

Mate choice when males are in patches: optimal strategies and good rules of thumb

John M.C. Hutchinson*, Konrad Halupka¹

Max Planck Institute for Human Development, Lentzeallee 94, 14195 Berlin, Germany

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Abstract

In standard mate-choice models, females encounter males sequentially and decide whether to inspect the quality of another male or to accept a male already inspected. What changes when males are clumped in patches and there is a significant cost to travel between patches? We use stochastic dynamic programming to derive optimum strategies under various assumptions. With zero costs to returning to a male in the current patch, the optimal strategy accepts males above a quality threshold which is constant whenever one or more males in the patch remain uninspected; this threshold drops when inspecting the last male in the patch, so returns may occur only then and are never to a male in a previously inspected patch. With non-zero within-patch return costs, such a two-threshold rule still performs extremely well, but a more gradual decline in acceptance threshold is optimal. Inability to return at all need not decrease performance by much. The acceptance threshold should also decline if it gets harder to discover the last males in a patch. Optimal strategies become more complex when mean male quality varies systematically between patches or years, and females estimate this in a Bayesian manner through inspecting male qualities. It can then be optimal to switch patch before inspecting all males on a patch, or, exceptionally, to return to an earlier patch. We compare performance of various rules of thumb in these environments and in ones without a patch structure. A two-threshold rule performs excellently, as do various simplifications of it. The best-of- N rule outperforms threshold rules only in non-patchy environments with between-year quality variation. The cutoff rule performs poorly.

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1. Introduction

Models with food distributed in patches have been prominent right from the start of foraging theory (e.g. Charnov, 1976). A patch structure allows models to capture phenomena both of local variation in resource richness and of local depletion (e.g. Iwasa et al., 1981). Empiricists have been able to investigate decision making in patchy systems which closely match such

models (e.g. Goulson, 2000; Waage, 1979), but the ideas have also inspired analysis of systems such as starlings foraging in a field in which the assumption of discrete readily recognizable patches is an abstraction from the real distribution pattern (Dall et al., 1997). There is a continuum between uniform and clustered distributions, and items may be randomly or uniformly distributed at one spatial scale, but clustered at another (Wiens, 1989). Patches have also long been a feature in models of population dynamics (Wiens, 1976), and are at the heart of metapopulation models (Hanski and Gilpin, 1999).

Models of mate choice, concerned with a female's decision whether to mate with a male of known quality or to examine further males, also have a respectably long pedigree in behavioural ecology (Janetos, 1980). It

*Corresponding author. Tel.: +49-30-82406352; fax: +49-30-82406394.

E-mail addresses: hutch@mpib-berlin.mpg.de (J.M.C. Hutchinson), halupka@biol.uni.wroc.pl (K. Halupka).

¹Present address: Department of Avian Ecology, University of Wrocław, ul. Sienkiewicza 21, 50 - 335 Wrocław, Poland.

is striking therefore that a patch structure has almost never been incorporated into models of female mate-choice behaviour. Bertorelle et al. (1997) provide the most prominent exception; they both document a patch structure in the distribution of male fish and simulate various decision rules in this environment to explain observed female behaviour. Our paper will seek more general results, both finding optimal behaviour and comparing the performance of suboptimal rules of thumb in a range of abstract patchy, and non-patchy, environments. Two other theoretical papers about mate choice involve a patch structure, but this patchiness matters only because of an extra assumption that males of like quality cluster: Roitberg et al. (1993) were interested in the advantage of a long memory of quality, and Benton and Evans (1998) were not concerned with which rules perform well but with the strength of the correlation between male success and attractiveness.

Could the lack of patch-based models of mate choice reflect a perception that males are rarely patchily distributed? In some species the territoriality of breeding males may indeed lead to their even dispersion, but many other species breed only in colonies. Nor need territoriality prevent clustering at broader spatial scales. This is strikingly the case in many leks, which are the best studied systems of mate choice (Höglund and Alatalo, 1995; Wiley, 1991), and which thus alone would justify the development of patch-based models. Although true non-resource-based leks are taxonomically rare, resource-based leks, in which males aggregate around resources required by females, are more common (Parker, 1978). Thus male dungflies aggregate around fresh dung where females will lay their eggs, just as male frogs aggregate at ponds. Even more commonly, both sexes have habitat requirements that lead to a patchy distribution of males simply because that habitat is patchy (Andrewartha and Birch, 1954; Hanski and Gilpin, 1999). Thus in modern Europe many bird and mammal species are restricted to small islands of woodland in a sea of open fields. Or insects may congregate around patches of flowers. Patchiness in the distribution of males therefore seems similarly as widespread a phenomenon as patchiness in the distribution of food.

Patch-based models of mate choice might nevertheless be unnecessary if females restrict their searching to a single patch (as do certain wood-boring beetles: Reid and Stamps, 1997). Gathering data on inter-patch movements is not easy, requiring either following females between patches or monitoring several patches for the presence of marked females, but such data are available for a variety of lekking species. Usually a substantial proportion of females visit more than one lek (Lanctot et al., 1997).

Another situation in which existing non-patch models could be applied with little modification is if females

visit several clusters of males, but choice of males within a cluster is simultaneous rather than sequential. This describes mate choice in the fiddler crab *Uca annulipes*, in which females select just one male to visit from each of several clusters (Backwell et al., 1998).

Despite the availability of patch-use models from foraging theory, it is not possible to apply them “off the shelf” to female choice of patchily distributed males. In the foraging models many items are consumed (so that depletion leads to a lowering of patch quality). In mate choice this may fit the behaviour of males (Parker and Stuart, 1976), but the usual assumption is that a female seeks a single male of high quality. Her decisions to move patch occur not because a patch deteriorates but because she learns about its contents. Female mate choice shares these characteristics with many other decision choices, such as where to set up a territory, where to build a nest, or on which leaf to oviposit (cf. Roitberg et al., 1993); so the models of mate choice that we develop apply more widely. Indeed we suspect that some of these systems may prove to be more amenable than mate choice to experimental testing of the models, because it may be easier to manipulate the quality of inanimate items. Our models may also apply when males are the choosy sex, but we ignore this possibility to keep the wording simpler.

Our model assumes that time spent looking for a mate has costs (Alatalo et al., 1988; Moore and Moore, 2001) and that movement between males within a patch is therefore less costly than the longer movements between males in different patches. This could be simply because of the longer time to find the next male (Wickman and Jansson, 1997), but also the habitat between patches may expose females to higher predation risk (Bertorelle et al., 1997; Hedrick and Dill, 1993). Also inherent in our model is that the female recognizes a patch, and thus knows that seeking a mate outside the current patch brings an increased cost. Indeed a more abstract version of the model can be framed in terms only of differing expected costs of travel to the next male. Thus the model also sometimes applies when the patchiness is in time rather than space. An example is an intertidal animal in which mate inspection is only possible at high tide, and the intervening low tides carry a predation risk.

Another aspect of our model is that females remember the qualities of males already encountered and may return to them, in some versions with a cost, which would be greater when returning to males in a previous patch. Returning to already visited males is frequently reported in empirical studies (Jennions and Petrie, 1997; Uy et al., 2001). This has often been interpreted as evidence for a best-of- N strategy and against a threshold strategy (see Wiegmann et al., 1996), the two rival decision rules which dominate the mate-choice literature (Janetos, 1980; Real, 1990a). With best-of- N strategies (also known as pooled comparison) the female decides

in advance to inspect N males, and only once she has inspected all of them can she return to select the best. Threshold strategies assume that females inspect a succession of males, deciding at each to accept him or continue. Usually threshold strategies have not allowed returning, probably because under the most common assumptions (notably an infinite time horizon), a fixed quality threshold for acceptance is optimal, so that return is never adaptive (Real, 1990a). This will turn out not to be the case in our patch models. We allow the possibility of returning to an earlier male without assuming that the number of males inspected is fixed in advance; rather, the decision depends on the qualities of males inspected earlier. Such a framework is also present in the “comparative Bayes tactic” of Luttbeg (1996), but he additionally assumed that revisits were often to gather more information about prospective mates. This confounding of mate choice with mate assessment seems entirely realistic, but for simplicity our models assume that quality is recognized fully at first encounter.

The theoretical literature on mate choice has borrowed from the extensive literature in economics and mathematics on the closely analogous job-search and secretary problems (Lippman and McCall, 1976; Freeman, 1983). The inspirations for these problems usually do not involve spatial search, so it is less surprising that appropriate patch-based models do not appear in that literature either, although some steps go in our direction. Gianini (1977) supposed that the chooser decides every N items either to accept the best of these N or inspect the next N , but choice within such “patches” was not analysed, and utility depended on rank rather than absolute quality. Similarly Lippman and McCall (1976) allowed a random number of items to be encountered simultaneously, but selection of the best of them was instantaneous, so the effect is merely a change in quality distribution of items considered sequentially. This fits the situation where the effort of selecting an item within a shop is negligible compared with that of moving between shops or towns (Meyer, 1997). Other models allow recall of earlier items within a moving window of the last N items (e.g. Smith and Deely, 1975).

Our aim in this paper is to understand the adaptive value of different behaviours when selecting patchily distributed mates. We are thus concerned not only with what behaviour is optimal, but with whether the optimal strategy is robust to variation in the environment, and with what simpler rules of thumb perform well. Rather than predicting optimal behaviour given real parameter values (in any case, almost never have the necessary parameters been measured), we seek to reveal general principles and to identify what broad patterns of behaviour are adaptive under what range of circumstances. Empiricists observing such patterns will then

have one or more potential explanations that they can test more thoroughly; or if they observe a different pattern they know to seek some other explanation. To expose the logic, we most thoroughly investigate an unrealistically simple model. Later sections elaborate it in various directions (specifically by introducing within-patch return costs, an increasing difficulty in finding the last males in a patch, and the need to learn the distribution of male quality from experience). Along the way, we highlight some further relevant elaborations worthy of future investigation, but can here merely make verbal arguments about their likely consequences. The final results section proposes some simplifications of the optimal strategy as rules of thumb, and compares their performance with that of other rules of thumb considered in the literature.

2. The framework of the model

We now explain the assumptions and parameters of the baseline version of our model (see Table 1 for a summary). We believe that the baseline parameter values are biologically plausible, but also frankly admit to choosing them partly so that the optimal behaviour resembled the real mate choice behaviour that we had in mind: i.e. females visiting several males and sometimes several patches. It did not require particularly careful tuning of the parameter values to achieve this (the sensitivity analysis in Table 2 will support this claim), but nor is it difficult to select other values with the uninteresting outcomes that the first male is always chosen or only one patch ever visited. As the baseline case we take travel time between patches to be 10 times the time to find and inspect a male in the same patch. This ratio generates results that contrast clearly with those from non-patchy environments, and may be quite realistic for many invertebrates, for instance. In other cases, such as some birds, travelling to a new patch takes less time than inspecting a new male, in which case optimal behaviour is very similar to that in a non-patchy environment.

In our model, male quality varies from 0 to 1. In the baseline case quality follows a normal distribution with mean $\mu = 0.5$ and s.d. $\sigma = 0.125$ (before very slight truncation at 0 and 1). For technical reasons we can allow only a number of discrete qualities within this range, but the number is chosen large enough (350–2000) to approximate a continuous distribution closely. Qualities of males are randomly drawn from the population so that the number and qualities of males in a patch are uncorrelated. In a real population of a monogamous species, the distribution of male quality and its correlation with patch size would change over the mating season as females progressively remove the

Table 1
Symbols used repeatedly in text

<i>Parameters with baseline values</i>		
N_μ	4	mean of patch size distribution prior to truncation ($0 < N \leq M$)
M	20	maximum patch size
w	0.01	rate at which opportunity to mate is interrupted
t_f	1	time to find and inspect next male in current patch
t_P	10	time to move to next patch
t_r	0	time to return to preceding male in current patch
t_R	10	time to return to preceding patch
μ	0.5	mean of quality distribution of current year/patch
σ^2	0.125 ²	variance of quality distribution of current year/patch
μ_0	0.5	mean of μ across years or patches
σ_0^2	0	variance of μ over years or patches
<i>Variables</i>		
n		number of males left to inspect in current patch
N		number of males in patch
l		number of males already inspected (either in current patch or overall)
q		quality of the current male = reward from mating with him now
m		observed mean quality of inspected males (either in current patch or overall)
r		expected reward from choosing the best option currently available
r_{cn}		when n uninspected males remain in patch, optimal strategy is to mate iff $r > r_{cn}$
r_{c0}		acceptance threshold when $n = 0$ (i.e. all males in patch inspected)
r_{c*}		acceptance threshold when $n > 0$ (i.e. males left to inspect in current patch)

best males (Collins and McNamara, 1993; Johnstone, 1997); we avoid this game-theoretic aspect.

A female must select just one male, and her reward is equal to the quality of the male with which she mates. Although she potentially has infinite time to find a mate, we specify a constant risk (rate = w) that the opportunity to mate will end, which results in a reward of 0. This risk might be predation or the unpredictable end of the breeding season. It ensures that females perform poorly if they continue sampling males until they find one of maximum quality. For simplicity the model contains no other costs such as energetic expenditure, but we expect that they would have roughly similar effects to an increased value of w . The cost of a behaviour in our model is thus simply a function of the time spent doing it. The model can incorporate an elevated predation risk when travelling outside patches by increasing between-patch travel times.

Males are encountered one at a time, and randomly with respect to quality (reasonable assumptions for some species, e.g. Reid and Stamps, 1997). The time to find and inspect the next male in the current patch is taken as a constant t_f , but the analysis would be similar if this time were a random variable $t_f(i)$ uncorrelated with quality or with how many males remain to be found in a patch. (What matters is the expected probability of surviving this time, so replace $\exp(-wt_f)$ with $\text{mean}[\exp(-wt_f(i))]$.) The same holds for the other time costs: time to find a new patch = t_P ; time to return to a male in the same patch = t_r ; time to return to a male in another patch = t_R . For tractability we assume that a

female can rely on each inspected male still being present if she returns.

We focus on the case of an infinite number of patches. In the baseline case the number of males per patch follows a Poisson distribution with mean $N_\mu = 4$, except that patches with no males are not visited, so that the actual mean patch size encountered is 4.07. Assuming instead that empty patches are visited would merely be equivalent to increasing the average travel time between non-empty patches. We also need to set a maximum patch size of M males, with M chosen to exclude only the extreme tail of the Poisson distribution (in the baseline case, $M = 20$).

In our initial optimality model we assume that the female knows w , the average travel times, the distribution of male qualities, and the distribution of the number of males in a patch. A female does not know a particular male's quality until he has been inspected. Nor does a female know the number of males in the next patch, but once there she knows both this and the number currently left to inspect.

3. Finding the optimal strategy

When a female has inspected a male she has several options. She can move on to an uninspected male in the same patch (if such males remain), she can move on to the next patch, she can accept the current male, or she can revisit and accept a male inspected earlier either in the current patch or in an earlier one. Inspecting a male

in the current patch is cheaper than moving patch to inspect another male, and their expected qualities are the same in the baseline case, so a female should never move to another patch until all males in the current patch are inspected.

The decision whether to continue inspecting males should depend in part on r , the expected reward from deciding to mate now, if necessary by returning to an earlier male. This acts as a state variable. It is simply the maximum of the product of each inspected male's quality and the probability that there will be time left to return to him. Whenever a new male is inspected, r should be updated if the new male provides a better option than the previous best option. With zero within-patch return costs, $r(l) = \max[r(l-1), q(l)]$, where l is the number of males inspected, and $q(l)$ is the quality of the present male. But having just moved to a new patch, $r(l) = \max[\exp(-wt_R)r(l-1), q(l)]$. The $\exp(-wt_R)$ term discounts the expected reward by the risk of being interrupted during the trip back to the preceding patch. The discounted value of r is thus just the weighted average of the reward should the return journey be successful (r) and the reward should it be interrupted (0). In fact, under the baseline assumptions it never pays to return to an earlier patch, so on moving to a new patch $r(l) = q(l)$.

If r exceeds the expected reward from continuing mate search, the current male or an earlier one should be accepted; if not, another male should be inspected. The reward from continuing the search depends on n (the number of uninspected males in the patch), on the reward if subsequent males are rejected in favour of a male already inspected (r in the case of no return costs), and on the quality of the next male. The latter is unknown, so we integrate over all possible qualities to calculate the expected reward of continuing. This expected reward also depends on the number of patches left, which we usually assume to be infinite, and on the female's future strategy, which we assume continues to be optimal. If $r = 0$ it must be better to continue searching and if $r = 1$ it must be better to accept a male. So, for each value of n , there must be a intermediate threshold level of r , r_{cn} , above which a male should be accepted immediately and below which search should continue. To find both the value of r_{cn} under the optimal strategy, and the expected reward when in each state of r and n , we use stochastic dynamic programming (McNamara and Houston, 1986; Mangel and Clark, 1988). This algorithm works backwards in time from when there are no further males to inspect in the patch to when none have been inspected, and from a last patch to when there are sufficient uninspected patches left that working further back has no effect on the optimal strategy or the expected rewards (see Appendix A). Having found the optimal strategy, we use Monte-Carlo simulation to calculate aspects of

behaviour such as the mean number of males or patches visited (Appendix A.5).

4. Zero within-patch return costs

The simplest version of our model assumes no costs of returning to males in the current patch. We treat this as a baseline version against which the results from less restrictive versions are compared.

Inspecting another male is less attractive an option if it requires moving patch rather than remaining within a patch, so it is not surprising that the optimal acceptance threshold with n males left to inspect, r_{cn} , is less for the last male in the patch than for earlier males. We expected r_{cn} to decline steadily as the number of males left to inspect in a patch declined. But r_{cn} turns out to be constant (r_{c*}) regardless of how many males are left to inspect in the patch, until the last male in the patch is inspected, when the threshold drops to r_{c0} . Appendix B proves this surprising result. It is related to a result known to economists, applying to the situation of a finite number of items with free recall of earlier options (Lippman and McCall, 1976). In that case also, a constant threshold should be applied until the last step, but then the threshold drops to 0 (because, with no option of continuing search, it must pay to return to the best item encountered, however poor).

The constancy of r_{c*} means that a female need not know how many males are left to inspect in a patch, but only whether any remain uninspected or not. This might be a much easier task. For instance if the female searches systematically through a patch, she would have a good idea near the end of her sweep that she has found the last male, but when halfway through could have only a rough estimate of the numbers yet to be found. The constancy of r_{c*} also means that she should never return to a male inspected earlier until she has inspected all males in a patch.

The value of r_{c*} is the same in the patch model as in non-patch models either with a finite time horizon and free recall or with an infinite time horizon with or without recall. As a corollary, r_{c*} is independent of the distribution of the number of males per patch, and of travel costs between patches. In the case of a finite number of patches, r_{c*} is independent of the number of unvisited patches. The easiest way to calculate r_{c*} analytically is to consider the infinite-time-horizon problem. There it is known that r_{c*} equals the expected reward, and that optimal decisions appear myopic in the sense that the cost of examining one more male exactly equals the increased reward expected from having one more male to choose from (Lippman and McCall, 1976)

$$r_{c*} = \exp(-wt_f) \left(r_{c*} \int_{-r_{c*}}^{r_{c*}} P(q) dq + \int_{r_{c*}}^{\infty} qP(q) dq \right)$$

Table 2
Optimal strategy and behaviour in the baseline model and a sensitivity analysis

	Results with baseline parameters	Percentage change to baseline results when:							
		Doubled time costs (w)	Doubled within-patch travel time (t_f)	Doubled inter-patch travel time (t_P)	Doubled patch-size parameter (N_μ)	Doubled s.d. of male quality (σ)	Additive within-patch return time ($t_r = t_f/2$)	One-off within-patch return time ($t_r = t_f/2$)	No return ($t_r = \infty$)
r_{c*}	0.654	-6.2	-6.2	0.0	0.0	+21.9	-3.1-0	-3.1-0	-12.5-0
r_{c0}	0.553	-13.8	-3.6	-11.0	+4.0	+19.3	-0.4	-0.2	-0.9
Expected reward	0.611	-4.8	-3.6	-1.6	+4.0	+19.4	-3.2	-0.2	-0.9
Proportion of ♀♀ interrupted	0.071	+6.6	+23.4	-20.9	-3.8	+35.7	+2.8	+1.9	+9.6
Mean number of ♂♂ inspected ^a	4.20	-27.3	-19.1	-14.3	+37.6	+15.8	-4.5	-1.9	-11.4
Mean number of patches inspected ^a	1.28	-16.3	-6.5	-14.5	-13.6	+13.8	+0.6	+0.4	+8.0
Proportion of ♀♀ revisiting ♂ ^a	0.358	-25.2	-36.5	+11.0	-20.8	-5.7	-24.0	-14.9	-100.0

Baseline parameters are $w = 0.01$, $t_f = 1$, $t_P = 10$, $t_r = 0$, $N_\mu = 4$, $\mu = 0.5$, $\sigma = 0.125$. Each column is based on 10^7 simulations.

^aThese figures exclude females that ran out of time before choosing and, if necessary, returning to a male.

where $P(q)$ is the probability that a male is of quality q . This simplifies to

$$r_{c*} = \int_{r_{c*}}^{\infty} (q - r_{c*})P(q) dq / (\exp(wt_f) - 1).$$

In contrast, the optimal threshold when inspecting the last male in a patch, r_{c0} , does depend on the other parameters of the model because it depends on the expected reward when moving patch. If there were a finite number of patches in the neighbourhood, it would also decrease as the number of patches left to inspect declines or as the expected time to find a new patch increases. The same happens if the time horizon is infinite but taking extra time has an extra penalty (such as later in the season the risk of interruption w increasing, or reproductive productivity decreasing: this would mean that all r_{c0} also decrease between and within patches). A consequence of a decrease in r_{c0} would be that some females return to previously rejected males in earlier patches. However, in the baseline case it never pays to return to a male in an earlier patch: if it was better once to reject all males in a patch in favour of an unknown patch, it remains the better choice were the female to find herself back there (because we assume an infinite local supply of unvisited patches). Later we will encounter another exception to this pattern, when females must learn the distribution of male qualities in the environment.

Table 2 reports the results of a sensitivity analysis in which we double various parameters of the model and examine the effect on the optimal thresholds and on various measures of female behaviour.

5. Robustness of the optimal strategy

Fig. 1 examines how the two thresholds, r_{c*} and r_{c0} , affect performance (found by simulation, see Appendix A.5). Here and elsewhere we use the same measure of relative performance of a suboptimal strategy, defined as the ratio of the improvement that that strategy shows over a null strategy, to the improvement that the optimal strategy shows.

Relative performance

$$= \frac{\text{performance of suboptimal strategy} - \text{performance of null strategy}}{\text{performance of optimal strategy} - \text{performance of null strategy}}$$

The null strategy is to accept the first male encountered.

It is evident that it is much safer to err on the side of having too low a value of r_{c0} than too high, and on having too high a value of r_{c*} than too low. In other words, there is little harm in inspecting more males than necessary within the current patch, but it is important to avoid the risk of continuing to search patch after patch. For a broad range of lower than optimal r_{c0} and higher than optimal r_{c*} the expected reward is only a few percent below the optimum, because these strategies mostly lead to the same behaviour, of searching the first patch completely and accepting the best male in it.

The solid curve in Fig. 1 indicates performance of a simplified rule in which $r_{c0} = r_{c*}$. This constancy of the acceptance threshold means that a female never returns to a male inspected earlier. The optimal single threshold is 0.583 (compared with 0.654 and 0.554 for r_{c*} and r_{c0} , respectively), and this gives a relative performance of 0.928. However, for this single threshold rule the cost of

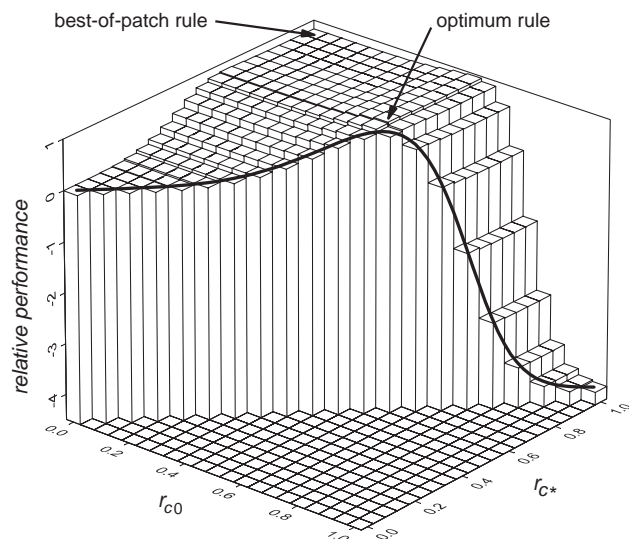


Fig. 1. *Relative performance* of two-threshold rules in the baseline case (see Table 1), depending on the acceptance thresholds (r_{c0} is when the last male in a patch has been inspected, r_{c*} is for all earlier males). *Relative performance* measures the improvement over a null strategy (taking the first male) relative to the improvement shown by the optimal strategy (see text). The heavy line highlights performance values where there is a single threshold ($r_{c0} = r_{c*}$). Cases where $r_{c*} < r_{c0}$ are not shown as they are consistently inferior. Each performance value is based on 10^7 simulations.

deviating from the optimum threshold increases quite sharply in both directions; there is no plateau of near optimal performance as with the two-threshold rule.

In different environments, the adaptive landscape in Fig. 1 will shift, and different thresholds will become optimal. The presence of the plateau suggests that the two-threshold strategy optimal in one environment may do well in many environments in which it is not optimal. However, the optimal combination of r_{c0} and r_{c*} lies not far from the edge of the plateau, so that a shift in landscape may take the formerly optimal combination of parameter values over the edge; thus a strategy further from the edge may be more robust. The strategy maximally far from the edge, which nevertheless has a *relative performance* of 0.829, is in the back corner of Fig. 1, with $r_{c*} = 1$ and $r_{c0} = 0$. This strategy is to visit every male on the first patch and then pick the best: we call it the “best-of-patch” rule.

To assess the robustness of the optimal rule directly, we have examined how well a version adapted to the baseline parameters performs when transplanted to environments with different parameters. Fig. 2 displays the performance of this transplanted optimum as a proportion of the performance of the true optimum rule adapted to each environment. The robustness of the best-of-patch rule is assessed similarly. The transplanted optimal rule performs well when male quality is higher or more variable, but can perform very poorly (worse even than the null strategy of accepting the first

male) when male quality is lower or less variable than the environment to which the thresholds are adapted (Figs. 2(a, b)); in these cases best-of-patch does much better. When w (roughly the risk of delaying mate choice) or mean patch size change, both rules are rather robust (Figs. 2(c, d)), and best-of-patch is not on average better. We expected the performance of best-of-patch to be more affected than it was by mean patch size, as this determines how many males are inspected. Relative to the optimum it does best with a mean patch size of about 7. Of course these results depend on the other parameters, particularly the costs of moving between and within patches.

Various other simple rules of thumb have been proposed as good solutions in sequential search. However, one of their supposed strengths is in coping with a situation of uncertainty about the distribution of quality. We therefore consider them later, in Section 9, after having derived the optimal strategies in such a situation.

6. Within-patch return costs

When there are within-patch return costs the optimal strategy is more complex since the threshold now does decline as the number of males in the patch left to inspect decreases (Fig. 3; see Appendix A.3 for method of solution). Nevertheless, the pattern remains that the drop in threshold is mostly when the last male in the patch is inspected.

With return costs one must specify whether returning to a male visited two or more steps ago takes no longer than returning to the previous male, or whether the time required accumulates additively (i.e. the female has to retrace her path). The situation in nature must usually lie between these extremes, depending on the spatial configuration of males within a patch, so we investigate both situations, which we term the cases of “one-off” and “additive” return costs respectively.

With additive return costs, accepting a male once l males on the patch have been inspected yields an expected reward $r(l) = \max[\exp(-wt_r)r(l-1), q(l)]$, where t_r is the time to return to the preceding male in the same patch, and $l > 1$. The expected reward for continuing is a non-decreasing function of $r(l)$. Thus males should be accepted if and only if $r(l)$ exceeds a threshold value r_{cn} , which declines as the number of uninspected males in the patch (n) decreases (Fig. 3).

In the case of one-off return costs, we define s as the undiscounted value of the best male encountered so far in the current patch ($s(l) = \max[s(l-1), q(l)]$); so s is identical to the baseline formulation for r , but this is no longer the expected reward from mating now. The expected reward from continuing depends on $s(l)$, whereas the reward from accepting a male is a function

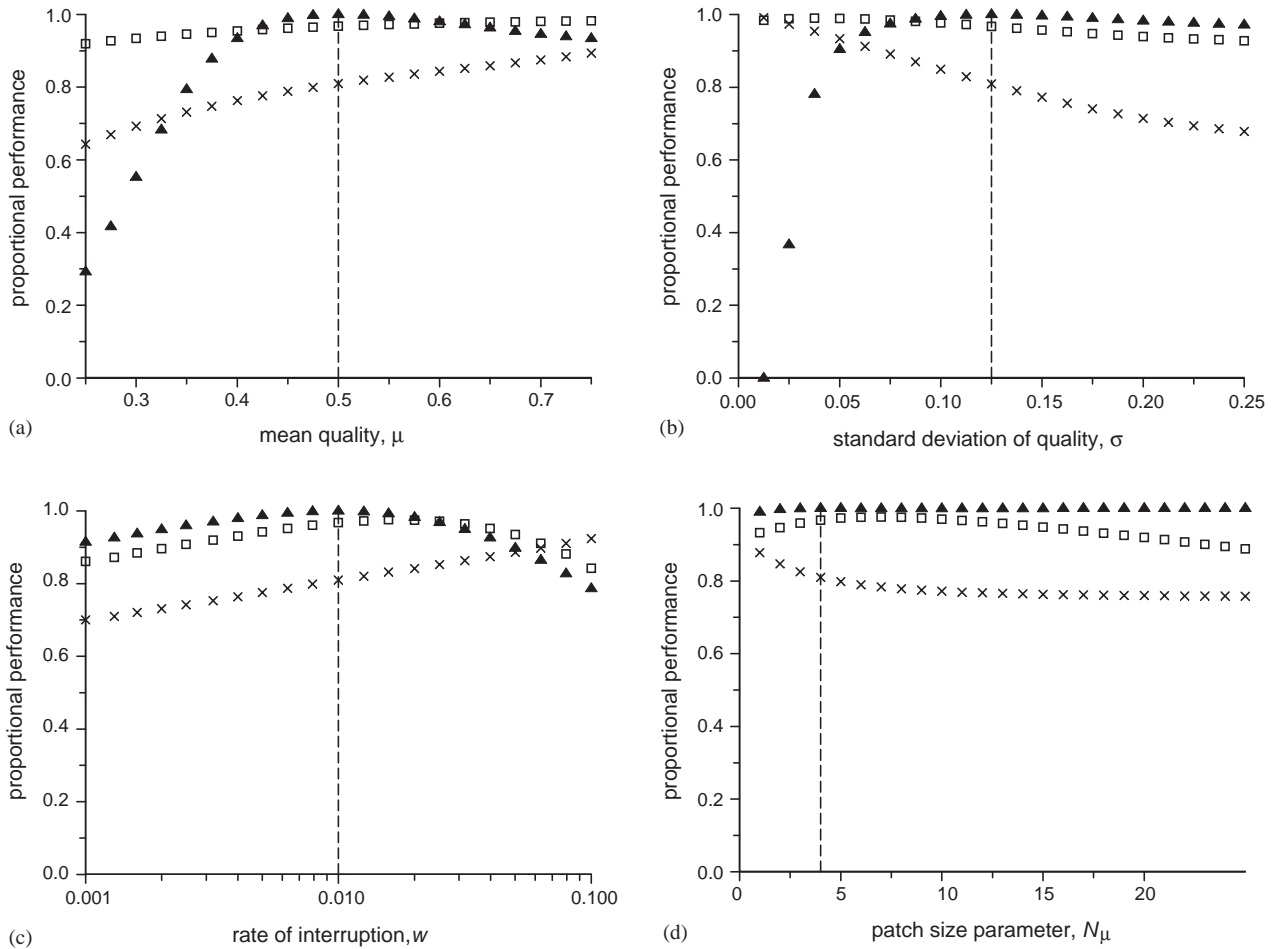


Fig. 2. Performance of the optimal strategy in a novel environment. In each part of the figure a different parameter of the environment is altered. Proportional performance = performance of given rule/performance of rule optimal in that environment. ▲ = fixed two-threshold rule which is optimal in the baseline environment indicated by the dashed line. □ = best-of-patch rule (inspect all males in a patch and accept the best). × = take the first male encountered. Default parameters are as in Table 1.

of both $s(l)$ and $q(l)$ (i.e. $\max[\exp(-wt_r) s(l - 1), q(l)]$, which equals $\max[\exp(-wt_r) s(l), q(l)]$). Consequently, there are two thresholds for each value of n . One is the value which the current male must exceed to be accepted. The second is the value that the best previously visited male must exceed if the female is to return to him. This second threshold is always higher than the first, and is independent of n except that it falls once $n = 0$ (Fig. 3). Consequently, as in the baseline case, a female returns to a previously inspected male only once all males in the current patch are inspected. This pattern of behaviour also holds with additive return costs.

Both with additive and with one-off return costs, the fewer the uninspected males left in the patch, the more likely that the female will get to the end of the patch and then return. She should try to avoid the cost of returning by progressively lowering her acceptance threshold. When there are many males still left in a patch it is unlikely that the female will return (she is likely to find

an above-threshold male before reaching the end of the patch). Consequently, however high the return costs, the acceptance threshold when many males are left to inspect converges to the same limit, the same as r_{c*} in the case of zero return costs (Fig. 3). It is also apparent from Fig. 3 that r_{c0} (the last-male threshold) decreases only very little with increased return costs. The value of r_{c0} depends on the expected reward having moved patch, which is the same as the expected reward initially. Introducing return costs has rather little effect on this expected reward and thus on r_{c0} . Table 2 shows that other measures of behaviour are little affected by increases in within-patch return costs from 0 to half t_f , the finding and inspection cost. Unsurprisingly, the greatest effect is a decrease in the proportion of females that return to a male inspected earlier.

Mostly it seems reasonable to consider only cases where return costs are no greater than the finding and inspection costs when first encountering each male. However, if attempts to return to a male are often

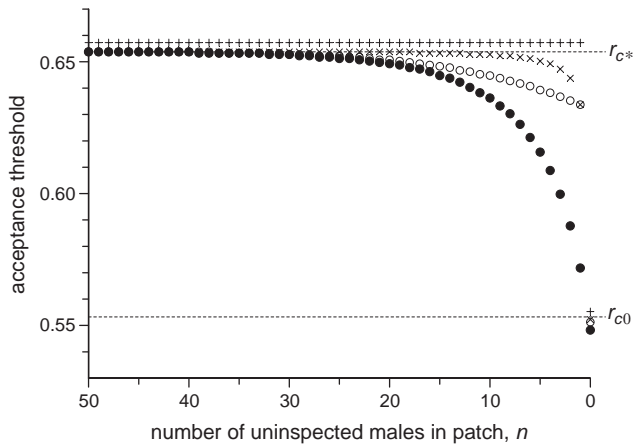


Fig. 3. The optimal strategy when return costs are added to the baseline model. Acceptance thresholds depend on n , the number of males left to inspect in the current patch. For the case of infinite return costs (so that recall of previously inspected males is disallowed), ● indicates the quality above which the current male is accepted. In other cases, return costs are set half that of the original discovery and inspection ($t_r = t_f/2$). For the case when the time to return to a male mounts up additively with each further male inspected, ○ shows the value of r (expected reward from mating, i.e. including discounting) above which a male is accepted. Both sorts of crosses refer to the case when returning to any male in the current patch takes the same time: × indicates the quality that the current male must exceed to be accepted now, and + the quality that a male encountered earlier must exceed. The dashed lines indicate values of the two optimal thresholds when within-patch return is costless. Parameter values as in Table 1.

unsuccessful, we might, in a rough and ready way, attempt to incorporate this decreased advantage of returning by increasing the return costs further. (Using dynamic programming to find the optimal strategy in a direct model of this situation becomes problematic, because the female should remember not only the best male encountered but also qualities of all the other males inspected, in case the best ones become unavailable. Karni and Schwartz (1977) show analytically, for a related problem, that the acceptance thresholds in such cases of partial recall lie between those with no return allowed and those when returning always succeeds.) When return costs are extremely high the effect is of course the same as when it is impossible to return to males inspected earlier, the more usual assumption of sequential search models (e.g. Dombrovsky and Perrin, 1994; Mazalov et al., 1996). In this situation the acceptance thresholds decline more smoothly as the number of males in the patch left to inspect declines (Fig. 3). Surprisingly, the *relative performance* of this strategy, compared with the optimal when return is possible and costless within a patch, is 0.951, which indicates the small advantage to the female of being able to remember the quality of previously inspected males in the patch and to relocate them. On the other hand if a female does have these capabilities and within-patch return costs are zero, her optimal decision rule is

simpler: she does not need to change threshold with every male inspected, nor know how many males are left to inspect in the patch.

When return costs are half that of finding and inspection costs, the decline in threshold is rather shallow until the last male is inspected (Fig. 3), suggesting that a two-threshold strategy might still perform rather well. We used Monte-Carlo simulation to find the best two-threshold strategies. They do indeed perform extremely well (*relative performance* > 0.996). The best-of-patch strategy also still does well (*relative performance* > 0.803). Indeed even when return is impossible a two-threshold strategy can have a *relative performance* of 0.990. Our conclusion is that within-patch return costs need have little consequence for fitness. Whether decision rules allow return is likely to depend more on cognitive abilities (e.g. to remember qualities) or on whether rejected males remain relocatable and available.

The non-return version of our patch model might apply best when males are steadily becoming unavailable (e.g. owing to mating, predation or an ebbing tide), explaining why attempting to revisit is unprofitable (but requiring slight alterations to the model since the number of unvisited males remaining in the patch declines faster than the rate of inspection). In other situations the biological basis of our non-return version of the model may be questioned. Other possible reasons for a female not to be able to revisit a male are that males move around making them impossible to refind, or that females cannot remember male positions or qualities. But in these cases females would keep encountering the same males repeatedly and the females seem unlikely to know how many males in the patch remain uninspected. A different form of model is then necessary. Such a model might well apply in many situations, particularly in mating aggregations of invertebrates. However, an optimal solution would be complex because females would need to remember the quality of not just the best male encountered but of other males that might be acceptable if reencountered.

7. Increasing search costs

So far we have assumed that t_f , the expected time to find and inspect the next male, is independent of the number of uninspected males in the patch. More plausibly, finding any of 20 uninspected males should be easier than finding the only one of 20 males that is uninspected. One might reasonably suppose that the rate of finding uninspected males is directly proportional to the number of them left in the patch, and here we make this assumption also about t_f (assuming time for inspection to be a negligible component of t_f in this extreme case). Whereas before $t_f = 1$, now $t_f = 2/n$,

where n is the number of males left to find in the patch and the factor 2 ensures rough comparability with the mean travel times and expected reward in the baseline version.

The optimal strategy is then an acceptance threshold that decreases progressively as the number of uninspected males declines (Fig. 4; see Appendix A.2 for method of solution): if the cost of finding another male is higher than earlier, it makes sense not to remain as picky. Unlike the earlier case of within-patch return costs, when the threshold also decreased, now females often return to a male before they reach the end of the patch (Table 3, last row). Indeed amongst cases where a return occurs, it may be in only a minority that all the males in the patch have been inspected.

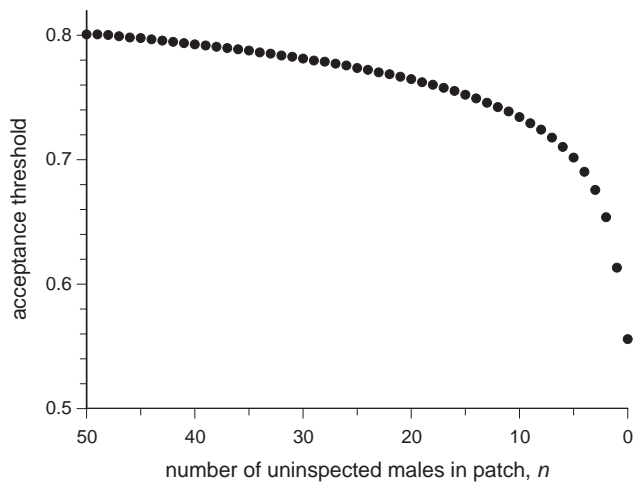


Fig. 4. The dependence of the optimal acceptance threshold on the number of males left to inspect in the current patch (n), in the case when it gets harder to find the last males in the patch ($t_f = 2/n$). The female continues searching until the best male in the patch encountered so far exceeds this threshold, which may involve returning to a male previously rejected. She never leaves the patch until $n = 0$. Parameter values as in Table 1.

The higher encounter rate when entering a new large patch can mean that it might pay to skip the last few hard-to-find males in the current patch. If females ever make such a decision, whether to skip or continue is independent of r , the quality of males encountered so far (proof in Appendix C). However, for most plausible parameter values, including those of our baseline case, skipping the last few males in a patch is never adaptive (Table 3). To get it to be so requires a much lower cost of moving between patches and a high average number of males per patch.

We considered another version of the model in which again the expected pay-offs from inspecting the next male decrease within a patch, but for another reason than increasing search costs. Females may follow a strategy that makes them likely to encounter better males in a patch earlier. For instance in leks the best males are often clustered in the middle (Kokko et al., 1998), and in non-lekking species also it seems plausible that the edges of suitable habitat hold lower quality males. If males are partially ordered in quality, the quality of males inspected early indicates something about the expected quality of males left to be inspected, but the optimal mate-choice strategy is not straightforward to derive. Another way in which females make themselves more likely to inspect better males earlier is to use preliminary cues that allow several males to be inspected simultaneously from afar, and then inspect more carefully those that on this basis appear the most promising (Rintamäki et al., 1995). Optimization is now more straightforward, because a female has more information than a rough ranking of the males; rather for each male she can estimate a different probability distribution of quality. Salop (1973) shows in an analogous job search problem how to find optimal acceptance thresholds at each step given a specified order of inspection and also sets out necessary conditions to check whether the order is optimal (he assumes

Table 3
Optimal behaviour in some major variants of the model. Environments are as the baseline (see Table 1) except in the parameters given

	Baseline ($t_r = 0, t_f = 1, \sigma = 0.125, \sigma_0 = 0$)	No return ($t_r = \infty$)	Search time increasing ($t_f = 2/n$)	Between-year variation in mean quality ($\sigma = \sigma_0 = 0.088$)	Between-year variation in mean quality ($\sigma = 0.125, \sigma_0 = 0.088$)	Between-patch variation in mean quality ($\sigma = \sigma_0 = 0.088$)	Between-patch variation in mean quality ($\sigma = 0.056, \sigma_0 = 0.112$)
Expected reward	0.611	0.606	0.614	0.566	0.606	0.585	0.564
Proportion of ♀♀ interrupted	0.071	0.077	0.066	0.053	0.070	0.088	0.098
Mean number of ♂♂ inspected ^a	4.20	3.72	4.21	3.98	4.44	4.61	4.17
Mean number of patches inspected ^a	1.28	1.38	1.29	1.14	1.25	1.41	1.55
Proportion of ♀♀ revisiting ♂ ^a	0.358	0	0.380	0.555	0.530	0.531	0.548
Proportion of returners before patch end ^a	0	—	0.486	0.186	0.134	0.251	0.371
Proportion of returners revisiting patch ^a	0	—	0	0.002	0.003	0	0
Proportion of patch departures before end	0	0	0	0	0	0.335	0.726

Each column is based on 10^7 simulations.

^aThese figures exclude females that ran out of time before choosing and, if necessary, returning to a mate.

no recall, but points out that the same framework can deal with recall). Acceptance thresholds decline with each male inspected. We do not deal further with these situations of ordered encounter of males, but we expect them to provide another reason for females sometimes not to finish inspecting all males on a patch before returning to an earlier male or leaving to seek another patch.

8. Learning the distribution of quality

So far we have assumed that the female “knows” the distribution of male qualities. A justification would be that, if this distribution were stable, the parameters of a mate-choice strategy could have evolved to be optimally hardwired. If instead the distribution varies, for instance so that in some years mean male quality is lower, the female would benefit from being able to lower her acceptance thresholds after encountering a succession of poor males, since that suggests a low population mean that year.

Rules that adjust their acceptance criteria in an optimum Bayesian manner to qualities encountered in the current environment have previously been considered by Mazalov et al. (1996) in a fixed-time-horizon problem without recall. Roitberg et al. (1993) found optimum rules under the constraint that only a small window of past qualities could be remembered. Certain other suboptimal decision rules can also be viewed as crudely adjusting standards of acceptance to what sampling suggests is the current quality distribution in the environment. The best-of- N rule has this property, as does any rule with a threshold that drops with time. The cutoff rule considered by Dombrovsky and Perrin (1994) and Todd and Miller (1999) explicitly sets an acceptance threshold dependent on an initial fixed sample of males. We consider such suboptimal rules of thumb in Section 9. Empirical evidence from a variety of taxa confirms that acceptance of a male may depend on the quality of males inspected earlier (the “previous male effect”: Gibson and Langen, 1996; Kavaliers et al., 2003; Wagner et al., 2001).

For demonstration purposes we consider two extreme patterns of variation in the distribution of male qualities. One is typified by the case of year-to-year variation in weather that affects the mean quality of the entire male population (e.g. Bryant and Jones, 1995). Males in each patch are, as before, drawn at random from this single population. Although we will refer to this as the case of between-year variation it might also apply to variation in population mean over a shorter time-scale. For instance, in many insect species individuals emerging later in the year are smaller (Yoshimura et al., 2003); similarly a female bird migrating late may find only the poorer males and territories still available.

Similarly, females dispersing to a new locality must gauge the standard of males in that general area.

With the second pattern of variation, we envisage that smaller-scale environmental conditions will tend to affect the quality of all males in one patch similarly, but conditions may differ in other patches. Similar patterns could arise if males of different qualities locate in different patches, for instance because only the best males can defend territories in the highest quality habitats or because males avoid displaying alongside much more attractive rivals (Sutherland, 1996, p. 96). Such systematic inter-patch variation in quality provides another important reason to incorporate patches in a model. The situation is to be distinguished from the variation in patch quality that is present even in the baseline model, due simply to random sampling from a common distribution. The new version of our model draws the males in each patch from a different quality distribution. There is thus a correlation in qualities within a patch, and no correlation between patches, even adjacent ones. Nor is there any correlation between the number of males per patch and their mean quality. The real world is often likely to show both our inter-year and inter-patch types of variation, but we avoid dealing with this situation because of its complexity (discussed below). It must also be the case in nature that females utilize cues from the environment that indicate the mean quality in a patch or in a year (e.g. Reid and Stamps, 1997), but we assume that such information is available only from sampling males directly.

With both patterns, we assume that the uncertainty is in the population mean (μ) of each distribution from which male qualities are sampled, whereas the shape of these distributions is always normal with variance σ^2 (cf. Mazalov et al., 1996, who did allow σ to vary). Values of μ are themselves sampled from a normal distribution with mean μ_0 and variance σ_0^2 . This distribution of the means is considered fixed, so that an animal would have had the chance to become adapted to it; technically it provides the prior distribution. In this scenario, a standard result of Bayesian probability is that responding optimally to the information learnt from male qualities requires remembering only the observed mean quality and the number inspected (e.g. Cox and Hinkley, 1974). These two statistics also allow us to calculate the posterior probability of the next male being of each possible quality, so that we can continue to use stochastic dynamic programming to calculate the optimal strategy (see Appendix A.4).

8.1. Between-year variation in quality

We consider first the case where males in all patches come from a single population, but where the mean quality of this population differs from year to year and

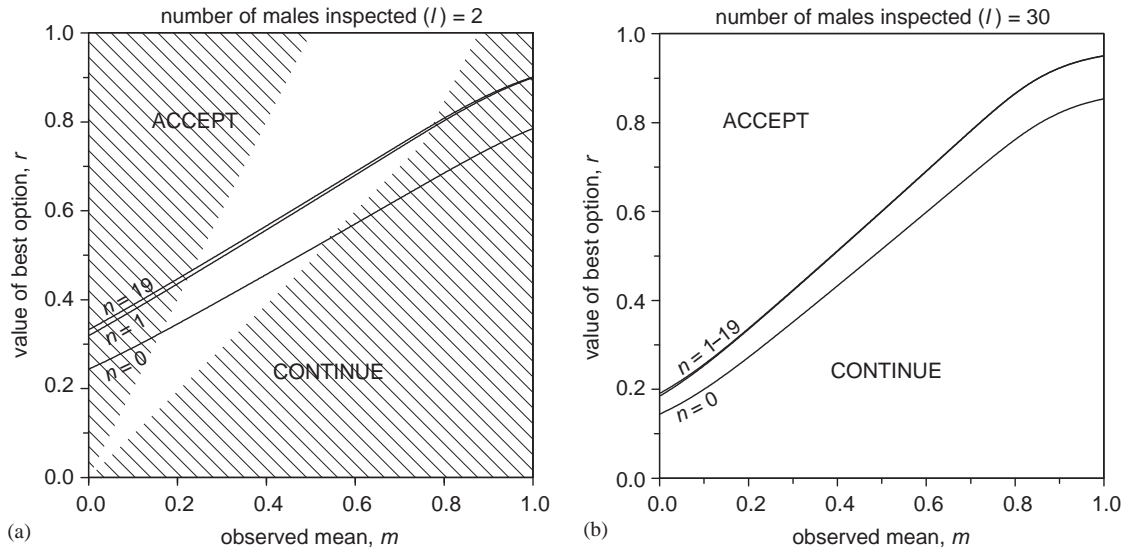


Fig. 5. The optimal strategy when quality varies between years. The female decides whether to continue to search or mate on the basis of r (expected reward from mating now), m (the mean of all qualities so far encountered), l (the number of males inspected), n (the number of males left to inspect in the current patch). The two diagrams, each corresponding to a different value of l , show where in the space of m and r acceptance should occur, with n affecting the position of the boundary line marking the acceptance threshold. For each value of l , the thresholds are so similar for n between 1 and $M - 1$ (19) that only lines for these two extreme values are shown, as well as that for $n = 0$. Some areas of the r - m space are inaccessible; in *a* those areas are shaded, in *b* such areas would be much smaller. Parameter values as in Table 1, except $\sigma_0^2 = \sigma^2 = 0.125^2/2$.

is initially unknown to the female. We focus on a case in which $\mu_0 = 0.5$, and $\sigma = \sigma_0 = 0.125/\sqrt{2} \approx 0.088$; the overall variance of male qualities (across all years) = $\sigma_0^2 + \sigma^2$, so this is unchanged from the baseline case. The other parameters are also as in the baseline version of the model (within a patch no return costs and no increase in the time to find the next male).

Which action is chosen should now depend on four state variables: the value of the best option so far available (r), the number of males left to inspect in the current patch (n), the observed mean quality of all males so far inspected including the current one (m), and the total number of males inspected, not just those in the current patch (l). The situation of between-year variation in mean quality is the only one investigated here where it can be optimal to return to a male from an earlier patch: he might have been rejected when less was known about the population mean, but becomes desirable if the population mean appears low. For simplicity we assume that each movement to a new patch increases the distance back to all earlier patches by the same amount (i.e. additive between-patch return costs), and that the return journey takes the same time as the forward journey between patches ($t_R = t_P$).

Fig. 5 shows the form of the optimal strategy. However many males have been inspected and however many are left to inspect in the current patch, the form of the dependence of the optimal action on best quality and mean quality is similar. Not surprisingly, with low r the search continues and with high r the female mates. When observed mean quality is high, better quality

males are to be expected in the future, so a higher r is needed for acceptance—hence the positive slope of the boundary lines.

For a given number of males inspected, the position of these lines is very similar regardless of how many males there are left to inspect in the patch, with the prominent exception that once all males in a patch have been inspected a lower quality becomes acceptable. This closely parallels the two-threshold form of the optimal strategy in the baseline case, and has the same explanation. So why are the threshold lines not exactly the same when one male is left to inspect as when 19 are left? The reason must be that, when each inspection increases certainty about the value of the population mean, delaying a decision to accept a borderline case is slightly more advantageous when there are several more males that can be inspected cheaply (i.e. without moving patch).

The positions of the threshold lines in Fig. 5 depend also on the total number of males inspected. When the observed mean is low, females are prepared to accept males of lower quality the greater their confidence that the population mean really is low (i.e. the more observations contribute to the mean). Conversely, when the observed mean is high, the more individuals on which this is based, the higher the quality of males that the females demand. Hence as the number of males encountered increases, the threshold lines become steeper.

A caveat must be made about Fig. 5. Not all of the r - m state space shown is accessible. For instance, when

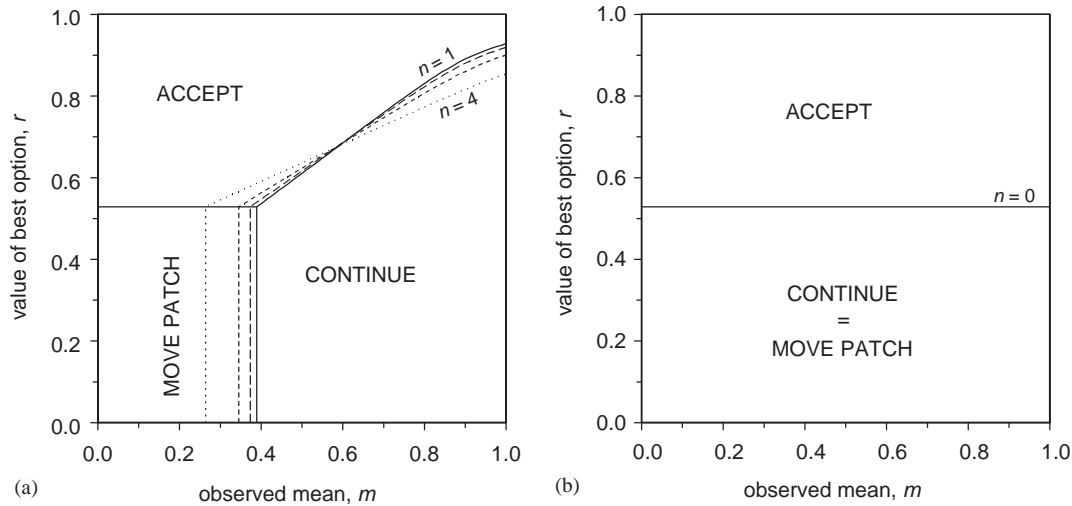


Fig. 6. The optimal strategy when quality varies between patches. The female decides whether to continue to search or mate on the basis of r (expected reward from mating now), m (the mean of all qualities so far encountered in the current patch), n (the number of males left to inspect in the current patch), and M (number of males in the patch). We show here only the strategy in patches of 5 males. In different regions of the space of m and r , different actions are optimal, with the exact position of the boundary lines between these regions depending on n . For clarity the configuration in the case of $n = 0$ is shown separately. Parameter values as in Table 1, except $\sigma_0^2 = \sigma^2 = 0.125^2/2$.

only one male has been inspected, the observed mean quality must equal the best quality. In the case when only two males have been inspected (Fig. 5(a)), we show the inaccessible regions by stippling; when more males have been inspected it becomes awkward to calculate these regions, but they also become smaller.

Table 3 summarizes the behaviours resulting from the optimal strategy. We have already mentioned the most distinctive behaviour, of moving back to previous patches. But of the cases where a female returns to a male inspected earlier, only 0.2% involve movements to an earlier patch. Females have no reason to jump to another patch before examining all males in the current patch, but more often than in other situations return to a male in the current patch before having inspected all that patch's males (of the 57% of females that return, 18% do so before checking the whole patch). Returns before the end of the patch occur when the quality acceptance threshold has dropped, because the number of males inspected has increased and/or because the observed mean has fallen.

Another aspect of performance which stands out is that the mean reward is rather lower than in the other cases in Table 3 (0.56 vs. 0.61 in the baseline version). Part of the reason is that in any 1 year the variance in quality is less, so a female cannot gain so much by good mate selection. Hence also, she spends less time searching. If instead we set the parameters so that the within-year variance in quality is the same as in the baseline case ($\sigma = 0.125$; still $\sigma_0 = 0.125/\sqrt{2}$), the mean reward and the number of males inspected is much more similar to the baseline case (Table 3).

8.2. Between-patch variation in quality

We now consider the situation where males in different patches come from populations with different mean qualities μ . We again focus on a case in which $\mu_0 = 0.5$ and $\sigma = \sigma_0 = 0.125/\sqrt{2}$, with other parameters as in the baseline version of the model. As with between-year variation, the optimal action depends on four state variables, but they are somewhat different. One is again r , but because returning to an earlier patch is now never optimal, r can simply be the best male so far encountered in the current patch. Another is the observed mean quality (m), but this is now just of males in the current patch. We take as the other two state variables patch size and n , the number of males left to inspect in the patch, but it would be equivalent to take n and l , the number of males already inspected in the patch (since $l + n = \text{patch size}$).

Fig. 6 illustrates the typical form of the optimal strategy, in this case for a patch of five males. When all males in the patch have been inspected ($n = 0$; see Fig. 6(b)) the form of the strategy is to mate if the best male in the patch exceeds a threshold quality r_{c0} which is independent of patch size and of the mean quality experienced in that patch. When there are males left to inspect in the patch, the form of the strategy is only slightly more complex (Fig. 6(a)). Below some level of observed mean quality, the decision is between mating or jumping to a new patch, with the threshold still the same value as r_{c0} . Above this level of observed mean quality, jumps to new patches should not occur; mating occurs if r is above some quality threshold, otherwise

search continues in the same patch. This threshold increases with the mean quality encountered, so that in patches which seem to be full of good males the female should be more picky.

Again it resembles the baseline case that the threshold values of r above which the best mate is accepted depend rather little on the number of males left to inspect in the patch, except when no males are left to inspect. But there is more difference than when the variation in population mean is between years (Fig. 5), because the number of males left in a patch now also reflects the number of males contributing to the observed mean, and thus its reliability as an indicator of the quality of uninspected males on the patch. Consider first the part of Fig. 6(a) above r_{c0} . If more males have been observed (smaller n) the female is prepared to accept lower quality males in the case of a low observed mean, and only higher quality males in the case of a high mean: hence the threshold line gets steeper as n decreases. Accompanying this change, there is a raising of the threshold value of the mean below which a jump to a new patch occurs if $r < r_{c0}$: when a low observed mean is based on more males (smaller n), jumping to a new patch occurs at higher observed means, because these low means then more reliably indicate a low μ .

In simulations, 33% of the movements to new patches occurred before all the males had been inspected (Table 3). This may happen even after inspecting only a single male (this occurs in 4.2% of patches with 2 males, and 2.8% of patches with 6). We discussed earlier how early leaving can also be optimal if males inspected later in a patch tended to be of poorer quality or if females reencounter males without realizing that they have already been inspected. In all these situations the low qualities of males already inspected suggests low quality of those to be encountered later in that patch.

Despite this tendency to leave patches early, the average number of patches inspected was only 10% more than in the baseline case; we expected that it would pay to sample more patches, but this must depend on the relative travel costs between and within patches compared with the relative variances in quality between and within patches. When there was relatively more variation between patches ($\sigma_0 = 2\sigma$), but the total quality variance was still the same, leaving patches before fully inspecting them became much more common (73% of moves, vs. 33% when $\sigma_0 = \sigma$), but the average number of patches inspected increased only from 1.41 to 1.55 (Table 3).

As in the situation of between-year variation in mean quality, females may return to mate with a previously inspected male before all males in a patch have been inspected. 53% of the matings involved returning to a previously encountered male and in 25% of these the return occurred before all males in the patch were inspected. In contrast to the situation of between-year

variation in mean quality, now females never return to an earlier patch. (The earlier patch remains less attractive than a new unvisited patch, so long as we assume that the local supply of new patches is not exhausted.)

If there were variation in population means both between patches and between years, a female may learn that all patches are likely to be worse than she expected when originally leaving the patch. It may then even make sense to return to a partially inspected patch to continue searching in it. One strategy might be first to visit several patches superficially and only later return to the one seeming the best. Unfortunately, for fully optimal behaviour the number of state variables becomes unmanageable: the female must remember means and best males of all patches left that are not fully inspected, because a revisited patch may on second inspection turn out worse than initially predicted, and then she needs this information about the other patches already visited.

9. Suboptimal rules of thumb

The optimal strategies when there is variation between years or between patches are not so complex in form that it is inconceivable that they might evolve. On the other hand they do require combining four pieces of information. We now consider what is the gain in using such strategies compared with various simpler suboptimal rules of thumb. Optimization models generally dominate in behavioural ecology, but mate choice is probably the domain in which consideration of rules of thumb has been most prominent (e.g. Bertorelle et al., 1997; Janetos and Cole, 1981; Real, 1990b; Todd and Miller, 1999).

We use simulation to assess *relative performance* of the decision rules in eight different environments (Table 4; Appendix A.5). The first is the baseline case, in which the distribution of male quality does not vary between years or patches and is known to the female. We then consider the two environments considered earlier in which there is equal variation in μ between years or between patches as there is about μ within each year or patch ($\sigma_0 = \sigma$). We also consider again the case when the standard deviation of μ between patches is double that of individual male qualities within a patch ($\sigma_0 = 2\sigma$). As examples of environments where patchiness is less marked, we double mean and maximum patch size and halve the cost of moving between patches (considering cases both of between-year and of between-patch variation in mean quality). Finally we compare environments with no patch structure (with and without between-year variation). Table 4 reports how well suboptimal strategies perform relative to the improvement that the optimal strategy achieves over picking the

Table 4
Performance of optimal strategy and relative performance of suboptimal rules of thumb

	Baseline ($t_P = t_R = 10$, $N_\mu = 4$, $M = 20$, $\sigma = 0.125$, $\sigma_0 = 0$)	Between-year variation ($\sigma = \sigma_0 =$ 0.088)	Between-patch variation ($\sigma = \sigma_0 =$ 0.088)	Greater between-patch variation ($\sigma = 0.056$, $\sigma_0 = 0.112$)	Less patchy: between-year variation ($t_P = t_R = 5$, $N_\mu = 8$, $M = 40$, $\sigma =$ $\sigma_0 = 0.088$)	Less patchy: between-patch variation ($t_P = t_R = 5$, $N_\mu = 8$, $M = 40$, $\sigma =$ $\sigma_0 = 0.088$)	Not patchy: between-year variation ($t_P = t_R = 0$, $M = 1$, $\sigma = \sigma_0$ $= 0.088$)	Not patchy: ($t_P = t_R = 0$, $M = 1$, $\sigma = 0.125$, $\sigma_0 = 0$)
Optimal	0.611	0.566	0.585	0.564	0.585	0.612	0.591	0.654
Optimal no-return ^a	0.951	0.802	0.883	0.847	0.893	0.934	0.937	1.000
Two-threshold	1.000 (0.654, 0.553)	0.954 (0.695, 0.403)	0.976 (0.693, 0.525)	0.904 (0.712, 0.505)	0.937 (0.664, 0.390)	0.882 (0.663, 0.570)		
r_{c0} -only	0.964 (0.550)	0.940 (0.397)	0.960 (0.526)	0.895 (0.505)	0.881 (0.404)	0.823 (0.565)		
r_{c*} -only ^a	0.928 (0.584)	0.541 (0.488)	0.818 (0.556)	0.718 (0.528)	0.615 (0.522)	0.817 (0.598)	0.659 (0.535)	1.000 (0.654)
Best-of-patch	0.829	0.905	0.715	0.506	0.876	0.671		
Best-of- N	0.638 (3)	0.642 (3)	0.550 (3)	0.390 (3)	0.824 (5)	0.652 (6)	0.857 (7)	0.827 (9)
Cutoff rule ^a	0.366 (1)	0.220 (1)	0.201 (1)	0.000 (0)	0.465 (1)	0.366 (1)	0.559 (2)	0.587 (3)
Candidate-count ^a	0.366 (2)	0.220 (2)	0.201 (2)	0.000 (1)	0.465 (2)	0.366 (2)	0.508 (2)	0.496 (2)
Sequential comparison	0.555	0.558	0.485	0.347	0.611	0.472	0.574	0.514
Quality-up	0.567	0.577	0.480	0.335	0.611	0.471	0.574	0.515
Quality-up, no return ^a	0.342	0.330	0.252	0.111	0.365	0.278	0.341	0.314
Mean-up	0.540	0.530	0.428	0.247	0.612	0.471	0.585	0.527
Mean-up, no return ^a	0.443	0.431	0.336	0.172	0.479	0.366	0.453	0.413
Non-candidate-count	0.507 (2)	0.222 (2)	0.394 (2)	0.191 (2)	0.756 (2)	0.615 (3)	0.825 (4)	0.802 (5)

Relative performance by definition is 1 for the optimal strategy and 0 for the null strategy of taking the first male. Parameter values of the constrained optima are given in brackets (except for the optimal no-return rule, which is too complex), but some may be inaccurate in the third decimal place because of the flatness of the optima. The rules are explained in the main text. Environments are as the baseline (see Table 1) except in the parameters given. Each performance figure is based on 10^7 simulations.

^aThese rules never involve returning to a previously rejected male.

first male encountered at random. For each of the eight environments, any parameters required by a rule have been set to values maximizing performance averaged across the conditions encountered in that environment.

One way to simplify the optimal decision rule is to forbid returns, removing the need to remember the quality and position of individual males; in some species the mobility of males or their pairing up with rival females will anyway make returning impossible. The optimum rules under this constraint of no return are not simple (even in non-varying environments—see Fig. 3(a)), but they provide a standard against which to assess performance of other rules that avoid returns. Since in each environment the relative performance of the no-return optimum exceeds 80% (and it is the optimum in the non-patchy environment without between-year variation), poor performance of other no-return rules cannot be explained purely by their avoiding returns.

Two-threshold strategies of the same form as the optimum in a non-variable environment still perform exceedingly well when the environment varies. The improvement in performance over a random strategy is often over 90% that achieved by the optimal strategy even though decisions are now much simpler to make: remember that a single constant threshold (r_{c*}) is used to

decide whether to accept a male or continue searching in the patch, and a lower threshold (r_{c0}) is applied once all males in a patch have been inspected. Naturally these thresholds should have different values from the situation when the mean of the quality distribution is known exactly (further back on the plateau in Fig. 1). Although the two-threshold strategy is so close in performance to the optimum, not only is the decision rule much simplified but also the range of behaviours observed: females never return to a male or leave a patch before inspecting all males in it, and never return to an earlier patch.

We tried three ways to simplify this strategy even further. One is to set r_{c*} to 1, so that all males in every visited patch are inspected, and then to use r_{c0} to decide whether to accept the best or to try another patch. (Naturally the value of r_{c0} is altered from that used in the two-threshold rule.) This strategy is called cluster sampling by Bertorelle et al. (1997) and r_{c0} -only by us. An alternative simplification is to use only r_{c*} , keeping the same threshold when having to decide whether to move to the next patch. Note that this r_{c*} -only strategy avoids ever having to remember or return to a male inspected earlier. Thirdly, the best-of-patch strategy, already considered in Fig. 2, chooses the best male of the first patch encountered.

It turns out that the r_{c0} -only strategy does almost as well as the high-performing two-threshold strategy; evidently even if a high-quality male is found, it is reasonable in our environments to check the rest of the males in the patch (although less so when the patches are larger). The r_{c*} -only strategy suffers particularly from between-year variation, probably because the threshold must be set low to avoid endless searching in poor years, and then is not selective enough in good years. However, when there is no patch structure and no between-year variation, the single constant threshold is optimal. The best-of-patch strategy is weaker when quality variation between patches is higher, because if μ is low in the first patch, a male must nevertheless be chosen from it.

The next best strategy overall is best-of- N , which inspects a predetermined number of males and then returns to the best. Note that in our version of best-of- N , the female is not forced to return to the male of the highest quality if he lies in an earlier patch and the expected reward is higher from returning to a male of somewhat lower quality in the current patch. Real (1990a) showed that earlier claims for the superiority of best-of- N over fixed threshold (i.e. r_{c*} -only) rules were invalid if there were costs to search. Luttbeg's (2002) contrary claims that it can nevertheless outperform threshold rules in particular situations (e.g. few males to inspect, fixed time, etc.) seem questionable: they rely on not allowing any recall in the threshold rule considered, or on comparing performances in environments to which neither rule's parameters are adapted. Our study has shown that if there is variation between years in male quality, best-of- N does outperform the simplest fixed-threshold rule, r_{c*} -only. It performs worse than r_{c*} -only otherwise, and in all our patchy environments it is also worse than the slightly more complex threshold rules that also allow return, r_{c0} -only and best-of-patch. However, with the combination of variation between years and no patchiness, best-of- N outperforms all the other rules of thumb.

Best-of-patch can be viewed as a best-of- N strategy in which $N = \text{patch size}$, so the superiority of best-of-patch demonstrates that it pays for decision rules to take account of patch structure. Also reflecting this, is that best-of- N uses a smaller value of N when mean patch size is smaller.

The cutoff rule (e.g. Seale and Rapoport, 1997) inspects N males, notes the quality of the best, and then searches until a better male than this is found. The rule has been much investigated because it is optimal if nothing is previously known or can be learnt about the distribution of quality in the environment, if no returns are possible, and if the aim is to maximize the chances of finding the highest quality male in a population of known size (e.g. Dombrovsky and Perrin, 1994). These are not the aims with which natural selection is likely to be concerned, but the rule has also been considered as a

means to achieve a high expected quality of partner when population size is uncertain (Dombrovsky and Perrin, 1994; Dudey and Todd, 2001; Todd and Miller, 1999). In our environments the rule does poorly compared even to the r_{c*} -only strategy, which also does not require the female to recall earlier males. Setting too high a threshold in our patchy environments is particularly costly because our fairly small patches mean that finding such a good male will likely require risky travelling between patches. The cutoff rule has only a crude method of avoiding a high threshold, which is to reduce the number of males in the initial sample. (It cannot for instance set the threshold at the second best rather than best of a sample of three.) Consequently in our patchy environments the acceptance criterion is based on a sample of no more than one male. This means that it may accept a low quality male if the first male happens to be low quality. In the environment with more variation between patches, the optimal value of N is 0, i.e. the first male encountered is chosen.

Because the cutoff rule has an optimal parameter value of $N = 1$ in most patchy environments, the rule turns out to be identical in effect to the candidate-count rule using its optimal parameter value of 2. "Candidate" is used in the special sense of a male that is better than all earlier males (Seale and Rapoport, 1997), with the first male inspected inevitably being the first candidate. With parameter value 2, search stops at the second candidate (half the time the second male inspected).

Another rule suggested in the literature (Wittenberger, 1983) is sequential comparison. Search continues until a male is worse than the preceding male, and then the preceding male is chosen (in our manifestation, unless the preceding male is in a different patch and discounting makes it better to take the current male instead). As a rule of thumb in the real world it has the attraction that memory need not be long, and there is little risk of the preceding male having disappeared by the time a female returns to him. In our environments it was always outperformed by best-of- N , but outperformed the cutoff rule in all but the non-patchy environment without between-year variation.

Almost the converse of this rule is what we call quality-up, which continues search until a male is better than the preceding male (even if neither is a candidate) and then chooses the male offering the highest expected reward (necessarily either the first inspected or the last). Quality-up performs very similarly to the sequential comparison rule, because the expected number of males until search stops must be the same for both rules (one waits for the first decrease the other for the first increase). They seem crude and unreliable ways of ensuring that a reasonable number of males are inspected, which explains their mediocre performance. Brown (1981) claimed that the behaviour of a freshwater fish was compatible with a modification of quality-up

rule in which the stopping rule is the same but then the last inspected is always chosen—by forgoing the option to take the first inspected if better than the last, this modification necessarily decreases performance. The decrease is enough to make performance worse in most environments than the other rules that avoid returns.

A similarly motivated rule, mean-up, stops when the current male exceeds the mean quality of all previously encountered males, and then chooses the male offering the highest discounted reward. It performs similarly to quality-up. However, a modification of not allowing returns results in a performance that is superior to several other no-return rules in patchy environments, although still well below the r_{c^*} -only no-return rule.

With the successive non-candidate count rule, non-candidates are males that are worse than the current best, and the count of non-candidates is reset once a new candidate is found. So with parameter value 2, two failures in succession to find a better male lead to stopping search. In our version of the rule (in contrast to the rule with this name in Seale and Rapoport, 1997; Dudey and Todd, 2001), we allow females then to return to the best male (if a subsequent change of patch has not lead to one of the non-candidates now being the better bet). In our environments the rule never does better than best-of- N .

This list of rules is inevitably not exhaustive; for instance, non-candidate count rules might be combined with the r_{c0} -only strategy, so that acceptance is possible without searching the whole patch (and responsive to what has been learnt about qualities within it), yet movement to new patches depends on a hardwired threshold. We have not investigated more such rules because there is so little room for improvement in performance over the very simple two-threshold and r_{c0} -only strategies. But note that in the non-patchy but variable environment both best-of- N and the non-candidate count rule are superior, so one important take-home lesson is that we might predict different types of decision rules in patchy than in non-patchy environments.

It is quite possible that the rank ordering of the various rules will change somewhat depending on other aspects of the environment, for instance search costs and perhaps variance in quality. A full sensitivity analysis is beyond the scope of this paper. Another limitation is that we consider that the environmental variation is only in mean quality, although the analysis of best-of-patch in Fig. 2 suggests that at least that rule copes well with other sorts of variation.

10. Discussion

The two-threshold rule and its simplification r_{c0} -only are the overall winners in this analysis, with another

simplification r_{c^*} -only winning the prize for the restriction of no returns. These threshold rules can be optimal in simple cases and they perform well in more complex and uncertain situations. They are also very simple, requiring natural selection to adjust only one or two parameters, and needing to judge only whether any males are left in the current patch, not the exact number. Gigerenzer et al. (1999) have made more general claims that simple rules of thumb can often perform surprisingly well in a wide variety of contexts. They have also associated this with criticisms of the optimality approach (e.g. Gigerenzer and Todd, 1999), so it is interesting that the most successful rule of thumb was derived from the optimal strategy in a simplified environment. We suspect that this approach, and the related one of simplifying the optimal strategy in the fully complex environment, may often prove more effective a method to choose good rules of thumb than more ad hoc approaches. On the other hand, one of the relative failures in our analysis, the cutoff rule, was also originally derived from an optimal rule in a simplified environment (albeit with a different optimization criterion).

The two-threshold rule is at least compatible with the most widespread pattern of mate choice reported, of the frequent occurrence of returns to males inspected earlier, but acceptance of the last inspected male occurring more often than expected by chance if the animal were using a best-of- N strategy (Wiegmann et al., 1996). It is difficult to use published data to judge more critically the extent to which animals use a two-threshold rule, because patchiness of the distribution of males has usually not been quantified. An exception is the study of Bertorelle et al. (1997) on a bottom-dwelling river fish where indeed the data did fit best the r_{c0} -only rule (which they called cluster sampling; our two-threshold rule was not considered). In many real environments the patch structure will not fit our simple assumptions, but then one may generalize the two-threshold rule to specify that acceptance thresholds should depend inversely on the perception of the travel costs, delays or risk required to find the next male. When the perception of these costs increases, the falling threshold may cause females to return to males earlier rejected. A human example that might roughly fit this pattern is the increased attractiveness of members of the opposite sex in dating bars as closing time approaches (Gladue and Delaney, 1990). Likewise female fiddler crabs are willing to accept smaller males nearer the time of the semi-lunar tidal cycle by which they must spawn (Backwell and Passmore, 1996).

If females do use something like the two-threshold rules that we predict, it should have consequences for how males distribute themselves around patches. In the baseline case, a male of quality $< r_{c0}$ has no chance of finding a female, so should try to delay breeding to

another year. A male of quality $>r_{c*}$ may succeed in winning a female even if other males in the same patch are better, with his chances dependent simply on how many other males in the patch also are of quality $>r_{c*}$; so he will tend to do better in a smaller patch. A male of intermediate quality ($r_{c0} < q < r_{c*}$) must be the best in his patch to mate, which again often favours him joining smaller patches. However, there may well be other processes opposing evolution towards smaller patches. We have assumed that females encounter patches at random, but in lekking species there is evidence that females should and do prefer larger leks where they can “comparison shop” to greater effect (Alexander, 1975; Hutchinson,). The extent to which this preference will predominate will depend on how often females have a choice of patches the sizes of which they can judge prior to a visit. Even in our model, in which females do not know patch size in advance, when there is between-year variation an isolated male of moderate quality can do better by joining a patch of lower quality males; these may convince a female that qualities are poor this year and that he is thus unusually good.

A game-theoretic analysis may thus become necessary even without the further complications of females removing the best males from the mating pool or of mutual mate choice (Collins and McNamara, 1993; Johnstone, 1997; McNamara and Collins, 1990). In the text we have also mentioned three other versions of a patch-based model that we avoided tackling because of the complexities entailed: no deliberate recall but random reencounter of males in the patch; a tendency to inspect higher quality males first; a combination of between-year and between-patch variation. We believe that all these situations occur frequently in nature and that therefore their analysis would be well worthwhile. However, optimization may prove too difficult (although finding optima constrained by limited memory might be possible), so the approach may have to be the more messy one of simulating rules of thumb.

We hope that the two-threshold rule will provide a simple example to blur an artificial dichotomy that we perceive to have persistently biased the literature on mate choice. We sense a tendency to try to shoehorn observed mating strategies into best-of- N or fixed threshold rule categories (Jennions and Petrie, 1997; Wiegmann et al., 1996), and the theoretical literature has often not helped by concentrating disproportionately on these two possibilities (e.g. Luttbeg, 2002; Wiegmann et al., 1999; Wiegmann and Mukhopadhyay, 1998). Returns have been taken as evidence for a best-of- N tactic, despite returns also being predicted by other threshold models. Although theoreticians have envisaged that with best-of- N the value of N is fixed in advance, empiricists have not worried that the data imply that N must vary widely between different females. The two-threshold rule has some characteristics

of both best-of- N and fixed threshold rules, and readily explains returns after a variable number of inspections. Equally misleading is to try to classify rules as either sample-based or threshold based (Valone et al., 1996). The two-threshold rule shows that acceptance criteria can depend both on qualities of males encountered and on a hardwired threshold. We think it most likely that real decision rules are of this kind, which will make them all the harder to uncover.

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Appendix A. SDP modelling and forward simulation

Stochastic dynamic programming is a numerical procedure to find an optimal decision rule for a sequence of actions. Decisions depend on the values of state variables, which in the baseline case are r (the maximum expected reward currently available from accepting an already inspected male), and n (the number of males left to inspect in the current patch). State variables must have a finite number of discrete options, but by making this number large we can approximate continuous variation. We allow male quality to take Q equidistant values from 0 to 1 inclusive, and, since quality is taken as the female’s reward from mating with a male, r is also analysed on this discrete scale. n varies from 0 to M , where M is a maximum patch size.

A.1. Baseline case

Consider a large but finite number of patches and that a female has inspected the last male in the last patch. The best male to select would give her expected fitness r (if that male is in the same patch his quality is r , otherwise r is his quality discounted by inter-patch return travel times—see below). With no further males left to inspect, the best option is clearly to accept that male, so the fitness associated with being in that state is r . We write this as,

$$F(\text{patches left} = 0, \text{males in patch left} = 0, \text{highest value of male} = r) = r,$$

i.e.

$$F(0, 0, r) = r.$$

Then consider one step earlier with one last male left to find and inspect, and with the female having just

inspected another male in the same patch. Should the remaining male be inspected or should the female accept the best option amongst males already inspected? Which is better depends on the value of the state variable r . The expected reward from accepting an already inspected male is r . The expected reward from continuing the search is the weighted average of all possible fitnesses one step later, which requires averaging over all possible qualities q_j of the next male.

$$F_{continue}(0, 1, r) = \exp(-wt_f) \sum_{j=0}^Q P(q_j) F(0, 0, \max[r, q_j]).$$

$P(q_j)$ is the probability that the next male has quality q_j . The $\exp(-wt_f)$ term is the discount due to the risk $1 - \exp(-wt_f)$ that the mating opportunity ceases before the next male can be inspected (e.g. because of predation), which would result in a fitness of 0. The optimal strategy chooses the higher of r and $F_{continue}(0, 1, r)$, so

$$F(0, 1, r) = \max \left[r, \exp(-wt_f) \sum_{j=0}^Q P(q_j) F(0, 0, \max[r, q_j]) \right]$$

and we simultaneously have now learnt the appropriate behaviour when in the state $(0, 1, r)$.

This process can be continued backwards within the last patch, and indeed within any patch x from last: for $n > 0$,

$$F(x, n, r) = \max \left[r, \exp(-wt_f) \sum_{j=0}^Q P(q_j) F(x, n - 1, \max[r, q_j]) \right].$$

When first entering a patch it makes sense always to inspect the first male, but the value of r inherited from the preceding patches must be discounted because of the risk associated with the return journey. So if a female has seen a male of quality r in an earlier patch, her expected fitness on joining a patch (x from the last) of N males is

$$G_N(x, r) = F_{continue}(x, N, \exp(-wt_R)r) \exp(-wt_f) \times \sum_{j=0}^Q P(q_j) F(x, N - 1, \max[\exp(-wt_R)r, q_j]).$$

A complication arises here because the value of $\exp(-wt_R)r$ will in general not fall on the discrete grid values of r for which $F(x, N - 1, r)$ has been calculated by backwards iteration; the solution is to interpolate linearly from the adjacent grid values. But in the baseline case, it should never pay to return if many patches are left (see main text), so one shortcut is to replace $\exp(-wt_R)r$ with 0. We now calculate the expected fitness on leaving the preceding patch, which is the weighted average of $G_N(x, r)$ over all patch sizes N , discounted by the expected risk of travelling forward to

the next patch:

$$F_{continue}(x + 1, 0, r) = \exp(-wt_p) \sum_{N=1}^M (\text{prob. patch size} = N) G_N(x, r).$$

And, $F(x + 1, 0, r) = \max[r, F_{continue}(x + 1, 0, r)]$.

The backwards iteration can now continue back between patches and then further back through earlier patches. It continues until there are enough patches left that $F(x + 1, n, r)$ converges closely to $F(x, n, r)$ for all n, r .

A.2. Time to encounter increasing

If the time to encounter an uninspected male depends on the number of uninspected males left on the patch, the main equation is modified slightly, firstly by making t_f a function of n , and secondly by providing the extra option to move to the next patch when $n > 0$. The expected reward from such a move is the same as when $n = 0$ when the move is obligatory (i.e. $F(x, 0, r)$). Thus for $n > 0$,

$$F(x, n, r) = \max \left[F(x, 0, r), r, \exp(-wt_f(n)) \times \sum_{j=0}^Q P(q_j) F(x, n - 1, \max[r, q_j]) \right].$$

A.3. Within-patch return costs

Other modifications are necessary to incorporate return costs within a patch. When time to move back to earlier males mounts up additively the more males that have been visited in-between, for $n > 0$,

$$F(x, n, r) = \max \left[r, \exp(-wt_f) \times \sum_{j=0}^Q P(q_j) F(x, n - 1, \max[\exp(-wt_r)r, q_j]) \right].$$

The $\exp(-wt_r)r$ term requires the values of $F(x, n - 1, r)$ to be interpolated from adjacent grid values of r . Now r is the larger of the present male's quality and the discounted reward for returning to earlier males:

$$r(n) = \max[\exp(-wt_r)r(n + 1), q(n)].$$

When return costs are one-off, the female must remember the value of the best male undiscounted by within-patch return costs (but maybe discounted by inter-patch return costs):

$$s(n) = \max[s(n + 1), q(n)].$$

The expected reward from accepting a male is $\max[q(n), \exp(-wt_r)s(n+1)]$, which equals $\max[q(n), \exp(-wt_r)s(n)]$. So F now depends on the current value only of $s(n)$, which we write as s :

$$F(x, n, s, q) = \max \left[q, \exp(-wt_r)s, \exp(-wt_f) \times \sum_{j=0}^Q P(q_j) F(x, n-1, \max[s, q_j], q_j) \right].$$

A.4. Variation in population mean quality

More complex modifications are necessary to deal with the situations where there is systematic variation between patches or years in the distribution of male quality. We allowed variation only in the population mean of the distribution (μ); the distribution of this mean was normal ($N(\mu_0, \sigma_0^2)$), and the quality distributions about μ were also normal (s.d. = σ). These assumptions make the problem particularly tractable, because, given an observed mean m based on l observations, the expected distribution of a subsequent observation is also normal (Cox and Hinkley, 1974, p. 391), with mean

$$(ml\sigma_0^2 + \mu_0\sigma^2)/(l\sigma_0^2 + \sigma^2)$$

and variance

$$\sigma^2(1 + \sigma_0^2/(l\sigma_0^2 + \sigma^2)).$$

The number of state variables must now be increased to include m and l .

We deal with between-year variation first. In this case m and l are over all observed males in whatever patch they occurred. For $n > 0$,

$$F(x, n, r, m, l) = \max \left[r, \exp(-wt_f) \sum_{j=0}^Q P(m, l, q_j) F(x, n-1, \max[r, q_j], (ml + q_j)/(l+1), l+1) \right].$$

Here $P(m, l, q_j)$ is the probability of observing a quality of q_j given the posterior distribution implied by m and l in the formulae above. The term $(ml + q_j)/(l+1)$ is simply the updated observed mean. Since in any year all males are drawn from the same population, swapping patches need be considered only when no males are left to inspect in the current patch. For backwards iteration between patches, the formulae for G_N and $F(x, 0, r, m, l)$ are straightforward analogues of the baseline case:

$$G_N(x, r, m, l) = \exp(-wt_f) \sum_{j=0}^Q P(m, l, q_j) F(x, N-1, \max[\exp(-wt_R)r, q_j], (ml + q_j)/(l+1), l+1),$$

$$F(x+1, 0, r, m, l) = \max \left[r, \exp(-wt_f) \sum_{N=1}^M (\text{prob. patch size} = N) G_N(x, r, m, l) \right].$$

The dynamic programming now starts with l , the number of males observed, set to a large number (e.g. 70) and $F(0, n, r, m, l)$ set to r . For each combination of values of r and m , for $n > 0$, we calculate $F(0, n, r, m, l-1)$. We can also calculate $G_N(0, r, m, l-1)$ for all N , and from these calculate $F(1, 0, r, m, l-1)$. We now calculate $F(0, n, r, m, l-2)$ for $n > 1$, and $F(1, 1, r, m, l-2)$. Similarly we can calculate $G_N(0, r, m, l-2)$ for $N > 1$, and $G_1(1, r, m, l-2)$. Because these have different values of x , it is not strictly correct to combine them in calculating $F(1, 0, r, m, l-2)$. But we are concerned with the situation of many patches left when fitness is independent of their number, and, since we will be iterating back through a large number of males, we do not worry about the value of x , considering an arbitrary large value of $x = X$. Further iteration leads eventually to calculation of $F(X, n, r, m, 1)$. During this procedure we have also found the optimal strategy, which is dependent on n, r, m and l .

When the variation in population means is between patches instead of between years, it is the observed mean qualities on the current patch only that matter. Correspondingly, l is now the number of males already inspected on the current patch, so $n = N - l$. Our program calculates a strategy dependent on N and l (besides m and r), but this is thus straightforward to convert to a strategy dependent on N and n (as presented in the main text and Fig. 6).

One difference from the case of between-year variation is that it can make sense to leave a patch before having examined all its males. So for $l < N$,

$$F(x, N, r, m, l) = \max \left[r, \exp(-wt_f) \sum_{N=1}^M (\text{prob. patch size} = N) G_N(x-1, r, F(x, N, \max[r, q_j], (ml + q_j)/(l+1), l+1)) \right]$$

and for $l = N$ the calculation is the same but without the third option of continuing in the patch. The fitness on entering a patch of N males is

$$G_N(x, r) = \exp(-wt_f) \sum_{j=0}^Q P(\mu_0, 0, q_j) F(x, N, \max[\exp(-wt_R)r, q_j], q_j, 1).$$

(Since it never makes sense to return to a patch, these formulae could be simplified by setting $G_N(x, r) = G_N(x, 0)$.)

The dynamic programming starts by setting $G_N(0, r) = r$ for all r and M . From these values, we can calculate for all values of r and m the fitness at the end of a preceding patch of size N , $F(1, N, r, m, M)$. We continue the backwards iteration within the patch until $l = 1$ and we have obtained $F(1, N, r, m, 1)$, which allows calculation of $G_N(1, r)$. This is calculated similarly for each patch size (N) in turn, after which we can repeat the whole procedure with $x = 2$. This backwards iteration through patches since the last is continued until the fitness values have converged from one value of x to the next.

A.5. Forward simulation

The simulation forward in time is a more straightforward procedure. For each female we first use a pseudo-random number generator (`ran1()` from Press et al., 1992) to calculate the time when she will be interrupted. As we work forward, any step to the next male takes time which is subtracted from this lifetime, and if the remaining lifetime falls below 0, the female is considered not to have mated before interruption. Qualities of each male encountered (and with variable environments values of μ) are also determined by random numbers, using `gasdev()` from Press et al. (1992), and calling the routine again if an individual quality falls outside the range of 0 to 1. Values of q are rounded to the nearest grid value since the optimal strategy has been calculated only for values of q , r and m that fall on the grid of $Q + 1$ values. When discounting or averaging takes values of r and m off the grid, they are converted to either of the two adjacent grid values with probabilities inversely proportional to their relative distances away.

Appendix B. Why r_{c*} is constant

Here we examine the case where there are no within-patch return costs and show analytically that the optimal acceptance threshold is constant except that it is lower at the last male in a patch.

Let $f(r) = \exp(-wt_f) \int_0^1 P(q) \max[r, q] dq$. This function describes the expected reward if a female continues to the next male and then mates (making the best choice from the males encountered). $P(q)$ is the probability density function for the next male to have quality q , and r is the expected reward if she stops search now. The expected reward from continuing must be a non-decreasing continuous function of r , since it cannot be a disadvantage to have encountered a better male earlier. Since q is distributed only between 0 and 1, $f(0) = \exp(-wt_f) \int_0^1 P(q) q dq > 0$, and $f(1) = \exp(-wt_f) < 1$. So there is a root r_* of the equation $f(r) = r$. If $P(q)$ is non-zero around r_* , then $f(r)$ is a locally increasing function there, and this root is unique

(we consider only this simplest case, but the arguments below are easy to amend if the distribution of q is discontinuous over a range around r_* , in which case all values over this range are roots). Thus $r \geq r_* \Leftrightarrow f(r) \leq r$, and $r \leq r_* \Leftrightarrow f(r) \geq r$.

A female has just inspected the $n + 1$ th last male in a patch, and if she stops search now her expected reward is r ; her expected reward without this restriction is the maximum of this and the expected reward if she continues: i.e.

$$F(n + 1, r) = \max \left[r, \exp(-wt_f) \int_0^1 P(q) F(n, \max[r, q]) dq \right].$$

Suppose for some n and r that $F(n, r) = r$. Then

$$\begin{aligned} F(n + 1, r) &= \max \left[r, \exp(-wt_f) \int_0^1 P(q) \max[r, q] dq \right] \\ &= \max[r, f(r)]. \end{aligned}$$

The female will choose the mate-now option (r) over the continue option ($f(r)$), iff $r \geq f(r)$, which is the case iff $r \geq r_*$. So $r_* = r_{cn+1}$, the acceptance threshold with $n + 1$ males left. Also, if $F(n, r_*) = r_*$, then $F(n + 1, r_*) = r_*$. Thus by induction, $F(n, r_*) = r_* \Rightarrow r_{cj} = r_*$ for all $j > n$.

Consider a last patch ($x = 0$). At the last male in this last patch, a female should mate because she cannot continue, so $r_{c0} = 0$ and $F(x = 0, n = 0, r_*) = r_*$. Hence, from the result above, $r_{cn} = r_*$ for all $n > 0$.

Consider now a female that has inspected the last male of the penultimate patch ($x = 1$). Suppose for the moment no costs of return to an earlier patch. If $r \geq r_*$, then if the female does continue to the last patch the values of r_{cn} derived above imply that she will certainly inspect no more than the first male, regardless of patch size. So

$$\begin{aligned} F(x = 1, n = 0, r_*) \\ = \max \left[r_*, \exp(-wt_p) \exp(-wt_f) \int_0^1 P(q) \max[r_*, q] dq \right]. \end{aligned}$$

The expected reward for continuing to another patch is now $\exp(-wt_p) f(r_*) = \exp(-wt_p) r_* < r_*$ (if between-patch travel time $t_p > 0$). Introducing costs of return to an earlier patch can only make this expected reward smaller, so it will still be $< r_*$. Thus for $r = r_*$ the expected reward is higher to stop search now, which implies $r_{c0} < r_*$ and that $F(x = 1, n = 0, r_*) = r_*$. As above, this implies that in the penultimate patch $r_{cn} = r_*$ for all $n > 0$. By induction this must be true for all patches. So $r_{c*} = r_*$, and $r_{c0} < r_{c*}$.

Appendix C. Why the decision to move patch or continue in the same patch is independent of r

This applies to the case where the expected time to encounter an uninspected male in the current patch

increases as the number of such males decreases (Section 7). For simplicity our algebra assumes no within-patch return costs, but they would not disrupt the argument. Consider a female having just inspected the $n + 1$ th last male, where $n > 0$. The female now has three options:

- (i) accept a male immediately, which brings reward r , the quality of the best male so far encountered in the patch;
- (ii) move to a new patch, with expected reward $H(r)$;
- (iii) continue in the present patch, with expected reward $F_{\text{continue}}(n, r)$.

If it makes sense to leave the best male on offer for an unknown patch now, it will make sense were the female ever to return to the patch (assuming an infinite number of patches), so returns to males in earlier patches should not occur. Thus if moving patch is the best option, the expected reward is independent of r ; call this reward H' .

So, $F_{\text{continue}}(1, r) = \exp(-wt_f) \int_0^1 P(q) \max[r, q, H'] dq$, and thus when $r \leq H'$ $F_{\text{continue}}(1, r) = F_{\text{continue}}(1, H')$. Similarly, for $n > 1$, $F_{\text{continue}}(n, r) = \exp(-wt_f) \int_0^1 P(q) \max[r, q, H', F_{\text{continue}}(n-1, \max[r, q])] dq$, and thus when $r \leq H'$ (by induction from the case $n = 1$) $F_{\text{continue}}(n, r) = F_{\text{continue}}(n, H')$.

For each value of n , $F_{\text{continue}}(n, r)$ must be a non-decreasing function of r (it cannot harm to have seen a higher quality male). Although we do not prove this rigorously, it clearly makes sense that for each n there is a single root \hat{r} where $r = F_{\text{continue}}(n, r)$; when $r > \hat{r}$ it is better to accept a male than to continue searching in the patch, and when $r < \hat{r}$ the converse.

Now, suppose for a value of n , that $F_{\text{continue}}(n, H') > H'$. Then for all $r < H'$, $F_{\text{continue}}(n, r) = F_{\text{continue}}(n, H') > H'$. Since $F_{\text{continue}}(n, r)$ is a non-decreasing function of r , it is also $> H'$ for all $r > H'$. Hence for this value of n , moving patch is never optimal.

Suppose for another value of n , that $F_{\text{continue}}(n, H') < H'$. Then for all $r < H'$, $F_{\text{continue}}(n, r) = F_{\text{continue}}(n, H') < H'$. $F_{\text{continue}}(n-1, H') < H'$ also implies that $H' > \hat{r}$, so for all $r > H'$, $r > F_{\text{continue}}(n, r)$. Hence for this value of n , continuing in the same patch is never optimal.

So whether a female not accepting a male continues in the patch or moves patch should never depend on the quality of males so far inspected, but may depend on the number of males left to inspect.

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