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Assessing the robustness and optimality of alternative decision rules with varying assumptions

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Several alternative decision rules have been proposed for how individuals assess and choose options, such as mates and territories. Three of these rules are the threshold rule, where individuals choose the first option that exceeds a preset level of quality, the best-of-*n* rule, where individuals assess a fixed number of options and then choose the best of those options, and the comparative Bayes rule, where individuals use estimates of options to selectively assess and choose options. It has been previously concluded that the threshold rule produces higher average fitness than the best-of-*n* rule when assessment costs are not trivial. However, previous comparisons assumed that time and options are infinite, individuals can estimate the distribution of option quality without uncertainty or mistakes, and individuals receive perfect information about the quality of assessed options. I found that the best-of-*n* rule produces higher average fitness than the threshold rule despite significant assessment costs, when time for choosing an option is limited, when individuals are choosing from a small pool of options, when estimates of the distribution of option quality are error-prone, and when there is uncertainty about the distribution of option quality. I also found that the comparative Bayes rule produces higher average fitness than the threshold and best-of-n rules when time or options are limited and when individuals receive imperfect information about the quality of assessed options. Therefore, the optimality of alternative decision rules depends on more than the size of assessment costs and the previous conclusions of empirical studies that have assumed such need to be re-examined.

Individuals often choose options from a set of candidates. Foraging individuals choose food items; dispersing individuals choose destinations; and mating individuals choose mates. Presumably, the fitness of these individuals depends on the quality of the options they choose. However, uncertainty about encountered and yet-to-be-encountered options and time and energy costs and constraints impede how accurately individuals can choose options and creates the need for decision rules that balance the costs of assessment and the benefits of good choices. The rules individuals use to make these choices can critically affect the dynamics of systems, such as mating systems (Gibson & Langen 1996) and predator–prey systems (Luttbeg & Schmitz 2000).

Various rules for assessment and decision making have been proposed. The rules vary in their assumptions about whether previously encountered options, such as mates or territories, can be remembered and returned to, whether encounters with options are random or controlled by the choosing individual, and whether encounters provide perfect or imperfect information about the quality of an option (Janetos 1980; Real 1990; Getty 1996; Luttbeg 1996; Mazalov et al. 1996). Three of the proposed decision-making rules are the best-of-*n* rule, the threshold rule and the comparative Bayes rule. For the best-of-*n* rule, individuals assess a fixed number of options (*n*) and then choose the option with the highest assessed quality (Janetos 1980). For the threshold rule, individuals set a threshold and choose the first option that has an assessed quality that exceeds the threshold (Real 1990). The threshold can either be fixed or adjustable to time or experience. For the comparative Bayes rule, individuals estimate the quality of each available option, use encounters with options to update these estimates, and then choose the option with the highest assessed quality when the cost of more information exceeds the expected benefit of that information (Luttbeg 1996).

One approach taken to try to determine the likelihood of various proposed decision-making rules has been to compare their relative performances. Janetos (1980) compared the performances of best-of-*n* and fixed threshold

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rules, and concluded that best-of-*n* rules achieve higher average fitness than fixed threshold rules. Janetos, however, assumed that there were no costs to assessing options. Real (1990) re-examined the comparison of best-of-*n* and threshold rules with assessment costs, and concluded that when assessment costs are not trivial, threshold rules achieve higher average fitness than best-of-*n* rules. Luttbeg (1996) compared comparative Bayes, best-of-*n* and threshold rules and concluded that comparative Bayes rules achieve higher fitness than the other two rules, particularly when assessment costs are small, but these comparisons were made only with small pools of options.

These conclusions have impacted how the decision-making process has been investigated, particularly for mate choice. For example, since it is generally assumed that mate assessment has relatively high costs, it has been suggested that individuals should more often use behaviours that match a threshold rule rather than a best-of-*n* rule when choosing a mate (Valone et al. 1996). Behavioural observations, however, have often suggested that females use a best-of-*n* or related rule (Valone et al. 1996; Jennions & Petrie 1997). This discrepancy has lead to the search for alternative explanations for why females might use best-of-*n* rules (Dale & Slagsvold 1996; Valone et al. 1996).

In addition, the conclusions have also suggested a tight link between assessment costs and the occurrence of decision rules, with best-of-*n* rules being used when assessment costs are very small and threshold rules being used when assessment costs are larger. This has led to the belief that mate choice rules can be inferred from or supported by the size of assessment costs (Dale et al. 1992; Gibson 1996; Reid & Stamps 1997). And, conversely, it has been believed that the size of assessment costs can be inferred from the mate choice rule apparently used by females (Rintamaki et al. 1995; Forsgren 1997).

In this paper, I test the robustness of the conclusion that optimal threshold rules achieve higher average fitness than optimal best-of-*n* rules when assessment costs are not small, and thus test how tight the link is between assessment costs and the occurrence of alternative decision rules. In my comparisons, I include the performance of the comparative Bayes rule, because there is some evidence that the comparative Bayes rule outperforms best-of-*n* and threshold rules when assessment costs are small (Luttbeg 1996). I compare the performances of the rules while varying the assumptions that went into Real's (1990) comparison, such as infinite time to make choices, infinite options from which to choose, individuals know the distribution of option quality, and individuals receive perfect information about encountered options. I show that the performances of alternative decision rules are very dependent on these assumptions and that there is a wide range of situations, other than very low assessment costs, that favour best-of-*n* rules over threshold rules.

METHODS

Under varying assumptions, I compare the average fitness of individuals choosing options using best-of-*n* (Janetos 1980), threshold (Real 1990) and comparative Bayes (Luttbeg 1996) rules. In each case, I assume that the distribution of the quality of options is normal ($\bar{\mu}$, ρ^2) and that the fitness of individuals matches the quality of the option they choose, μ, minus incurred assessment costs. An assessment cost, c, is paid each time an option is assessed. Before comparing the performances of rules, I find the optimal version of each rule, such as the optimal threshold for the threshold rule and the optimal *n* for the best-of-*n* rule.

I use Real's (1990) comparison of best-of-*n* and threshold rules as a starting point. In this comparison, it was assumed that individuals have infinite time to choose an option, infinite options from which to choose, know the underlying distribution of the quality of options, and receive perfect information when they assess an option. I start my comparison of the three decision rules using these assumptions and then vary each of the assumptions to see how they affect the relative performances of the three rules. In some cases analytical solutions for the performances of these rules are not possible, such as the threshold rule with finite options and the comparative Bayes rule in all cases. Thus, I use simulations to measure the fitness outcomes of the rules.

Best-of-*n* Rule

The best-of-*n* rule (sometimes referred to as a pool comparison rule) states that an individual should assess a fixed number (*n*) of options and then return to and choose the option with the highest assessed quality (Janetos 1980). The optimal level of *n* depends on assessment costs and the variance in the distribution of option quality, but is independent of the mean of the distribution of option quality. Following the common formulation of the best-of-*n* rule (Janetos 1980; Real 1990), I assume that options are randomly encountered, and individuals behave as if they know the distribution of option quality and receive perfect information about the quality of options. I find the optimal level of *n* by conducting 3000 replicates of an individual choosing an option from an infinite pool of options using a range of *n*s. I use the level of *n* producing the highest average fitness in subsequent comparisons of the three rules.

Threshold Rule

The threshold rule states that an individual should set a quality threshold and choose the first option that appears to have a quality that exceeds the threshold. The optimal threshold depends on the mean and variance of the distribution of option quality, assessment costs and time constraints. Again, like the best-of-*n* rule, I follow the common formulation of the rule (Real 1990) and assume that options are encountered randomly and individuals gain perfect information about the quality of encountered options. I also assume that individuals know the distribution of option quality, so that the mean of the estimated distribution of option quality, $\hat{\mu}$, equals the mean of the actual distribution of option quality, $\bar{\mu}$, and the variances are equal.

I use a dynamic state variable model (Clark & Mangel 2000) to find optimal thresholds. In some cases, I assume that finite time is available for selecting an option (see Real 1990 for this variation of the model), and if an individual reaches the final time period, T, without choosing an option, they randomly select an option, as in Real (1990). The chooser's expected fitness from a randomly selected option at time T is

$$F(T)=E(\mu)=\hat{\mu}. \tag{1}$$

For the time period prior to the terminal time, $T-1$, the individual sets a threshold (w), pays an assessment cost, randomly encounters an option with quality μ, and chooses the option if it exceeds the threshold. The optimal threshold, w, for time step $T-1$ maximizes,

$$F(w_{T-1},T-1)=\max_{w}\sum_{0}^{\mu<w}p(\mu)(F(T)-c)+\sum_{\mu>w}^{\infty}p(\mu)\mu \tag{2}$$

which I solve for w=0 to 12 at steps of 0.1 and for the cumulative distribution of μ at steps of 0.001, with $p(\mu)$ being the probability density function of μ. If the quality of the encountered option is below the threshold (the first half of the right side of equation 2), then the individual rejects the assessed option, receives the fitness associated with randomly choosing an option in time step T, and pays an assessment cost, c. If the quality of the encountered option is above the threshold (the second half of the right side of equation 2), then the individual chooses that option and receives the associated fitness, μ. The assessment cost, c, does not appear in the second half, because that cost is paid regardless of the level of the threshold.

I use the same procedure to find optimal thresholds for earlier time steps, but if an individual rejects an encountered option, the individual then assesses another option in the next time step. Thus, optimal thresholds for earlier time steps maximize,

$$F(w_t,t)=\max_{w}\sum_{0}^{\mu<w}p(\mu)(w_{t+1},t+1)-c)+\sum_{\mu>w}^{\infty}p(\mu)\mu. \tag{3}$$

When comparing the performances of the three decision rules with infinite time, I used the optimal threshold for the first time step of 1000 available time steps. At time step one of 1000 steps, thresholds are very weakly affected by time constraints and thus accurately represent the optimal threshold with infinite time.

Comparative Bayes Rule

The comparative Bayes rule states that individuals should assess the option that maximizes their expected future fitness, and if the cost of assessment exceeds the expected fitness benefit of assessment, an individual should choose the option with the highest associated expected fitness (Luttbeg 1996). I assume that individuals have prior estimates of the quality of each available option and these prior estimates are normal distributions ($\hat{\mu}$,ρ^2) that initially match the estimated distribution of option quality.

If individuals assess an option and the information they receive is perfect, they receive a signal, x, that equals the option's quality. If information is imperfect, the signal they receive is drawn from a normal distribution centred at the option's quality and with a signal variance, σ^2. The signal variance increases as information becomes more imperfect. Thus, if individuals base their estimate of an option's quality on their prior estimates of that option's quality ($\hat{\mu}$,ρ^2), then the signal, x, they would expect to receive from that option would be

$$Pr(X=x|\hat{\mu},\rho^2)=\frac{1}{\rho\sigma 2\pi}\int_{-\infty}^{\infty}\exp\left[\frac{-(x-\mu)^2}{2\sigma^2}-\frac{(\mu-\hat{\mu})^2}{2\rho^2}\right]d\mu \tag{4}$$

with μ being the actual quality of the option. When individuals assess an option, they receive information about the quality of that option, and that information is combined, using Bayesian updating, with the prior estimate of the option to form a new posterior estimate of the option. The new mean, $\hat{\mu}$, and variance, ρ^2, of the posterior estimate are

$$\hat{\mu}_{\text{new}}=\frac{x\tau+\hat{\mu}_{\text{old}}R}{\tau+R} \tag{5}$$

$$\rho^2_{\text{new}}=\frac{1}{\tau+R} \tag{6}$$

$$\text{with } \tau=\frac{1}{\sigma^2} \text{ and } R=\frac{1}{\rho^2_{\text{old}}}$$

(Luttbeg 1996). When individuals choose an option without any further assessment, their expected fitness (E) is

$$E\{\text{fitness (choose option)}\}=\hat{\mu} \tag{7}$$

and the expected fitness of choosing the option that is estimated to be the best is

$$\psi=\max\,(E\{\text{fitness (choose option)}\}). \tag{8}$$

To quantify the expected fitness of assessing an option, I assume that individuals myopically base their decisions to assess or choose options only on how those decisions will affect their behaviour in the next time step. This is a necessary assumption because the combinations of potential pieces of information received over future time periods are too numerous to set end conditions. This prevents the use of backward iteration over many time periods. So, if individuals assess an option, receive a signal (x), and update their estimate of the quality of that option (equations 5 and 6), the expected fitness of choosing that option in the next time step is

$$E\{\text{fitness (choose option)}|x\}=\hat{\mu}_{\text{new}}. \tag{9}$$

However, when individuals assess an option, they can choose a different option in the next time step based on the signal received and how it changed their estimate of the option. An individual's expected fitness after assessing an option is

$$E\{\text{fitness (assess option)}\} = \sum_{x=-\infty}^{\infty} p(x)\max(\hat{\mu}_{new}, \psi) - c \quad (10)$$

with $p(x)$ being equation (4). I calculate the expected fitness after assessing each of the available options. If an individual assesses the option associated with the highest expected fitness prior to assessment (ψ), then ψ is replaced with the expected fitness of choosing the next best option.

When the maximum expected fitness of choosing an option (equation 8) is greater than the maximum expected fitness of assessing an option (equation 10), an individual chooses the option associated with equation (8). If the maximum expected fitness of assessing an option (equation 10) is greater than the maximum expected fitness of choosing an option (equation 8), then the individual assesses the option associated with the maximum of equation (10). I assume that if time expires, an individual chooses the option with the maximum expected fitness of choosing (equation 8).

Uncertainty about the mean population quality

The only manipulation that changes the equations used to find optimal behavioural rules is my manipulation of the mean option quality. To test the effects of uncertainty about the distribution of option quality on the performances of the three decision rules, I alter the scenario so that the mean option quality, $\bar{\mu}$, can take three values (3, 5 or 7) with the probabilities

$$Pr(\bar{\mu}=3)=\frac{\gamma}{2}$$

$$Pr(\bar{\mu}=5)=1-\gamma$$

$$Pr(\bar{\mu}=7)=\frac{\gamma}{2}.$$

The mean option quality is unknown to individuals, but does not change as they choose an option. As γ increases, there is greater uncertainty about the distribution of option quality, but the expected value of the mean option quality is unchanged.

The optimal n for the best-of-n rule is unaffected by a shifting mean, because the qualities of options are compared only to each other, rather than to a population estimate. For the comparative Bayes rule, the variances in the prior estimates could increase with the increasing uncertainty, but I chose to leave them unaffected.

The formulation of optimal thresholds, however, is affected. Thresholds are determined in the same manner as equations 2 and 3, but equation 3 is altered to reflect that the probability that μ exceeds the threshold and the value of μ when it exceeds the threshold are altered by the shifting μ,

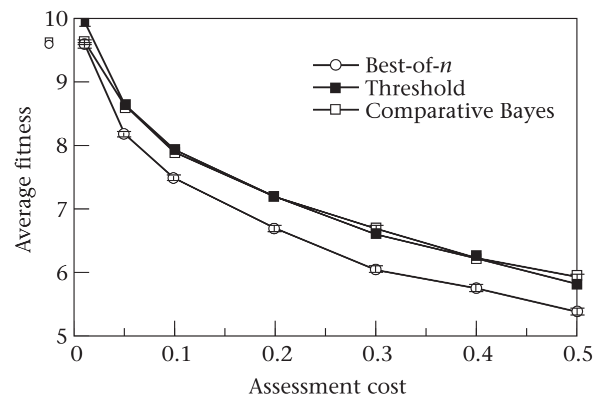

Figure 1. Average fitness outcomes of the best-of-*n*, threshold and comparative Bayes decision rules (±SD) versus assessment costs, with infinite time and infinite options (*N*=1000 for each rule). For the comparative Bayes rule, the time limit and number of options are 70.

$$F(w_t, t) = \max_{w} \left[\frac{\gamma}{2}\left(\sum_{0}^{\mu<w} p_3(\mu)(F(w_{t+1}, t+1)-c) + \sum_{\mu>w}^{\infty} p_3(\mu)\mu \right) + (1-\gamma)\left(\sum_{0}^{\mu<w} p_5(\mu)(F(w_{t+1}, t+1)-c) + \sum_{\mu>w}^{\infty} p_5(\mu)\mu \right) + \frac{\gamma}{2}\left(\sum_{0}^{\mu<w} p_7(\mu)(F(w_{t+1}, t+1)-c) + \sum_{\mu>w}^{\infty} p_7(\mu)\mu \right) \right] \quad (11)$$

with p_3, p_5 and p_7 referring to equation (4) with means of 3, 5 and 7, respectively.

RESULTS

Assessment Costs

I first compare the performances of the three decision rules using the same assumptions as Real's (1990) comparison, that is, infinite time, infinite options, individuals know the distribution of option quality, and individuals receive perfect information. I vary assessment costs to measure their effect on the relative performances of the three rules. I assume that individuals know the cost of assessment as it varies, and thus they use rules, such as thresholds, that match the cost. I find that the threshold rule outperforms the best-of-n rule when there are assessment costs, even as low as 0.01 (Fig. 1), which is very small compared with the expected fitness of a randomly selected option, which is 5. This matches Real's (1990) conclusion. I find that the comparative Bayes rule does as well as the threshold rule for all assessment costs, except for very small assessment costs where it only does as well as the best-of-n rule (Fig. 1).

Finite Time

The assumption that individuals have infinite time to choose an option seems inconsistent with many situations. For example, mate choice decisions are often

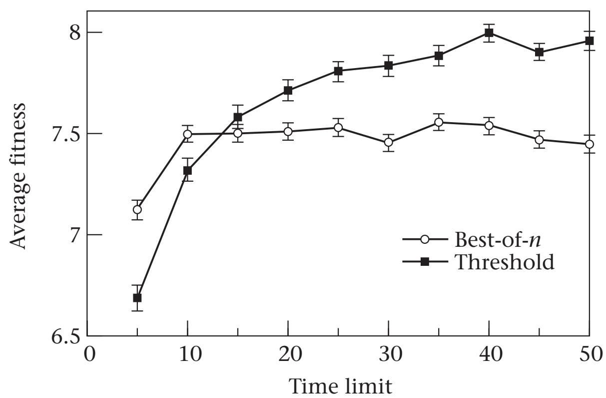

Figure 2. Average fitness outcomes of the best-of-*n* and threshold decision rules (±SD) versus time limits, with infinite options and an assessment cost of 0.1 (*N*=1000 for each rule).

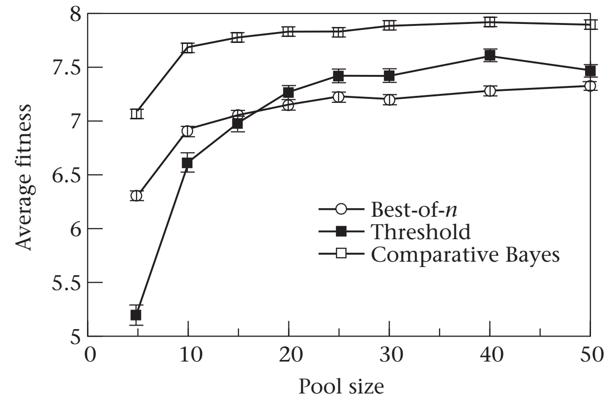

Figure 3. Average fitness of the best-of-*n*, threshold and comparative Bayes decision rules (±SD) versus pool sizes, with a time limit of 30 periods and an assessment cost of 0.1 (*N*=1000 for each rule).

constrained by the length of breeding seasons and physiological limitations to how long females can delay mating (see Sullivan 1994; Backwell & Passmore 1996). I vary the amount of time individuals have for making a choice to measure how time constraints affect the relative performances of the best-of-*n* and threshold rules. I do not include the comparative Bayes rule in this comparison because individuals using this rule never resample an option when they receive perfect information. Therefore, the smaller of either the pool size or the time limit determines how many samples can occur, and thus the two variables cannot be manipulated independently. I assume that individuals know how much time is available and adjust their rules accordingly. Individuals using the threshold rule randomly choose a mate if time expires. Individuals using the best-of-*n* rule always set *n* to be less than or equal to the time constraint and thus never run out of time.

Because I am interested in whether finite time can lead to the best-of-*n* rule outperforming the threshold rule, I want the threshold rule to outperform the best-of-*n* rule prior to the addition of finite time. Thus, I set the assessment cost to 0.1, a level at which the threshold rule outperformed the best-of-*n* rule (Fig. 1). The best-of-*n* rule has higher average fitness than the threshold rule when there are 14 or fewer time steps in which to choose an option (Fig. 2). Although limited time for choosing a mate has been interpreted as a form of higher assessment costs (Gotthard et al. 1999), these results show that limited time favours the best-of-*n* rule, while high assessment costs favour the threshold rule. Therefore, limited time for choosing a mate should not be interpreted as simply a form of higher assessment costs.

Finite Pool of Options

Obviously, individuals never have an infinite number of options from which to choose, and in many cases the number of options is quite small. For example, females have been observed to choose mates from small pools of available mates (10 peacocks, *Pavo cristatus*, Petrie et al. 1991; 13 and 14 male great reed warblers, *Acrocephalus arundinaceus*, Bensch & Hasselquist 1992; 12 male pied flycatchers, *Ficedula hypoleuca*, Dale et al. 1992). In addition, the pool sizes are likely to vary over time. I vary the number of options available to individuals to measure how pool size affects the relative performances of the three decision rules. I assume individuals using the best-of-*n* and threshold rules do not know the size of the pool, and their rules are based on infinite pools.

I construct pools of available options by randomly drawing the quality of each option from a normal distribution. When an option is assessed, it is either chosen or placed back into the pool of options. The best-of-*n* (Janetos 1980) and threshold (Real 1990) rules assume that options are randomly encountered, and thus previously assessed options can be randomly re-encountered. The comparative Bayes rule allows re-encounters, but they have no fitness benefit when information is perfect and thus do not occur. Many mate choice studies have observed that females often re-encounter males (Gibson & Langen 1996).

For these comparisons, I use an assessment cost of 0.1 and a time limit of 30 periods. The threshold rule outperforms the best-of-*n* rule at these parameters with an infinite pool of options (Fig. 2). In addition, the average fitness of the threshold rule appears to reach a plateau at approximately 30 time steps. I chose to use a finite time limit because the threshold rule does particularly poorly if forced to choose an option from a finite pool, but with infinite time. In those situations, individuals can set a threshold that exceeds all available options, and they will continue to assess their options without ever choosing one because their thresholds do not decline when time is infinite. Pool size and assessment costs interact to determine when the best-of-*n* rule outperforms the threshold rule. The best-of-*n* rule has higher average fitness than the threshold rule when there are 16 or fewer options from which to choose (Fig. 3). Thus, as pool sizes decrease and assessment costs become increasingly larger, the best-of-*n* rule can outperform the threshold rule (Fig. 4). The average fitnesses of both rules increase slightly as pool size increases beyond the size of the time limit. Individuals cannot sample more options than allowed by the

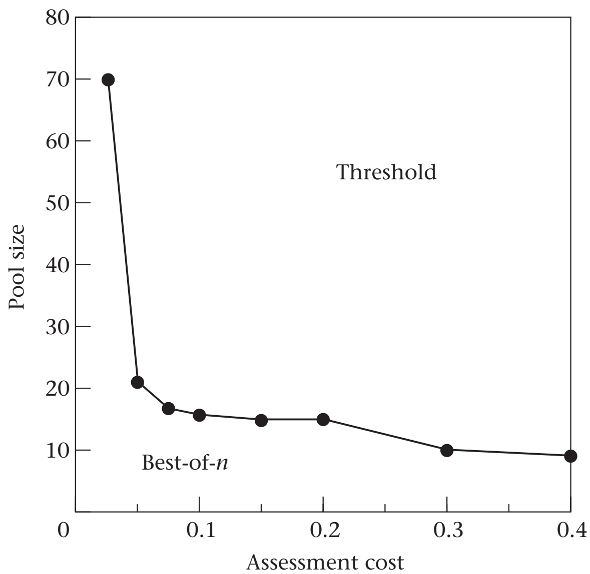

Figure 4. Regions of assessment costs and pool sizes in which either the best-of-*n* or the threshold decision rules are favoured over the other. Points represent the pool size at which the dominance of the two rules switched for a given assessment cost.

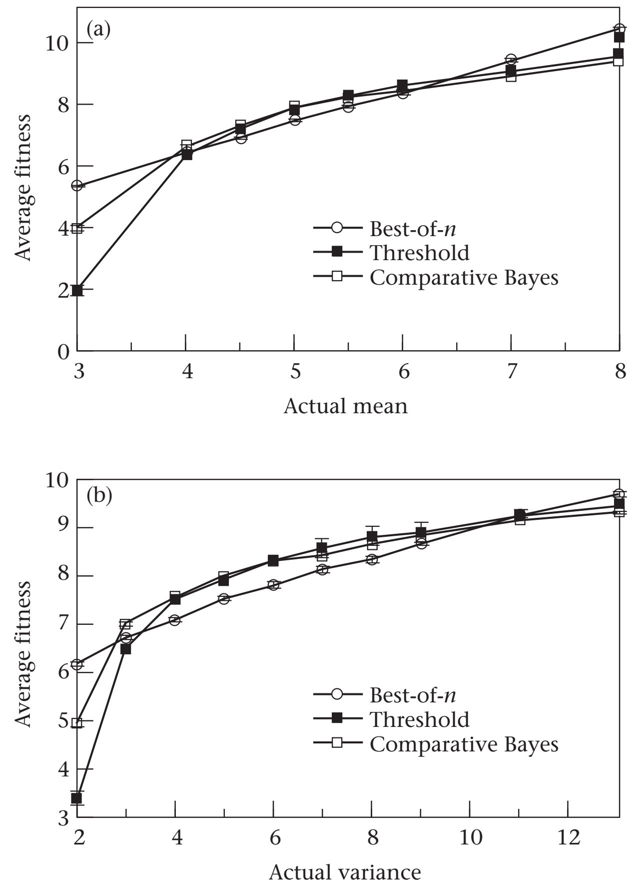

Figure 5. Average fitness of the best-of-*n*, threshold and comparative Bayes decision rules (±SD) versus (a) incorrectly estimated mean option quality and (b) incorrectly estimated variance in option quality, with infinite time, infinite options and an assessment cost of 0.1 (N=1000 for each rule). For the comparative Bayes rule, the time limit and number of options are 70. The estimated mean and variance are each 5, while the actual means and variances are varied.

time limit, but bigger pool sizes decrease the chance of random re-encounters and thus increase the success of the rules. The comparative Bayes rule produces higher average fitness than the threshold and best-of-*n* rules for all observed pool sizes. Increasing the pool size above the time limit, 30, had no noticeable effect on the average fitness of the comparative Bayes rule, because individuals using this rule do not randomly re-encounter options.

Inaccurate and Uncertain Estimates of the Distribution of Option Quality

In natural situations, the distribution of option quality is certain to vary. For infinite pools of options, the distribution of option quality may vary with environmental conditions. For finite pools of options, the distribution of the quality of available options will vary because of random sampling. Individuals may have estimates of the distribution of option quality that are the product of natural selection or the product of assessing the current assortment of available options (Mazalov et al. 1996). Either way, it is unlikely that individuals can perfectly estimate the current distribution of option quality. However, the three rules each depend on these estimates. In particular, the threshold rule uses the estimate to predict the quality of options to be encountered in the future time periods (equations 1–3). The optimal number of samples for the best-of-*n* rule depends on the estimate. The comparative Bayes rule uses the estimate as the initial prior estimate of each option. I first test how robust the three rules are to incorrect estimates of the distribution of option quality. I vary the mean and the variance of the actual distribution of option quality while holding the individual's estimate of the distribution constant, and compare the performances of the three rules.

For these comparisons, I use infinite time, infinite options and an assessment cost of 0.1. When individuals have the correct estimate of the mean, 5, of the distribution of option quality, the threshold and comparative Bayes rules perform very similarly and both outperform the best-of-*n* rule. However, the best-of-*n* rule has higher average fitness than the threshold rule when the actual mean option quality is less than 4.5 or greater than 6 (Fig. 5a). The best-of-*n* rule is more robust than the threshold rule (and to a lesser degree, the comparative Bayes rule), when mistakes are made in estimating the mean of the distribution. The effect is asymmetric, with a decrease in the actual mean having a greater effect on the relative advantage of the best-of-*n* rule over the other two rules than an increase in the actual mean. The comparative Bayes rule does much better than the threshold rule when the actual mean is less than the estimated mean, but the threshold rule does slightly better than the comparative Bayes rule when the actual mean is greater than the estimated mean.

The effects of incorrect estimates of the variance in the distribution of option quality are smaller than the effects

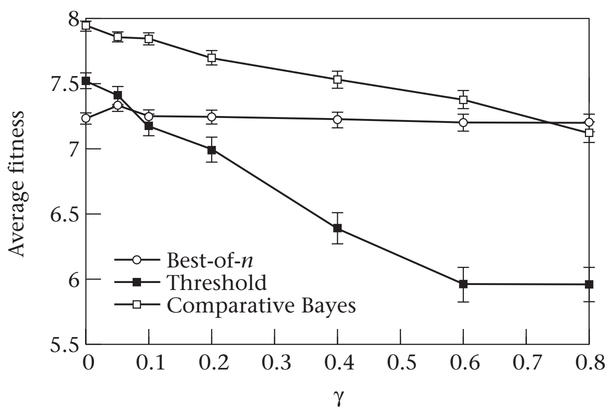

Figure 6. Average fitness of the best-of-*n*, threshold and comparative Bayes decision rules (±SD) versus γ, the probability that the mean option quality is either 3 or 7, with a pool size of 30, a time limit of 30 periods and an assessment cost of 0.1 (*N*=1000 for each rule).

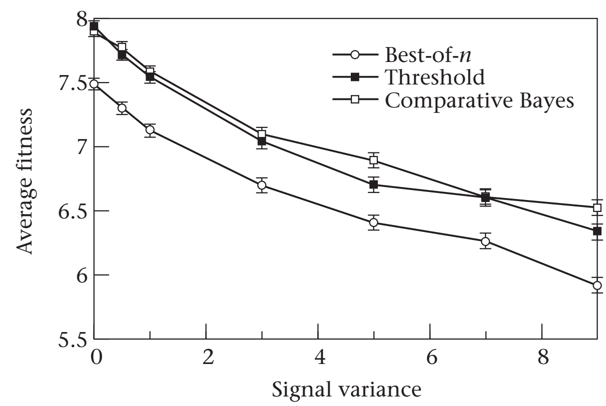

Figure 7. Average fitness of the best-of-*n*, threshold and comparative Bayes decision rules (±SD) versus signal variance, with infinite time, infinite options and an assessment cost of 0.1 (*N*=1000 for each rule). For the comparative Bayes rule, the time limit and number of options are 70.

of incorrect estimates of the mean. The best-of-*n* rule has higher average fitness than the threshold rule when the actual variance in option quality is less than 4 or greater than 9, when individuals estimate the variance to be 5 (Fig. 5b). Overestimating the variance in the distribution, which leads to thresholds being set too high, clearly leads to the best-of-*n* rule outperforming the threshold rule, but a large underestimate of the variance is needed for the best-of-*n* rule to outperform the threshold rule. The comparative Bayes rule also does better than the threshold rule when the variance is overestimated.

Next, I test how uncertainty about the mean option quality affects the performances of the three decision rules. I assume that the mean option quality can take one of three values (3, 5 and 7) and individuals do not know the current mean quality, but do know probabilities of these means occurring and adjust their rules accordingly. For these comparisons, I use a time limit of 30, a pool size of 30 and an assessment cost of 0.1. I chose to use finite time because the threshold rule does very poorly with infinite time and incorrect estimates of the distribution, and I chose to use finite options because I want to include the comparative Bayes rule in the comparison, and for that rule, time and options cannot be varied independently. The performance of the best-of-*n* rule is unaffected by changes in the probabilities (γ) of different option quality means (Fig. 6). The threshold rule is the least robust to uncertainty about the mean option quality, with the performance of the rule declining as the probabilities of different mean qualities increase. And finally, the comparative Bayes rule is intermediate in its robustness, with a moderate decline in performance as the probabilities of different mean qualities increase. Therefore, if the distribution of the quality of options changes and individuals do not know the current distribution, this uncertainty can lead to the best-of-*n* rule performing better than the threshold rule even if individuals know the probabilities of different distributions.

Imperfect Information

Finally, previous comparisons have assumed that when an individual assesses an option they receive perfect information about that quality of the option. However, because of variance in the production of signals from the option and variance in an individual's perception and interpretation of those signals, it is unlikely that individuals ever receive perfect information about the quality of options. I assume that the information an individual receives is randomly drawn from a normal distribution with the mean being the actual quality of the option and the variance being the signal variance (Luttbeg 1996). When the signal variance is zero, the signal gives perfect information about the option's quality. As the signal variance increases, the signal gives more imperfect information about the option's quality. I assume that the threshold and best-of-*n* rules use the rules that are optimal for perfect information. The threshold and best-of-*n* rules have no mechanisms for dealing with imperfect information, and because of a linear fitness function and symmetric signal variance, simply adding variance to signals without having individuals tracking and updating estimates of option quality would have no effect. I vary the signal variance to measure how imperfect information affects the relative performances of the three decision rules.

For these comparisons, I use an assessment cost of 0.1 with infinite time and infinite options. Signal variance has no noticeable effect on the relative performances of the best-of-*n* and threshold rules (Fig. 7). However, the comparative Bayes rules goes from matching the performance of the threshold rule when signal variance is zero to outperforming the threshold rule when signal variance is greater than zero.

DISCUSSION

Based on Janetos's (1980) and Real's (1990) conclusions, there has been the belief that assessment costs determine

Table 1. Summary of the effects of the various factors on the relative performances of the three decision rules

	Best-of-*n*	Threshold	Comparative Bayes
Increased assessment costs	2	1	2
Less time	1	2	—
Fewer options	2	3	1
Estimates more incorrect	1	3	2
Estimates more uncertain	1	3	2
Information less perfect	2	2	1

The assigned numbers reflect the relative performances of the rules. For example, as there are fewer options, the relative performance of the comparative Bayes rule improves the most, and it is given a value of one. The relative performance of the threshold improves the least, and it is given a value of 3.

the relative fitness payoffs of threshold and best-of-*n* rules, with threshold rules outperforming best-of-*n* rules when there are assessment costs. I have shown that the relative success of the two rules also depend on the amount of time available for choosing an option, the size of the option pool, how accurately individuals can estimate the distribution of option quality, and how much uncertainty there is about the present distribution of option quality. The best-of-*n* rule is more robust than the threshold rule to limited time, limited options, incorrect estimates of the distribution of option quality and uncertain environments (Table 1).

The advantage of the threshold rule over the best-of-*n* rule comes from its reliance on estimates of the distribution of option quality. The threshold rule outperforms the best-of-*n* rule when there are assessment costs, given infinite time, infinite options and perfect estimates of the distribution of option quality, because individuals using a threshold rule cease assessing options when a good option is encountered, thus avoiding unnecessary assessment costs (Real 1990). In contrast, individuals using a best-of-*n* rule assess *n* options regardless of the quality of the encountered options. For this reason the threshold rule does better than the best-of-*n* rule when there are assessment costs, and the advantage decreases as assessment costs decrease. However, the ability of the threshold rule to cease assessment depends on individuals having accurate estimates of the distribution of option quality to which encountered options are being compared.

The threshold rule's reliance on estimates of the distribution of option quality makes it less robust to constraints that cause the estimates to vary from the actual distribution. I find that the best-of-*n* rule outperforms the threshold rule when time and options are limited, when estimates of the distribution of option quality are incorrect, and when the actual distribution varies. All of these factors lead to the expected distribution of option quality not matching the actual distribution. Obviously, mistaken estimates of the mean and variance of the distribution of option quality cause the estimated distribution to vary from the actual distribution. Likewise, when the actual distribution varies and individuals do not know the current distribution, the expected distribution will often not match the actual distribution. Perhaps a little less intuitive is that as time or options become more limited, individuals encounter a smaller sample of options drawn from the population distribution of option quality. These smaller sample sizes cause the encountered distribution of option quality to vary more widely from the expected distribution.

How well the decision rules handle the actual distribution of option quality varying from the estimated distribution can be most clearly seen in the manipulations in which individuals incorrectly estimate the mean or variance of the distribution. When individuals overestimate the mean or the variance of the distribution of option quality, they set thresholds or sample sizes (*n*) that are too high and they thus over-sample their options. This has a greater negative effect on the performance of the threshold rule than on the performance of the best-of-*n* rule (Fig. 5). Likewise, when individuals underestimate the mean or the variance of the distribution of option quality, they set thresholds or sample sizes (*n*) that are too low and they thus under-sample their options. This too has a greater negative effect on the performance of the threshold rule than the best-of-*n* rule.

The comparative Bayes rule has two strengths over threshold and best-of-*n* rules. The first is that it allows individuals to choose which options they assess. For example, when information is perfect, individuals avoid accidentally re-encountering options and avoid gathering redundant information. When random re-encounters are not possible because of infinite options, the performance of the comparative Bayes rule is very similar to the performance of the threshold rule (Fig. 1). However, when pools are finite and thus random re-encounters are possible, the comparative Bayes rule outperforms the other two rules by a fairly wide margin (Fig. 3, Table 1).

The second strength of the comparative Bayes rule is that it allows individuals to incorporate the imperfection of information into their estimates of the quality of options and thus into their assessment and choice decisions (Fig. 7). When information is imperfect, individuals using the threshold and best-of-*n* rules will occasionally, by chance, receive signals that appear to indicate that an option has very high quality, thus leading to that option being chosen. The comparative Bayes rule, however, incorporates the imperfection of information, and often leads individuals to resample options that are estimated to be of high quality. This resampling reduces the chance that an aberrant signal will lead to an incorrect choice by the individual.

Implications

Based on the expectation that the threshold rule will outperform the best-of-*n* rule when there are assessment costs, some have predicted that thresholds will be a more common decision rule than best-of-*n*. However, attempts to discern what rule is used in mate choice have often concluded that a best-of-*n* or related rule is used (Valone et al. 1996; Jennions & Petrie 1997). The apparent excess of females using mate choice rules similar to a best-of-*n* rule has led to alternative explanations. Valone et al. (1996) suggested that the apparent excessive use of best-of-*n* by females is due to experimental protocols that lower assessment costs and thus lead females to adopt best-of-*n* rules. Dale & Slagsvold (1996) concluded that female pied flycatchers use a rule similar to a best-of-*n* rule and that assessment costs are not small. They suggested that this apparent inconsistency was due to females using multiple male cues when choosing a mate and that multiple cues require females to visit males multiple times for accurate assessments. Since the threshold rule has no mechanisms for multiple visits, they concluded that females are forced to use a mate choice rule similar to a best-of-*n* rule. However, the results here suggest that limited time, limited options, limited accuracy in estimates of the distribution of option quality, and uncertainty about the distribution of option quality can lead to a broader range of circumstances in which the best-of-*n* rule outperforms the threshold rule. Thus, the apparent excessive use of best-of-*n* rules in mate choice may not be so puzzling after all.

The expectation that the threshold rule will outperform the best-of-*n* rule when there are assessment costs has also led to the belief that decision rules can be inferred based on the size of assessment costs. For example, the demonstration of assessment costs has been used as an argument for the existence of thresholds for mate choice. Several studies that have concluded that females use thresholds have further supported their findings by stating that thresholds should be expected given apparent assessment costs (Gibson 1996; Reid & Stamps 1997). That support is weakened if the best-of-*n* rule can outperform the threshold rule despite assessment costs.

It has also been argued that thresholds should be found in mating systems with high assessment costs and best-of-*n* should be found in mating systems with small assessment costs, particularly in leks (Dale et al. 1992; Rintamaki et al. 1995). The results of this paper do not dispute that high assessment costs will tend to favour the threshold rule over the best-of-*n* rule and that low costs will tend to favour the best-of-*n* rule. But the results do suggest that predictions based solely on assessment costs may fail because they ignore other important factors. We can now predict that the best-of-*n* rule will be more commonly used in systems with fewer options, short assessment periods, and with more uncertain or harder to estimate option quality distributions.

Conversely, the expectation that the threshold rule will outperform the best-of-*n* rule when there are assessment costs has also led to the belief that the apparent use of a decision rule can be used to infer the existence or absence of assessment costs. For example, sand gobies, *Pomatoschistus minutus*, apparently use thresholds when choosing a mate, and it was inferred that assessment costs are not small in this mating system, because, if they were, females would be using a best-of-*n* rule (Forsgren 1997). Small assessment costs are likely to favour the best-of-*n* rule, but there may be plausible circumstances in which the threshold rule would be favoured over the best-of-*n* rule despite low assessment costs. One of the strengths of the best-of-*n* rule over the threshold rule is its ability to return to previously encountered options. Reducing the ability or the benefit of returning to previously encountered options would reduce the relative success of the best-of-*n* rule. For example, if males are removed from the pool of eligible mates when selected by a female (Dale et al. 1992) or if the size or mixing of the pool makes it difficult to locate previously encountered males, then the relative success of the best-of-*n* rule is reduced. Thus, it may be incorrect to infer the existence of assessment costs when it is concluded that females are using thresholds to choose mates.

Similarly, the apparent use of a decision rule similar to best-of-*n* has been used to infer that assessment costs are small. Female black grouses, *Tetrao tetrix*, apparently use mate choice rules that are similar to best-of-*n*, and from this it was inferred that assessment costs must be small, because otherwise females would use thresholds (Rintamaki et al. 1995). The results in this paper have shown that the best-of-*n* rule can outperform the threshold rule when options or time are limited or when estimates of the distribution of option quality are uncertain or incorrect, even when assessment costs are not small. Therefore, the apparent use of a best-of-*n* rule is not a good indication that assessment costs are small. (The number of black grouse males available for mating was unclear, but the maximum number visited by a female was nine (Rintamaki et al. 1995); thus the best-of-*n* rule may have performed better than a threshold rule because of finite males, despite assessment costs.)

Attempts to determine what decision rules are used when females choose mates have typically focused only on the best-of-*n* and threshold rules. There are other proposed mate choice rules that vary key assumptions, such as nonrandom encounters (Luttbeg 1996), imperfect information (Getty 1996), and using experience to estimate the distribution of male qualities (Mazalov et al. 1996). Comparing empirical data to only a small subset of mate choice rules carries the risk of overlooking important factors that can affect the relative performances of rules. For example, in comparing the best-of-*n* and the threshold rules, imperfect information did not affect the relative performances of the two rules. However, including the comparative Bayes rule in the comparison made it clear that the clarity or reliability of information can affect the relative performances of decision rules. The inclusion of the comparative Bayes rule also showed that the ability to choose which options to assess can significantly increase fitness. This suggests that imperfect assessment and nonrandom mate assessment should be examined in studies of mate choice behaviour.

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References

Backwell, P. R. Y. & Passmore, N. I. 1996. Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. *Behavioral Ecology and Sociobiology*, **38,** 407–416.

Bensch, S. & Hasselquist, D. 1992. Evidence for active female choice in a polygynous warbler. *Animal Behaviour*, **44,** 301–312.

Clark, C. W. & Mangel, M. 2000. *Dynamic State Variable Models in Ecology*. New York: Oxford University Press.

Dale, S. & Slagsvold, T. 1996. Mate choice on multiple cues, decision rules and sampling strategies in female pied flycatchers. *Behaviour*, **133,** 903–944.

Dale, S., Rinden, H. & Slagsvold, T. 1992. Competition for a mate restricts mate search of female pied flycatchers. *Behavioral Ecology and Sociobiology*, **30,** 165–176.

Forsgren, E. 1997. Mate sampling in a population of sand gobies. *Animal Behaviour*, **53,** 267–276.

Getty, T. 1996. Mate selection by repeated inspection: more on pied flycatchers. *Animal Behaviour*, **51,** 739–745.

Gibson, R. M. 1996. Female choice in sage grouse: the roles of attraction and active comparison. *Behavioral Ecology and Sociobiology*, **39,** 55–59.

Gibson, R. M. & Langen, T. 1996. How do animals choose their mates? *Trends in Ecology and Evolution*, **11,** 468–470.

Gotthard, K., Nylin, S. & Wiklund, C. 1999. Mating system evolution in response to search costs in the speckled wood butterfly, *Pararge aegeria*. *Behavioral Ecology and Sociobiology*, **45,** 424–429.

Janetos, A. C. 1980. Strategies of female mate choice: a theoretical analysis. *Behavioral Ecology and Sociobiology*, **7,** 107–112.

Jennions, M. D. & Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society*, **7,** 283–327.

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

Luttbeg, B. & Schmitz, O. J. 2000. Predator and prey models with flexible individual behavior and imperfect information. *American Naturalist*, **155,** 669–683.

Mazalov, V., Perrin, N. & Dombrovsky, Y. 1996. Adaptive search and information updating in sequential mate choice. *American Naturalist*, **148,** 123–137.

Petrie, M., Halliday, T. & Sanders, C. 1991. Peahens prefer peacocks with elaborate trains. *Animal Behaviour*, **41,** 323–331.

Real, L. 1990. Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist*, **136,** 376–405.

Reid, M. L. & Stamps, J. A. 1997. Female mate choice tactics in a resource-based mating system: field tests of alternative models. *American Naturalist*, **150,** 98–121.

Rintamaki, P. T., Alatalo, R. V., Hoglund, J. & Lundberg, A. 1995. Mate sampling behaviour of black grouse females (*Tetrao tetrix*). *Behavioral Ecology and Sociobiology*, **37,** 209–215.

Sullivan, M. S. 1994. Mate choice as an information gathering process under time constraint: implications for behaviour and signal design. *Animal Behaviour*, **47,** 141–151.

Valone, T. J., Nordell, S. E., Giraldeau, L.-A. & Templeton, J. 1996. The empirical question of thresholds and mechanisms of mate choice. *Evolutionary Ecology*, **10,** 447–455.