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ORIGINAL ARTICLE

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Optimal divorce and re-mating strategies for monogamous female birds: a simulation model

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Abstract Although the extensive variation in divorce rates among monogamous bird species has stimulated several theoretical accounts, the mechanisms underlying divorce strategies remain poorly understood. Here, we use an individual-based simulation model to investigate the adaptiveness of mechanisms of mate choice in the context of remating. Our model compares the fitness of females that choose a mate during each breeding season using one of two different decision rules; "best-of-*n*" females sample *n* potential partners and then select the male with the highest quality, whereas "better option" females choose a mate whose quality is maximal among the non-mated individuals they sampled the season before. It is assumed in the model that best-of-*n* females have no a priori information about the quality of potential partners and systematically decide to divorce at the beginning of each breeding season before searching for a new mate. Conversely, better option females use the information they gained the season before, and may retain their previous partner if they have no opportunity to mate with an individual of better quality. Results from simulations indicate that the best-of-*n* decision rule should be favoured when there is a large variation in male quality and low costs of mate sampling. On the other hand, the probability that the better option rule may invade the population is predicted to increase with male survival rate. However, changes in male mortality had no marked influence on the expected proportion of divorcing pairs, contrary to previous theoretical expectations.

Keywords Avian monogamy · Divorce · Female mate choice · Simulation model

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Introduction

In a majority of monogamous bird species, individuals have more than one mate during their reproductive career. Although mate changes may be due to the death of one pair member, mate switching or "divorce" can occur when both partners from a previous breeding attempt are present together on the breeding grounds and at least one partner breeds with a new mate (Choudhury 1995; Black 1996). The reasons for divorce in monogamous birds have received much attention (Choudhury 1995; Black 1996; Dubois et al. 1998; Cézilly et al. 2000a; Dubois and Cézilly 2002). In particular, it has been predicted that pairs with low breeding performance should be more likely to divorce than successful breeders (Coulson 1972; Johnston and Ryder 1987; Ens et al. 1993) and that divorces should increase in frequency with increasing availability of unpaired individuals in the population (Ens et al. 1993; see Choudhury 1995 for a review). However, although both the costs and benefits of divorce are directly related to the outcome of mate choice, the mechanisms underlying divorce strategies remain poorly understood.

From a theoretical point of view, a considerable number of mate choice models have been developed to date (e.g. Janetos 1980; Parker 1983; Real 1990; Luttbeg 2002), but they do not apply to re-mating in monogamous species. In particular, mate choice models generally assume that females have to assess the quality of all potential partners they successively encounter before making a choice. This, however, is not true in the case of remating in monogamous species (see Black 1996). Indeed, in most long-lived monogamous species, females, at the onset of each breeding season, have to choose a mate among potential partners, some of which they have previously encountered (Uy et al. 2000). If females can use the information they gained the season before to choose a mate, the cost of sampling will be reduced. Accordingly, Otter and Ratcliffe (1996) found that females black-capped chickadees *Parus atricapilus* most often desert their mates to pair with experimentally "widowed" males of higher social rank from neighbouring territories. Furthermore, mate choice models typically assume that females using a "threshold decision rule" reproduce with the first encountered mate exceeding some pre-defined quality threshold (Janetos 1980; Wittenberger 1983; Real 1990). Although the threshold value of acceptability can be either constant (fixed-threshold rule) or attuned to the expectancy from continued search (one-step decision rule), most often it does not vary between females according to their previous experience (but see Mazalov et al. 1996). However, given that divorcing is advantageous for females only if they can obtain a better quality mate, a more realistic assumption for monogamous species would allow females to modify their threshold value of acceptability according to the quality of their previous partner. Finally, previous studies of female mate choice have considered that males remain available for mating after copulation with one female (Janetos 1980; Real 1990; Luttbeg 2002). This hypothesis makes sense when males reproduce with several females during each reproductive season. In monogamous species, however, males tend to pair with only one female in each breeding season, and hence become unavailable for other females following pair formation. In this situation, the larger the number of potential partners individuals can sample before making a choice, the more they gain information and improve their probability of acquiring a high-quality partner. However, when all individuals within the population search for a mate simultaneously, the number of available partners may decrease as selective individuals accept a potential mate to reproduce, which in turn should lead to a reduction in choosiness.

Here we present results from an individual-based simulation model, built to identify optimal strategies of re-mating for monogamous females. In this study we have compared the fitness of females that choose a mate during each breeding season using best-of-*n* (Janetos 1980) and better option decision rules. For simplicity's sake, we decided to consider only two decision rules in our analysis. It has recently been predicted that the best-of-*n* rule should outperform the threshold rule when time and options from which to choose are limited and when individuals have incorrect estimate of the distribution of option quality (Luttbeg 2002). Because these conditions are likely to be met in most monogamous species, then we excluded the threshold decision rule from our analysis. Following the common formulation of the best-of-*n* rule (Janetos 1980; Real 1990; Luttbeg 2002), best-of-*n* females sample *n* potential partners and then select the male with highest quality to reproduce (Janetos 1980; Real 1990). However, given that all females search for a mate simultaneously and that individuals have only one breeding partner during each season in monogamous species, we have considered that males are no longer available as potential mates after forming a pair-bond. For the better option rule, females choose a mate at the beginning of each breeding season among the non-mated individuals they sampled the season before. The two decision rules differ in the quantity of information females can use before making a choice, but also in the time required to search and sample for mates. Moreover, the most important difference between the two decision rules is that better option females may retain their previous partner if they have no opportunity to pair with another individual of better quality, whereas best-of-*n* females search a new partner at the beginning of each breeding season.

Methods

The model

Assumptions of the model

In our model we focused on the mating decisions of females, and we thus considered males as the non-discriminating sex (see Cézilly et al. 2000b). Accordingly, we assume that males vary in quality *q*, but we ignore variation in female quality. The population has a constant size, and contains N_m males and N_f females. Individuals are dispersed in a two-dimensional space, that is represented by a $k{\times}k$ square grid. All of the $k{\times}k$ cells of the grid are considered to be equivalent breeding sites, and each of them cannot be occupied by more than one breeding pair. Individuals can move only between adjacent territories. Each movement is costly, as it requires a time T_M during which females cannot search for a mate. The time horizon for pairing is restricted to the breeding season, whose length is the number of time steps *t*. Individuals mate only once in each breeding season, and become unavailable for additional mates after forming a pair-bond. Therefore, we did not consider mate switching within-season, nor extra-pair copulations. Each male is characterised by an index of quality *q*, which is supposed to follow a discrete normal distribution of mean μ and variance σ^2, but truncated to range from 0 to $q_{\max}$, where $q_{\max}$ represents the index of highest male quality. The quality of each male does not vary according to its age, but is fixed during its life. The breeding performance of a pair $\omega(q)$ corresponds to the number of offspring produced by each pair and depends exclusively on the male's quality *q*,

$$\omega(q) = q + b$$

The parameter *b* is a benefit of mate retention. Pair members that reproduce together consecutively at least twice, even by chance, improve their breeding performance by this factor *b*. Note that the benefit of mate retention does not depend on the age of the pair bond. The breeding performance of pairs that reproduce together over several breeding seasons consecutively, therefore, increases only between the first and the second breeding attempt and then remains constant.

Between two consecutive breeding seasons, each male dies with a probability which depends upon its own quality. So let $\mathrm{S_m}(q)$ denote the rate of survival for a male whose quality is *q*:

$$S_m(q) = \frac{S_m(0) \times (q_{\max} - q) + q}{q_{\max}}$$

where $q_{\max}$ is the index of highest male quality, and $S_m(0)$ is the survival rate of males whose quality is equal to zero. According to this equation, males survival rate increases linearly with *q*, reaching 1 when $q = q_{\max}$. There is empirical support to this assumption. For instance several studies report that males of higher social ranks have access to the territories of better quality (Barnard and Sibly 1981; Møller 1987). Since factors related to habitat quality (e.g. food supply or safety from predators) may influence both reproductive performance and survival, then we would expect a positive correlation between breeding success and survival rate. Since female quality variation was considered unimportant, we assumed that all females have a fixed probability S_f to survive between two consecutive breeding seasons.

As the population size is kept constant through years, each individual that dies at the end of a breeding season is replaced at the beginning of the next one by another individual of the same sex. Moreover, we assume that the distribution of male quality does not vary from one breeding season to the next. Therefore males that do not survive between two consecutive breeding seasons are replaced by individuals of the same quality. Males that are recruited for the first time in the population choose a breeding site randomly, whereas males which survive between two consecutive breeding seasons return on their previous breeding site with a probability f, or choose randomly a new territory with a probability $(1-f)$.

Females inherit the mating strategy from their mother. Therefore, the probability that a female which is recruited to the population at the beginning of a breeding season uses a particular strategy is set by the relative performances (estimated in numbers of offspring) of the strategies during the previous breeding season.

Overview of the decision rules

The first decision rule (best-of-*n*) is based on an a posteriori knowledge of the quality of potential mates. Females using this decision rule have no information about the quality of males at the beginning of each breeding season, and have to remain during a time T_A on the territory of all the potential mates (i.e. unpaired males) they successively encounter to assess their quality. However, females can rely on a priori knowledge of the mean and variance of the distribution of male quality, and hence can sample the optimal number of potential partners that maximises their breeding performance. Time for assessment is the same for all females, and corresponds to the time needed to estimate the quality of each potential mate without error. At the beginning of each breeding season, females choose a breeding site randomly and then move between adjacent territories and successively assess the quality of n potential mates. Given that potential partners are randomly encountered, previously assessed males can be randomly reencountered. In this case, however, females have no interest in remaining on the male's territory during a time T_A, and hence leave the territory immediately. After mate sampling is completed, females return to the territory of the male with the highest index of quality. Females are capable of evaluating the shorter itinerary from one breeding location to another, and thus travel time needed to get back to a given territory is equal to the minimum number of territories they have to cross. Because searching and sampling for mates is time-costly, there is a risk for females, at the end of the sampling process, of returning to the territory of males which are no longer available as potential mates. In such a case, they select the male with the highest quality among the remaining mates they previously encountered, and so on until they succeed in pairing. If females do not find a mate among the n potential partners, they reproduce randomly with the first available male encountered. In all cases, females reproduce with a new partner during each breeding season, unless they choose by chance the same male in two consecutve breeding seasons.

The second decision rule (better option) is based on an a priori knowledge of male quality, obtained during the season before mate choice occurs. We considered that, during a reproductive season, females are able to assess the quality of males present on neighbouring territories. The maximum number of males that females can sample and for which they can subsequently remember the quality and location, depends on their distance of perception, d. When the distance is equal to zero, females can only estimate the quality of their partner. Increasing the distance of perception raises the number of males among whom females can choose a mate, all the more quickly since the density of males is high. At the beginning of each breeding season, females return to their breeding territory, and reproduce with the male whose quality is maximal, among the non-mated individuals they previously sampled. Given that better option females use the information they gained the season before to choose a mate, they can reproduce immediately after the beginning of the breeding season. Unlike best-of-*n* females, therefore, they have no risk at the end of the sampling process of returning to the territory of males which are no longer available as potential mates. It may happen, however, that several females decide at the beginning of a breeding season to reproduce with the same male. In this case, a randomly chosen female reproduces with the male, while the others reproduce with the male with the highest quality among the remaining non-mated individuals they previously sampled. Females which did not reproduce the season before because they failed to find a mate or have been recruited in the population for the first year, have no information and then mate with the first encountered available potential partner, whatever its quality.

Simulations

We compared the average performance of the best-of-*n* and better option decision rules, by restricting our analysis to the main parameters that are thought to affect directly the intensity of competition between females, and hence the costs and benefits of mate sampling. More precisely, we investigated the effects of the operational sex-ratio, the density of potential mates, the extent of variation in male quality and the rate of male survival. Only one parameter was allowed to vary at one time, with other parameters fixed to their values given in Table 1. Each simulation was started with equal proportions of females using each decision rule, and the population was followed for 500 consecutive breeding seasons. Considering only 500 breeding seasons was justified in the present study since we found that an equilibrium point was reached after this period and that the relative proportion of each decision rule at the end of the simulation did not depend on the starting conditions (Fig. 1). At the end of each breeding season, both the relative proportion of each decision rule and divorce rate were calculated. Divorce rate was estimated as the number of pairs where at least one partner bred with a different partner the following year although its previous mate was still alive and present in the population, divided by the total number of pairs where both partners were present in the population the following year. For each set of parameters, means and variances were estimated from 20 repetitions.

Because it is assumed that females do not differ in quality, we considered that best-of-*n* females all sample the same number of potential partners before making a decision. The optimal level of n was chosen for each set of parameters in such a way that the average performance of the best-of-*n* decision rule was maximal once the equilibrium point was reached. More precisely, we made vary n from 1 to 15 for each set of parameters, and retained the value for which the average proportion of best-of-*n* females, estimated from 20 repetitions, was maximal after 500 consecutive breeding seasons, or the value that allowed best-of-*n* females to resist the longest time when all females were predicted to employ the better option rule at equilibrium (i.e. when the equilibrium proportion of best-of-*n* females was 0 for any value of n). Although an increase in the use of the better option decision rule is likely to reduce the number of available partners, which should in turn decrease the benefits of mate sampling and hence the number of potential partners sampled by best-of-*n* females, we have considered that n is fixed for a given set of parameters, whatever the relative proportion of each decision rule. Unlike previous studies, however, it would have been incorrect here to assess the optimal level of n after only one breeding season (Luttbeg 2002), since the relative performance of each decision rule may vary from one breeding season to the next, regardless of their relative proportion. Best-of-*n* females, for instance, do better than better option females during the first re-

Table 1 Definition of the parameters used in the model

Symbol	Values by default	Meaning
k	35×35	Dimension of the grid
N_m	600	Number of males
N_f	400	Number of females
d	1	Distance of perception
μ	4.0	Mean of the males quality
σ^2	4.0	Variance of the males quality
$S_m(0)$	0.6	Survival rate of males whose quality is zero
S_f	0.8	Mean female survival rate
f	0.5	Male rate of site fidelity
b	1	Improvement of the breeding success of pair members that reproduce together at least for the second consecutive reproductive season.
t	100	Length of a breeding season (in time steps)
T_A	1	Time (in time steps) for mate assessment
T_M	1	Time (in time steps) needed to move between two adjacent territories

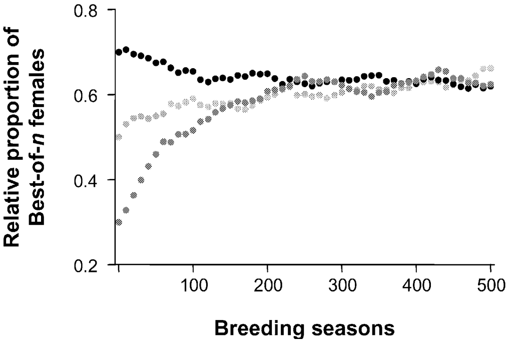

Fig. 1 Evolution of the relative proportion of best-of-*n* females over 500 consecutive breeding seasons when the initial proportion of females using this decision rule is 30%, 50% and 70%

productive season since they sample *n* potential partners before choosing a mate, whereas better option females reproduce with the first encountered available male. In subsequent reproductive attempts, however, better option females can improve their breeding success either by keeping the same partner or by deciding to divorce in favour of a better quality one. Therefore, the optimal level of *n* reported in this study does not necessarily maximise the average expected gain of best-of-*n* females at the end of each breeding season, but maximises the proportion of females using this rule after 500 consecutive breeding seasons. To control for the effect of other potential confounding factors that could have affected the optimal level of *n*, all other parameters, such as the mean or variance in male quality, were kept constant.

To investigate the influence of the operational sex-ratio we considered a constant number of males and allowed the number of females to vary. The effect of mate density was investigated through increasing or decreasing the number of males and females, while keeping a constant sex-ratio. Finally the effect of male survival rate was investigated by varying the parameter $S_m(0)$, which corresponds to the survival rate of lowest quality individuals.

Results

Predictions

Operational sex-ratio

The probability that the best-of-*n* decision rule may invade the population is predicted to increase as the operational sex-ratio becomes male-biased (Fig. 2A). When all the females cannot reproduce during a breeding season, because of an insufficient number of potential mates, it never pays females using the best-of-*n* decision rule to sample a large number of potential partners, since the longer they wait before accepting a mate the higher is their probability of remaining unpaired. As a consequence, their breeding performance is maximal when they reproduce randomly with the first available mate, that is when they do not sample more than one or two potential partners before reproducing (Fig. 2A). In this

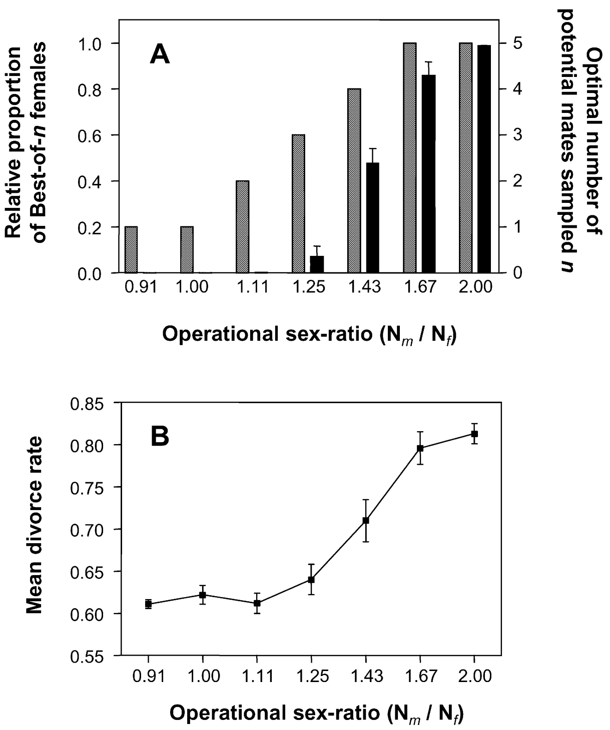

Fig. 2 **A** Influence of the operational sex-ratio (N_m / N_f) on the mean (+SEM) expected proportion of best-of-*n* females after 500 consecutive breeding seasons (*dark columns*) and on the optimal number of potential mates sampled by females using this decision rule (*light columns*). **B** Mean (+SEM) divorce rate in relation to the operational sex-ratio

case, however, their expected fitness is lower than that of females employing the better option decision rule, allowing that strategy to invade the population (Fig. 2A). Decreasing the number of females while keeping the number of males constant tends to increase the breeding success of best-of-*n* females, but has little or no effect on the average performance of the better option decision rule. This arises because increasing the relative proportion of males reduces the intensity of competition between females. As a consequence, females that employ the best-of-*n* decision rule can afford to be more selective, which in turn increases their expected fitness. Females using the better option decision rule, on the other hand, can reproduce immediately after the beginning of the breeding season, since they use the information they gained the season before to choose a mate and hence have no time cost of sampling. Thus, their probability of finding a mate is unlikely to be affected by the intensity of competition between females when the number of males within the population remains constant. Our model predicts that the proportion of females using the best-of-*n* decision rule should increase as the operational sex-ratio becomes male-biased (Fig. 2A). Since best-of-*n* females may reproduce with a different partner every season, divorce rate is also predicted to increase as the relative proportion of males increases (Fig. 2B).

Mate density

The model predicts that the relative proportion of females using the best-of-*n* decision rule should increase with male density (Fig. 3A). At low male densities, the mean inter-individual distance between mates is likely to be large. Thus, if females decide to sample a large number of potential mates, the time required to gain the information is likely to be longer than the duration of the breeding season. As the density of males increases, the time cost to sampling is reduced, allowing best-of-*n* females to sample a larger number of potential mates (Fig. 3A), which in turn increases their probability of acquiring a high-quality partner and hence their average breeding success. Increasing the density of males is also likely to improve the average breeding performance of better option females, although at a slower rate. This is due to the fact that better option females can assess the quality of a larger number of males at high density. However, they can use this information to choose a mate only if the males remain faithful to their territory from one breeding season to the next. Given that only a proportion *f* of males return on the same territory at the beginning of each breeding season, we would expect a weak influence of male density on the average performance of the better option rule, especially when males exhibit a low rate of site fidelity. Therefore we predict that under most circumstances the use of the best-of-*n* decision rule should increase with male density (Fig. 3A), and so should divorce rate (Fig. 33).

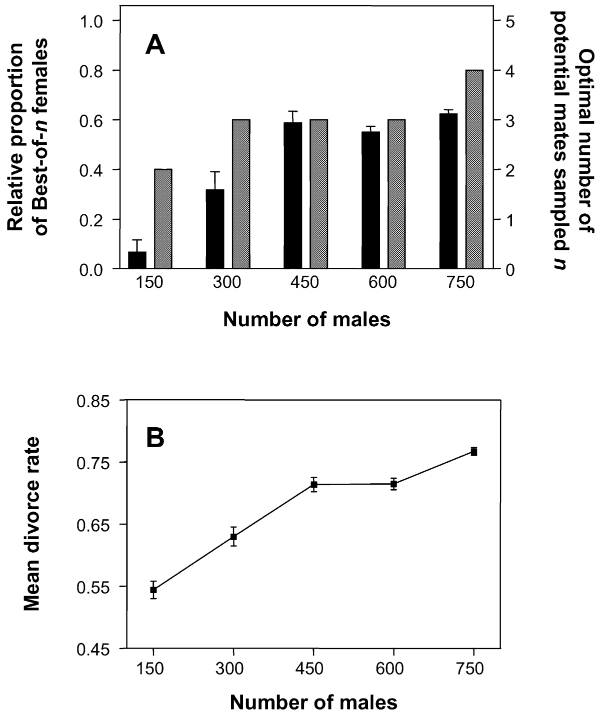

Fig. 3 **A** Influence of male density on the mean (+SEM) expected proportion of best-of-*n* females after 500 consecutive breeding seasons (*dark columns*) and on the optimal number of potential mates sampled by females using this decision rule (*light columns*). **B** Mean (+SEM) divorce rate in relation to male density

Extent of variation in male quality

Searching and sampling for mates before reproducing is advantageous for females only if they can obtain a partner whose quality is higher than that of the male they would have obtained if they had reproduced randomly. So when there is no variation in male quality, there is little to gain by being selective, and hence we predict that females using the best-of-*n* decision rule should reproduce with the first available mate. Inversely, when the extent of variation in male quality is high, the probability of mating with a high-quality partner increases as females sample a larger number of potential mates before making a decision (Fig. 4A). Therefore, females are predicted to become more choosy as the extent of variation in male quality increases. Moreover, the model predicts that both the relative proportion of females using the best-of-*n* decision rule (Fig. 4A) and divorce rate (Fig. 4B) should increase with the extent of variation in male quality. When there is no variation in male quality, females that employ the better option decision rule have no opportunity to find a better quality mate, and hence are expected to keep the same mate whenever it is possible. If there is a benefit associated with remating, then the average performance of the better option decision rule will outweigh that of the best-of-*n* decision rule, and divorce will be rare. Increasing the extent of variation in male quality increases the number of potential partners among which

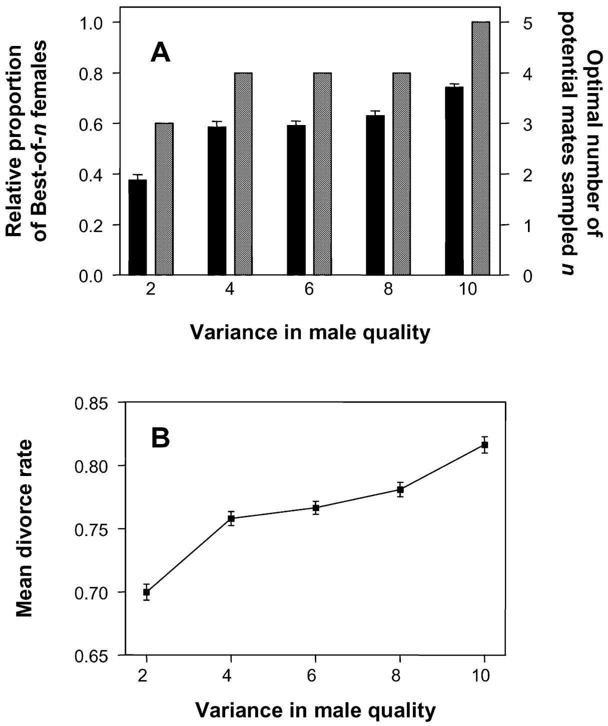

Fig. 4 **A** Influence of the extent of variation in male quality on the mean (+SEM) expected proportion of best-of-*n* females after 500 consecutive breeding seasons (*dark columns*) and on the optimal number of potential mates sampled by females using this decision rule (*light columns*). **B** Mean (+SEM) divorce rate in relation to the extent of variation in male quality

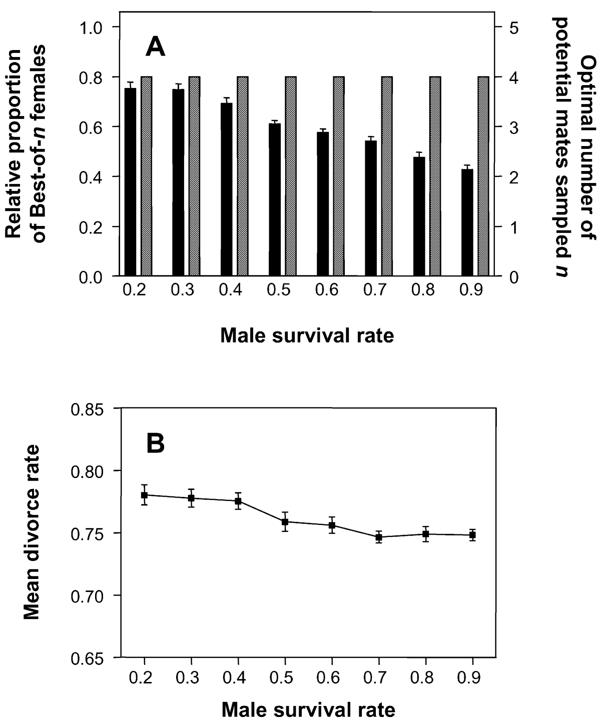

Fig. 5 **A** Influence of male survival rate of lowest quality individuals on the mean (+SEM) expected proportion of best-of-*n* females after 500 consecutive breeding seasons (*dark columns*) and on the optimal number of potential mates sampled by females using this decision rule (*light columns*). **B** Mean (+SEM) divorce rate in relation to male survival rate of lowest quality individuals

best-of-*n* females can choose a mate, but has no effect on the number of potential partners among which better option females can choose a mate. Therefore, the relative performance of the best-of-*n* decision rule will increase as the extent of variation in male quality increases, leading to an increase in divorce rate (Fig. 4B).

Male survival rate

Our model predicts no effect of male survival rate on the number of potential mates best-of-*n* females should sample before making a choice (Fig. 5A). Whether females decide to reproduce or to continue searching and sampling for mates depends on the costs and benefits of sampling. In particular, we would expect that females will become more selective as the benefits of sampling increase, but less choosy when the costs of sampling increase. In the model, we assumed that males that do not survive between two consecutive breeding seasons are replaced by individuals of the same quality. As a consequence, increasing male survival rate does not affect the number of potential mates that are present in the population during each breeding season, or the variance in male quality. So fluctuations in mortality rate are unlikely to influence sampling tactics of females.

Our model predicts a decrease in the expected proportion of females using the best-of-*n* decision rule with increased male survival rate (Fig. 5A). When male mortality rate is high, the number of potential mates among which better option females can choose a mate is likely to be low. Females that employ the best-of-*n* decision rule are then likely to have more information about potential mates and hence a higher probability of mating with a high-quality partner. Moreover, when male survival rate is low, better option females cannot remate with their previous partner in most cases. Thus, not only do they choose a mate among a smaller number of options than best-of-*n* females, but also they rarely get the benefit of mate retention. When mortality rate is low, the opposite is more likely to occur, which is expected to lead to an increase in the use of the better option decision rule. Although male survival is predicted to affect the use of each decision rule, it has no marked influence on divorce rate (Fig. 5B). When male survival rate is low, the proportion of females using the best-of-*n* decision rule is predicted to be high, which implies that mate retention should be very rare. Given that better option females may reproduce with their previous partner if there is no available male of better quality, increasing the use of this decision rule by increasing survival rate should lead to an increase in the rate of mate fidelity. However, as male survival rate increases so does the number of potential partners among which better option females can choose a mate, which in turn increases their chance of finding a better quality partner and hence their probability of divorcing. As a result, we predict that divorce rate should remain high when male survival rate increases, despite the increase in the proportion of better option females. However, the effect of male survival on divorce rate is likely to depend on male density. In particular, when the density of males is very low, the number of potential mates for which better option females can assess the quality during a breeding season is very small. As a consequence, they have very few opportunities to find a better quality partner at the beginning of the following season, even if male survival rate is high, and under these conditions we would expect that the increase in the proportion of better option females with increasing male survival rate will be paralleled by a decline in divorce rate.

Discussion

Divorce is advantageous for females only if they can improve their breeding performance by mating with a higher-quality partner. Among other parameters, the scope for improvement depends on the number of potential partners among which females can choose a mate. However, because searching and sampling for mates is time costly, females are most often limited in the number of potential partners they can sample before making a decision. Moreover, the benefits of mate sampling depends on the ability of females to assess the quality of potential partners among which they choose mate. We then predict that the use of one or the other decision rule should vary according to various factors such as the availability of unpaired individuals, the cost of mate sampling and the level of stability of the environment.

The main difference between the two decision rules is that females employing the best-of-*n* rule systematically decide to divorce at the beginning of each breeding season before searching for a new mate, whereas females using the better option rule initiate a divorce if they perceive an opportunity to mate with a higher-quality partner or otherwise retain their previous partner. Thus, when females have few prospects to improve their breeding performance, they benefit by using the better option decision rule, since this strategy reduces their risk of divorcing in favour of a lower-quality partner. The model therefore predicts that the better option decision rule should be favoured within populations exhibiting low or no variance in male quality. Although best-of-*n* females can gain more information about potential partners than better option females since they are not limited in the number of males they successively visit before making a choice, they have to invest both time and energy to search and sample for mates. So, it is advantageous for females to sample a large number of potential mates, only if they can use this information as they make a decision and reproduce with the better quality male. Conversely, when the males they successively visit have a high probability of becoming unavailable as they make a choice, they have no interest in being selective, since the longer they wait before accepting a mate the higher is their probability of remaining unpaired. Thus, our model predicts that the proportion of females using the best-of-*n* decision rule should decrease as the sex-ratio becomes more female-biased, since in this case there is an increased competition between females, forcing them to mate with the first encountered available male, whatever its quality. Similarly, when the time available to reproduce is reduced or when searching for potential mates requires a long time, we would expect that females will choose a partner before they have been able to acquire sufficient information. Since decreasing male density increases the inter-individual distance between potential partners, and hence the energetic and time costs of sampling (Real 1990), it follows that the proportion of females using the best-of-*n* decision rule should be higher at high male density. Conversely, when the quantity of information females can obtain without any cost is relatively large, the proportion of females using the better option decision rule should increase. The number of potential partners among which better option females can choose a mate depends directly on the proportion of males that re-use the same nest over consecutive breeding seasons. Hence we predict that the use of the better option decision rule should increase as site fidelity rate increases, but decrease with increased rate of male mortality. Given that variation in female quality was ignored in this study, we have considered that females using the best-of-*n* decision rule all sample the same number of potential partners before making a decision. However, because there may be considerable variability among females in the quality of potential mates sampled as well as in the time required to assess the quality of *n* potential partners, the optimal level of *n* is also likely to vary among females. Allowing females to use different levels of *n* would have probably changed the expected proportion of each decision rule at equilibrium, but not the qualitative results of this study. For instance, when the density of males is high, the costs of mate sampling are reduced, and then we predict that best-of-*n* females should sample a large number of potential partners before making a decision. However, as females become more selective, they increase not only their chance of finding a high quality partner, but also their probability of remaining unpaired. This is expected to favour the persistence of the better option decision rule since females using this decision rule can reproduce immediately after the beginning of the breeding season. Nevertheless, the frequency of females using the better option decision rule would probably be reduced if best-of-*n* females were allowed to use different levels of *n*, because those that have found a high quality male early in the sequence could make a decision earlier, increasing thereby their chance of reproducing.

While females using the best-of-*n* decision rule reproduce with a new partner every season, those that employ the better option decision rule can remate with their previous partner when there is no opportunity to obtain a better quality mate. As a consequence, we would expect that divorce rate will increase with the proportion of females using the best-of-*n* decision rule. Accordingly, our model predicts that divorces should occur more frequently when there is a large variation in male quality, and when the sex-ratio is male-biased. Moreover, divorce rate is predicted to increase as the density of males within the population increases. However, despite our model predicting that the use of one of the other decision rule should vary with male survival rate, changes in mortality rate had no marked influence on the expected proportion of divorcing pairs at high male densities. Although several hypotheses for divorce predict a negative correlation between divorce rate and survival rate (Rowley 1983; Ens et al. 1993), Ens et al. (1996) found no evidence for such a relationship at the interspecific level, even after controlling for the effects of phylogenetic inertia and potential confounding variables.

Depending on the decision rule females employ to choose a mate, they do not use the same information. In particular, the better option rule is based on an a priori knowledge of male quality obtained during the season before mate choice occurs, whereas the best-of-*n* rule is based on an a posteriori knowledge of the quality of potential mates. We have considered in this model that females can accurately assess the quality of potential mates, whatever the decision rule they use, although it is unlikely to be the case. Because females that employ the best-of-*n* rule do not have any information about the quality of males at the beginning of each breeding season, they can rely only on phenotypic attributes of potential partners to assess their quality. On the other hand, females that employ the better option decision rule can use both the phenotypic attributes and the breeding performance of potential mates as clues to assess their quality. Since phenotypic traits are not necessarily honest signals of individuals' quality (Camplani et al. 1999), then better option females are likely to have a better estimate of males' quality than females using the best-of-*n* rule, under many circumstances. Furthermore, it is assumed in the model that male quality remains constant throughout the individual's lifespan. However, in many bird species, reproductive performance may vary according to the age or the experience of the pair members, but also to environmental factors (Curio 1983; Newton 1989). When males' quality does not remain constant from one breeding season to the next, females cannot perfectly predict the reproductive success they will obtain by choosing a mate whose quality has been estimated during the previous breeding season. As a consequence, we would expect that the proportion of females using the best-of-*n* decision rule will be higher when they breed in unstable habitats, because in this case, environmental conditions can vary considerably between consecutive breeding seasons. Finally, we have assumed in the model that the time for mate assessment is constant, for any male's quality. However, it has been demonstrated in many species that females do not provide the same effort to estimate the quality of all potential mates, because low quality males generally require a reduced observation time compared to high quality ones (Cox and Leboeuf 1977; Montgomerie and Thornill 1989; Wagner 1991; Sullivan 1994). Thus, future extensions to this model should take into account differences not only in the quantity of information, but also in the quality of the assessment females use to select a breeding partner.

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