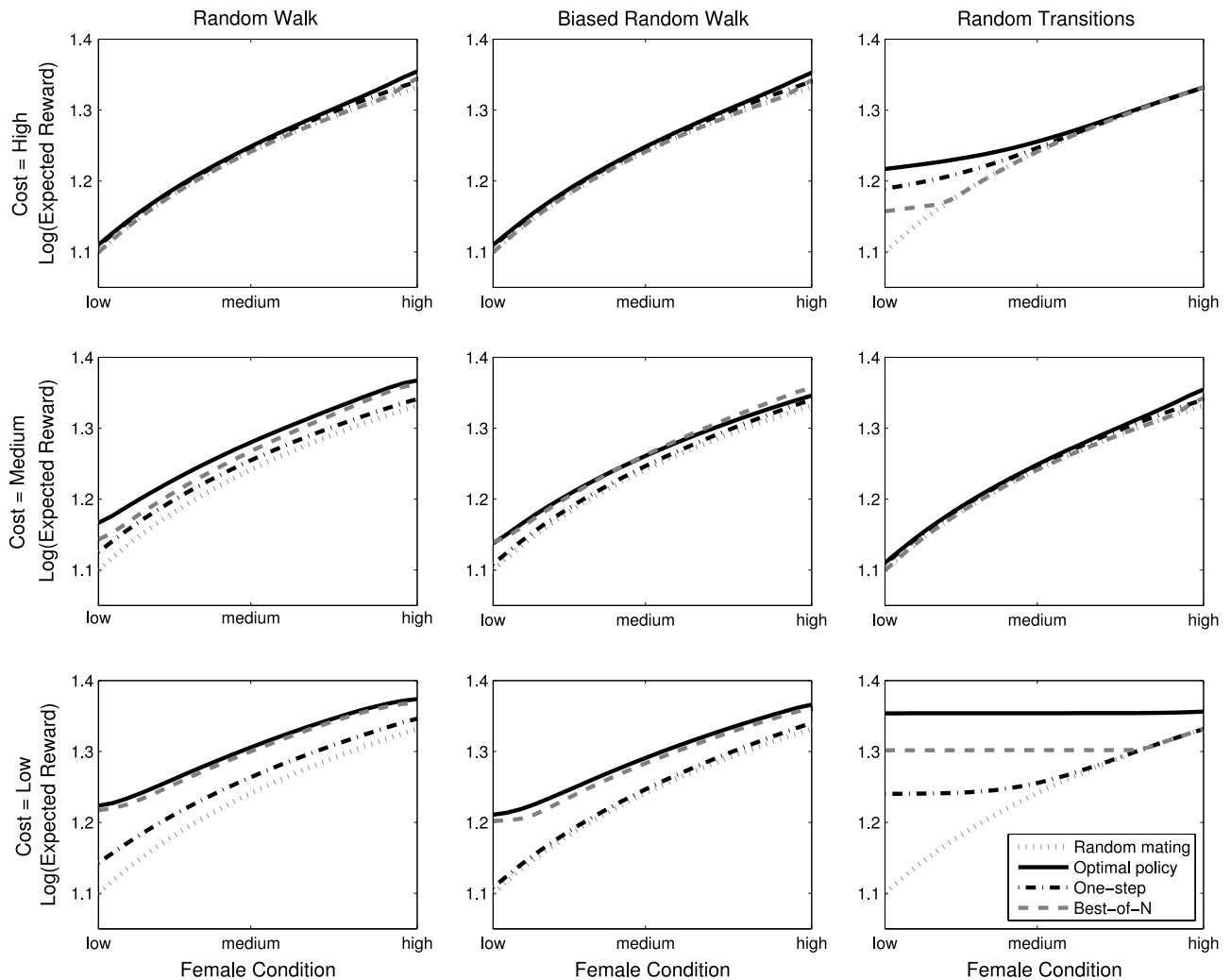


Fig. 1. Net expected rewards for different mate choice policies. We calculated the net expected rewards for the optimal policy, the one step look ahead policy, and best-of- n . The rows, from top to bottom, show high, medium, and low search costs. The columns each represent a different type of transition matrix, P : the right most column corresponds to a random walk, the middle column to a biased random walk (more likely to decrease over time) and the left most column corresponds to random transitions in quality. For this plot, $N_S = N_Q = 24$. On the x axis, initial female condition varies from 1 to 24.

the simulations, the extremely poor rewards for females with low condition bring the population average reward down substantially.

As the granularity of information about male quality decreases, the net expected reward decreases for both best-of- n and the optimal threshold. Under best-of- n , females actually search longer (i.e., the optimal value of n is larger) when they have less information. However, because the optimal threshold adapts to female state, females can stop searching when it becomes costly.

This result shows the robustness of the optimal threshold policy in making the best decision given the available information, and its adaptability to changing conditions. With perfect information and low costs, the optimal threshold policy performs on par with a best-of- n policy. However, when information is imperfect the optimal threshold policy is the clear winner: intuitively, there is no use in sampling a large number of males when the female cannot clearly tell the difference between them, and this fact becomes even more pronounced as costs increase. Finally, the optimal policy outperforms random mating (the dashed line in each figure) in all scenarios, even when mate choice is costly and information is poor.

3. Discussion

In this paper, we have constructed a model of female mate choice where female condition changes stochastically over time,

search costs are a function of female condition, and the ultimate reward of mating (i.e., offspring quality) is a function of both maternal and paternal condition values. We proved that the optimal policy to maximize a female's net expected reward is a condition-dependent threshold, we analytically derived lower bounds on the optimal thresholds, and we demonstrated that the optimal threshold can be found using the value iteration algorithm. We showed that the optimal condition-dependent threshold policy outperforms best-of- n and random mating under three different stochastic regimes: a random walk, an aging process, and completely random transitions. The condition-dependent threshold policy is indistinguishable from random mating when costs are very high, and performs on par with best-of- n when costs are very low. Finally, we showed through simulation that the condition-dependent threshold policy is robust to imperfect information, outperforming the baseline strategies even with very little information about male quality.

Mate choice strategies have been relatively well studied. Early models considered simple heuristics in constant environments (Janetos, 1980), while more recent models have dealt with incorporating search costs (Real, 1990), and complex problems such as learning (Luttbeg, 1996) and stochasticity in male quality (Collins et al., 2006). However, the model presented in this article is unique in that we consider the impact of female condition on mate choice

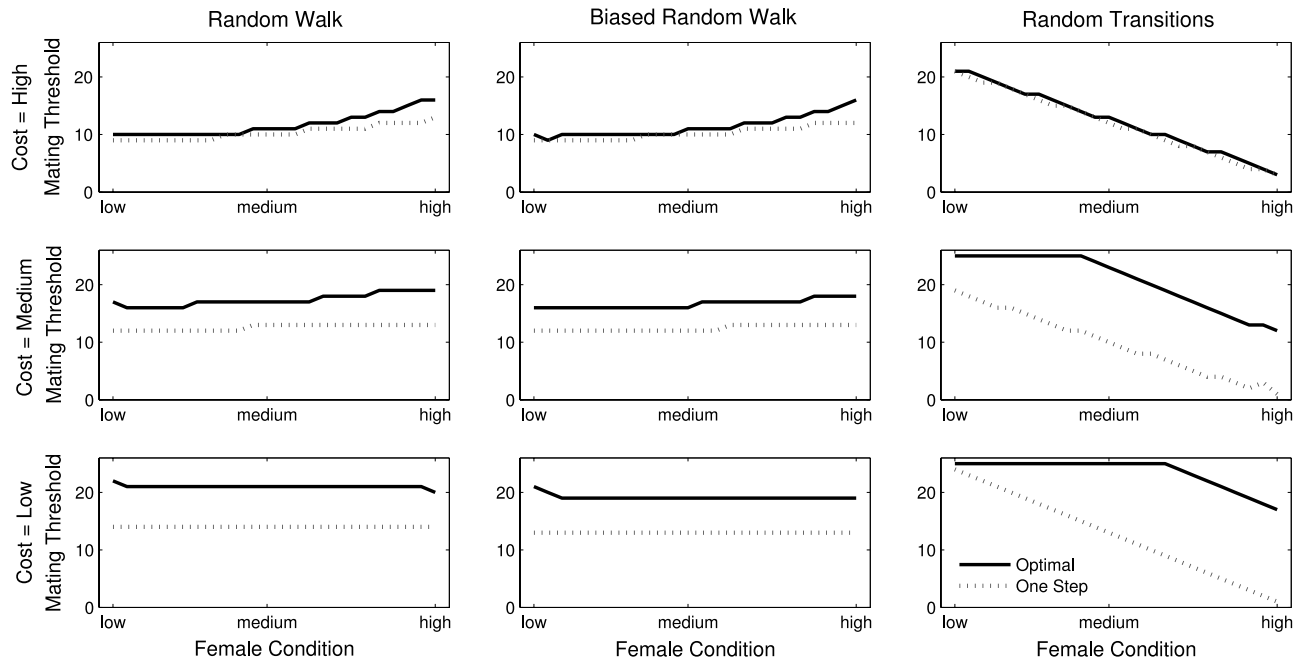


Fig. 2. Mating thresholds for females under the optimal policy and the one step look ahead policy (here, $N_S = N_Q = 24$). From top to bottom, we plotted low, medium, and high search costs. The thresholds for the two policies are generally similar, where thresholds are lower with high costs or a high probability of decreasing in condition, and high thresholds when searching is inexpensive.

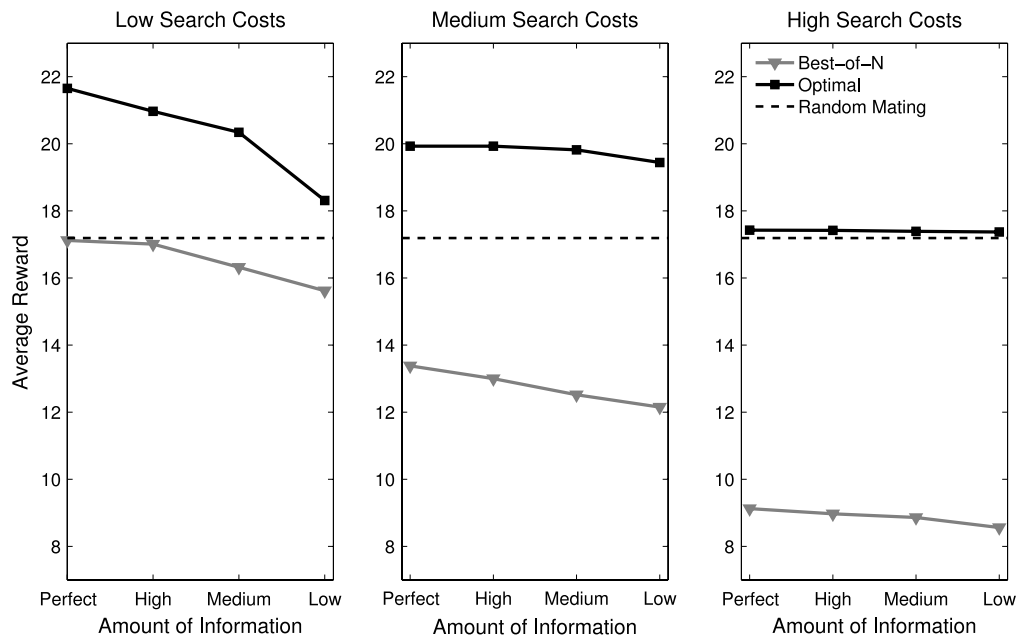


Fig. 3. Comparison of simulation results for policy performance under uncertainty about male quality. The three panels, from left to right, show the net expected rewards under low, medium, and high search costs. In each figure, the x axis depicts the ability to perceive male quality, going from perfect (at the left) to poor (at the right). In these simulations, $N_S = N_Q = 24$, $\mu = 12$, and $\sigma = 1.67$. With high information, females perceived 12 male classes, with medium information, 6, and with poor information, 3.

decisions: the offspring quality is a function of both male and female condition, and female condition changes stochastically during the search process.

The model presented in this paper predicts thresholds based on a female's state. Many policies that have been shown to perform well rely on complex calculations involving differential equations and prior probability distributions. Our policy calculates thresholds based solely on male trait distribution, female search costs, and state transition probabilities; given those values, an optimal

threshold can be calculated for each female state, and no dynamic updates need to be made. Generally, a female in poor condition with little hope for improvement has weaker preferences than a high quality female that can take the extra time to find a better mate. Interestingly, [Janetos \(1980\)](#) did suggest that an 'optimal one-step process' would be a useful strategy: if females had a finite time horizon for mating, they should be very picky at the beginning of their search, and gradually decrease their threshold. This result is analogous to our finite time horizon model with a single state.

Our results complement the empirical findings that female condition impacts preferences, and that females may exhibit plasticity in their preferences in order to maximize reproductive success (Cotton et al., 2006). Observational studies have correlated decreased preference strength with poor condition (Rintamäki et al., 1995; Bakker et al., 1999). Experimentally, both condition (Burley and Foster, 2006; Hunt et al., 2005; Hingle et al., 2001) and variation in search costs (Milinski and Bakker, 1992; Alatalo et al., 1988) have been shown to moderate female preferences.

Unlike some previous works that used models with Bayesian updating (such as Luttbeg, 1996 and Collins et al., 2006), in our model we do not assume that the female changes her belief about the male population as she encounters males. Assuming that females update their beliefs over time can markedly increase the complexity of the strategy that the female would have to employ. Rather, we supposed that the female already has knowledge of the distribution of male quality. In reality, it is likely that females can acquire social information about the distribution of male quality prior to mate choice (Doligez et al., 2002; Valone and Templeton, 2002; White, 2004). Furthermore, our simulations with imperfect information show that the optimal threshold policy under our model is robust to scenarios where females know very little about male quality. We also made the assumption that females would have some awareness of their own condition, based on the evidence of condition-dependent mate choice (Cotton et al., 2006).

Unlike in proposed best-of- n policies (Janetos, 1980), we do not assume the female can return to any previously-encountered male; this is consistent with Real (1990). The option to return to one of a set of previously-encountered males (while paying another search cost) could be incorporated in future work, which would increase the complexity of the policy (i.e., the policy would have to depend on the quality of the currently-encountered male and the quality of the best previously-encountered male). Adding such an option would only increase the payoff, since it would increase the actions available to the female.

Our results suggest an interesting mechanism for mate choice, and this mechanism may have evolutionary implications. Our finding that females are likely to alter their preferences in response to changes in condition and related search costs may have important evolutionary implications. It is possible that if females adaptively lower their threshold for mate quality, such a strategy could contribute to the maintenance of variability in male traits. It is also possible that females could evolve alternative strategies to compensate for variable environments, such as mate choice copying or mating with multiple males. Mate choice copying is a well documented phenomenon (Stöhr, 1998), and may be especially likely under scenarios where mate choice is costly (Frommen et al., 2009); if a low condition female were to observe a high condition female mating with a male, she could avoid further search costs and maximize her reproductive fitness by copying the high condition female's choice. Multiple matings could also offer females a hedging strategy—mate with a lower quality male to avoid the possibility of dying before reproducing, but mate with any higher quality males encountered later on (Caspers et al., 2014). Both of these possibilities might, however, result in female–female competition or decreased fitness due to male resource depletion, which could change female mating strategies (Orians, 1969; Weatherhead and Robertson, 1979; Tazzyman et al., 2012; Frame, 2012). In the future, a multi-generational genetic model of female mate choice with dynamic female fitness would greatly enhance our understanding of this process and its evolutionary outcomes. The results of this article highlight the need for increased awareness of female condition in experimental studies of mate choice, and the importance of sequential mate choice tests.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.tpb.2014.06.001>.

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