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An ESS model for divorce strategies in birds

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We present a theoretical investigation of divorce. Arguments are couched in terms of birds, but should be applicable to other groups of organisms. We model a population in which there is a range of both male and female qualities, and decisions on whether to divorce are made by both members of a breeding pair. The reproductive success of a pair is additive in male and female qualities in the baseline case, but we also consider the effect of quality interactions. The availability of new mates depends on the divorce strategy of all population members. We allow for the possibility that mate choice is associative in quality, although we do not explicitly model the mate choice process. Using a game-theoretical model which incorporates these factors we investigate the following issues: the form of the evolutionary stable strategy, and the implications of this strategy for quality correlations in breeding pairs and for the distribution of qualities among unpaired individuals; divorce rates, reproductive success and mate quality changes over the lifetime of an individual, and the dependence of these qualtities on the individual's quality; mean population divorce rates and their dependence on costs of divorce, longevity and the extent of quality variation in the two sexes; initiators of divorce and reproductive success before and after divorce.

Keywords: mate change; better option hypothesis; game theory; lifetime reproductive success; quality variation; sequential search

1. INTRODUCTION

Empirical studies of monogamous bird species have revealed wide variation in whether mates are retained from year to year (reviewed in Rowley 1983; Ens *et al.* 1996). For example, the majority of house martins, *Delichon urbica*, mate with a different individual each year (Bryant 1979), whereas mate change in barnacle geese, *Branta leucopsis*, is rare (Forslund & Larsson 1991). There are several reasons why an individual may find a new mate. In barnacle geese, individuals usually only form new pair bonds following the death of their previous mate (Forslund & Larsson 1991). In other species, individuals may breed with a new partner even though their previous partner is still alive. This phenomenon of mate change is commonly referred to as divorce. There have been several hypotheses proposed to explain this behaviour (see Choudhury (1995) for a review). It is now generally accepted that divorce is a strategic decision by an individual to maximize its fitness. We investigate divorce strategies using a model in which there are annual decisions after breeding. The model is based on the assumption that individuals divorce their current mate to mate with an individual of higher quality as proposed by the 'better option hypothesis' (Rowley 1983; Johnston & Ryder 1987; Ens *et al.* 1993; McNamara & Forslund 1996). Ens *et al.* (1996) review factors that affect the breeding quality of birds. Reproductive success is usually related to age and breeding experience, but may also be affected by lifelong phenotypic characteristics. In this paper we ignore aspects of quality that change over an individual's lifetime and concentrate on aspects that are fixed.

In our model the advantage of divorce is that a better mate may be found. Individuals who divorce are also likely to pay a cost (Rowley 1983; Johnston & Ryder 1987; Ens *et al.* 1993). A bird that has divorced has to obtain a new mate. Finding a mate may be energetically costly and waste time (Ens *et al.* 1996). Consequently, reproductive success with the new mate may be less on first breeding than on subsequent breeding attempts. Our model allows for this possibility.

The form of the model is described in detail later; here we give a brief introduction. A large population composed of equal numbers of males and females is considered. Within this population, individuals vary in quality and the quality of each individual is fixed throughout its life. The reproductive success of a pair depends on the quality of each member of the pair. After a breeding attempt, each member of the pair knows the other's quality and each then makes the decision whether or not to divorce. The pair splits if either member of the pair decides to divorce. After divorce, pair members seek a new mate. Reproductive success at the first breeding with a new mate is less when compared with subsequent breeding attempts with that mate. Within this population, all individuals follow a strategy of divorce that maximizes their expected total lifetime reproductive success. The problem of whether or not to divorce is game theoretical. One reason is that the likelihood of a particular female finding a better-quality mate after divorce depends on the qualities of males who are seeking mates. Males become available as potential mates through recruitment to the breeding population, through the death of their current mate and as a result of divorcing or being divorced.

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Because of this last cause, the quality of the mate obtained by a female depends on the divorce strategy of all population members. Similarly, the quality of the mate obtained by a male depends on the divorce strategy of all population members. The problem is also a state-dependent game, in that each individual has to take its own quality into account in deciding whether to divorce. This is because an individual's quality affects whether a new mate will subsequently divorce that individual. Results presented are at the evolutionarily stable strategy (ESS) for this game.

Factors that may account for differences in divorce rates between populations are reviewed by Ens *et al.* (1996). These include survival rates, cost of mate change and quality variation. Previously, McNamara & Forslund (1996) used an optimality model to investigate how these factors affected the divorce decisions of a focal female and described corresponding changes in population divorce rates. In that model, only females made divorce decisions and the distribution of available mates was not generated by population behaviour. Ens *et al.* (1996) review empirical evidence of initiators of divorce. In several species, including house wrens *Troglodytes aedon*, great tits, *Parus major*, and ptarmigan, *Lagopus* spp., divorce is usually due to females deserting their current mate. In magpies, *Pica pica*, male desertions are more common. In some species, including oystercatchers, *Haematopus ostralegus*, and blue ducks, *Hymenolaimus malacorhynchos*, although female desertions are more common than male desertions, individuals of both sexes divorce their mates. Thus, there are examples of divorce decisions made by both sexes and of divorce decisions made by only one sex.

Using the ESS model we compare how divorce decisions and resultant divorce rates depend on whether one or both sexes are allowed to initiate divorce. We re-examine the effects of survival rates, costs of mate change and quality variation on individual decisions and population divorce rates. In addition, we can explore whether these factors affect individuals of different qualities to the same extent. We then consider two other reasons why the divorce strategies may differ between the sexes. Reducing the variation in the quality of individuals of one sex will affect the probability that an individual of the other sex can find a better mate if it divorces. Similarly, if the reproductive success of a pair is primarily dependent on the quality of one sex, we would expect different divorce strategies for each sex. We then examine the reproductive success of pairs that have divorced to investigate the prediction of Ens *et al.* (1993) that the individual that initiated the divorce was likely to increase its reproductive success in the year following a divorce.

The single-female model of McNamara & Forslund (1996) described the pattern of divorce over the focal individual's life. They showed that the probability of an individual divorcing declines with increasing age. In this single-female model, males never divorce and so results do not depend on the quality of the focal female. This limitation no longer applies in our ESS model and so we are able to investigate whether patterns with age are different for individuals of different quality. We also look at how the changing divorce rate affects the pattern of mate quality and reproductive success through the lifetime of individuals. These issues are investigated for our baseline model and for a number of variants on it.

In the baseline case, the qualities of the individuals in a pair contribute to the reproductive success additively. Other interactions between male and female quality are also analysed. It is possible that the reproductive success of a pair may depend primarily on the quality of the best member of a pair. Alternatively, the qualities of the members of a pair may interact positively, so that the reproductive success of a pair of high quality birds is much greater than that of a pair consisting of one high-quality bird and one mid-quality bird. We also explore different forms of divorce costs. In the baseline model costs of divorce result in a fixed reduction in reproductive success in the year following divorce. Quality-dependent costs are also examined.

We do not explicitly model the details of how an unpaired bird chooses its mate from the pool of single birds. However, we allow for the possibility that this process leads to the formation of pairs where the qualities of the male and female are positively correlated. Such assortative pairing is expected to reduce the population divorce rate, as individuals should find suitable partners after fewer divorces of unsuitable ones. We explore the effect of assortative pairing on individual decisions and on population divorce rates.

Assortative pairing leads to a positive correlation in the quality of individuals within a breeding pair. But even when there is random pairing, the divorce strategy of population members can lead to such a positive correlation. We investigate how the correlation of quality depends on model parameters.

2. THE MODEL

Each male in a population is characterized by a measure of quality (usually denoted by x) which he keeps throughout life. Similarly each female has a quality measure (usually denoted by y), which she keeps through life. Our analysis is mainly focused on a baseline case in which male and female qualities are (approximately) normally distributed with means μ_{m} and μ_{f} and variances σ^2_{m} and σ^2_{f} respectively.

There are equal numbers of males and females within the breeding population. This population is large and of constant size. During winter, each population member dies with probability $1-s$ independently of other population members, the quality and age of the individual, and whether the individual has a mate. Each bird that dies is replaced by another of the same sex and quality which is entering the breeding population for the first time.

As in McNamara & Forslund (1996) the annual cycle is divided into four distinct non-overlapping phases: (i) winter, when mortality occurs; (ii) pairing, when any unpaired birds obtain a mate; (iii) breeding; and (iv) divorce or mate retention, when the breeding pair may or may not split up. Winter mortality has already been discussed. Details of the other phases are as follows.

(a) *Pairing*

At the end of winter an individual may be single for one of three reason: (i) it is breeding for the first time; (ii) it is divorced from its partner after the last breeding season; or (iii) it bred last season and no divorce occurred, but the mate died over the winter.

All single population members enter a pairing pool. By virtue of the assumptions we have made, this pool contains equal numbers of males and females. However, because divorce of a pair may depend on the qualities of both partners (see below), the distribution of qualities within the pairing pool need not be the same as in the population as a whole. During pairing, all individuals pair up with a member of the opposite sex and subsequently breed with this partner. The degree of assortative pairing is described by a parameter $\rho (\rho \geqslant 0)$. To obtain pairing that is assortative by quality, the distribution of qualities within each sex is transformed to have a normal distribution (Appendix A). Pairs are then formed with the rescaled qualities of pair members having a bivariate normal distribution with correlation coefficient ρ. Qualities of pair members are then scaled back to their true values. This gives a correlation coefficient of true qualities in pairs which is close to ρ. The case $\rho = 0$ corresponds to random pairing within the pairing pool.

(b) *Breeding*

Suppose that a male of quality x and a female of quality y breed together. The reproductive success of the pair depends on the quality of both partners. Since repairing may be energetically costly and can lead to late breeding, reproductive success also depends on whether the pair have bred before. Let $r_0(x,y)$ denote the success of the pair on first breeding and $r(x,y)$ the success on subsequent breeding. We assume that $r_0(x,y)$ and $r(x,y)$ are increasing functions of both x and y. We also assume that $r_0(x,y) \leqslant r(x,y)$.

In our baseline model we take

$$r_0(x,y) = x + y - c, \tag{1}$$

where $c \geqslant 0$, and

$$r(x,y) = x + y. \tag{2}$$

For this form of r_0 and r the reduction in reproductive success on first breeding, c, does not depend on the qualities of pair members. The constant c can thus be regarded as the cost of divorce.

Almost all computations which assume the baseline model take $\mu_m = \mu_f$ $(= \mu$, say). Without costs, the mean reproductive success in the population in a breeding season is then 2μ. Since the units in which reproductive success is measured is irrelevant, we shall quote costs as the percentage reduction in mean success $100 \times c/2\mu$. Also, variation in quality will be given in terms of the ratio of standard deviation to the mean success of a pair. Thus variation in female quality is given as $\sigma_f/2\mu$ and represents the component of the coefficient of variation in reproductive success due to variation in female quality.

(c) *Divorce*

Each population member has full knowledge of their own quality. After breeding, each individual also knows the quality of their mate. The female then decides, on the basis of her quality and that of the male, whether to initiate divorce of the pair. Similarly, the male decides, on the basis of his quality and that of the female, whether to initiate divorce. If either or both initiate divorce, the pair splits up. Provided they survive the winter, recently divorced individuals then enter the pairing pool. If neither partner initiates divorce the pair remains together. Provided both pairs members survive the winter they then breed together in the following year. If there is no divorce, but one of the pair dies during the winter, the other pair member enters the pairing pool after winter.

(d) *Optimization criterion*

The optimization criterion adopted is maximization of total lifetime reproductive success.

A divorce strategy is a rule that specifies whether or not to initiate divorce. This is a contingent rule specifying how behaviour depends on the sex and quality of the focal bird and on the quality of its current mate. If (almost) all members of the population adopt a particular strategy, this strategy will be referred to as the resident population strategy. Given a resident population strategy, π, there is a unique strategy, $B(\pi)$, which we refer to as the best response to π. This best response has the property that, whatever the sex and quality of a single 'mutant' individual within the population, the mutant does best by following strategy $B(\pi)$. Here we are interested in an ESS. An ESS strategy π^* must necessarily satisfy $B(\pi^*) = \pi^*$. The equations satisfied by an ESS strategy are given in Appendix A.

The dynamic game outlined above is too complex to solve analytically, and must be solved by numerical computation. Whatever the form of r_0, r, the distributions of qualities, and the value of ρ, the computational procedure outlined in Appendix B has always enabled us to find a solution to the ESS equations given in Appendix A. This suggests that an ESS may always exist.

Suppose that mating is random $(\rho = 0)$ and that the functions r_0 and r are given by equations (1) and (2), respectively. Then the methods used by McNamara & Collins (1990) can be used to show that the divorce strategy given by equations (A1*a*)–(A1*g*) of Appendix A is unique for a given composition of the pairing pool. However, since the composition of the pairing pool is determined by the solution to equations (A1*a*)–(A1*g*) this does not logically imply that the ESS is unique, even in this simple case. To investigate uniqueness we have computed ESS's using different starting distributions for the iterative procedure described in Appendix B. In all cases that we have investigated, the ESS obtained is independent of the starting distribution. This tentatively suggests that for given ρ, r_0, r and the distributions of qualities, the ESS is unique.

3. THE FORM OF THE ESS STRATEGY

Suppose that population members are following a particular ESS strategy. Within this population let

$$R_m(x) = E\{\text{annual reproductive success of a male of quality } x\},$$

be the mean annual reproductive success of a male of quality x averaged over the male's lifetime. Then a male of quality x which has bred with a female of quality y will initiate divorce if

$$r(x,y) < R_m(x) \tag{3}$$

try to keep his mate if

$$r(x,y) > R_m(x). \tag{4}$$

This result follows from the analysis of McNamara & Forslund (1996, Appendix A). Condition (3) says that the male should initiate divorce if the reproductive success on next breeding with the female is less than the mean annual reproductive success of the male. Since $r(x,y)$ is a strictly increasing function of y for fixed x there is a unique $y^*(x)$ such that

$$r(x,y^*(x)) = R_m(x). \tag{5}$$

Conditions (3) and (4) can then be reformulated as

if $y < y^*(x)$ a male (x) initiates divorce of a female (y) (6)

if $y > y^*(x)$ a male (x) attempts to keep a female (y). (7)

We will refer to $y^*(x)$ as the acceptance threshold of a male of quality x. (When $y = y^*(x)$ the pay-off to the male for mate retention is the same as the pay-off for divorce. In describing the logic of the ESS it is convenient to describe the male's action as one of mate retention when $y = y^*(x)$. This is not, however, what is assumed in computations, where small errors in decision making are introduced to avoid grid effects (see Appendix B).)

In a similar way we can define

$$R_f(y) = E\{\text{annual reproductive success of a female of quality } y\}.$$

Then a female of quality y initiates divorce of a male of quality x if $r(x,y) < R_f(y)$. Thus if we define $x^*(y)$ by $r(x^*(y),y) = R_f(y)$ the female initiates divorce if $x < x^*(y)$; and $x^*(y)$ is the acceptance threshold of the female.

Suppose a male of quality x mates with a female of quality y, then after breeding there are four possible scenarios.

(i) $x < x^*(y)$ and $y < y^*(x)$. Then both partners will initiate divorce and the pair will divorce.
(ii) $x < x^*(y)$ and $y \geqslant y^*(x)$. Then the female will initiate divorce, but the male will not wish to divorce. The outcome will be divorce of the pair.
(iii) $x \geqslant x^*(y)$ and $y < y^*(x)$. Then the female will not wish to divorce, but the male will initiate divorce and the pair will divorce.
(iv) $x \geqslant x^*(y)$ and $y \geqslant y^*(x)$. Only in this case will both partners wish to keep their mate and the pair will remain together.

Figure 1 illustrates the ESS strategy and these four scenarios.

(a) *The ESS strategy in the baseline case*

Suppose that r_0 and r are given by equations (1) and (2), respectively, and consider first the case $\rho = 0$. Then the arguments of McNamara & Collins (1990) can be adapted to show that $x^*(y)$ must be a non-decreasing function of y and $y^*(x)$ must be a non-decreasing function of x. In other words, as the quality of an individual increases, so does its acceptance threshold. These conclusions, and the block structure of strategies described below, hold regardless of whether or not quality distributions are normally distributed.

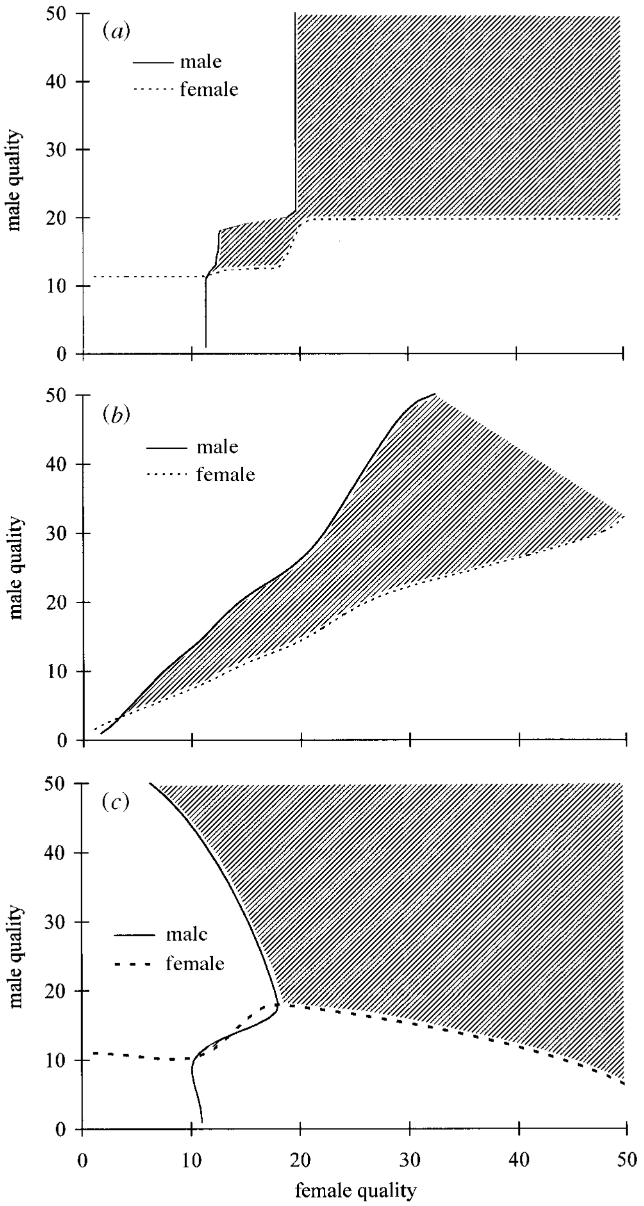

Figure 1. The ESS divorce strategy. A female will divorce her partner after breeding unless his quality exceeds her acceptance threshold (dashed line). Similarly a male will divorce his partner unless her quality exceeds his acceptance threshold (solid line). The shaded area thus shows the combinations of female and male qualities for which the pair will stay together after breeding. (*a*) Baseline model with random pairing ($\rho = 0$). (*b*) Baseline model with $\rho = 0.4$. (*c*) Reproductive success of a pair given by equation (9), $\rho = 0$. In all cases survival probability $s = 0.75$, cost = 25%, variation $\sigma_m/2\mu = \sigma_f/2\mu = 0.2$.

Individuals with qualities below the acceptance thresholds of all members of the opposite sex will always be divorced after breeding (in figure 1*a* individuals of quality below 13 always divorce). At the other extreme, there will be individuals whose quality exceeds the acceptance threshold of all members of the opposite sex (in figure 1*a*

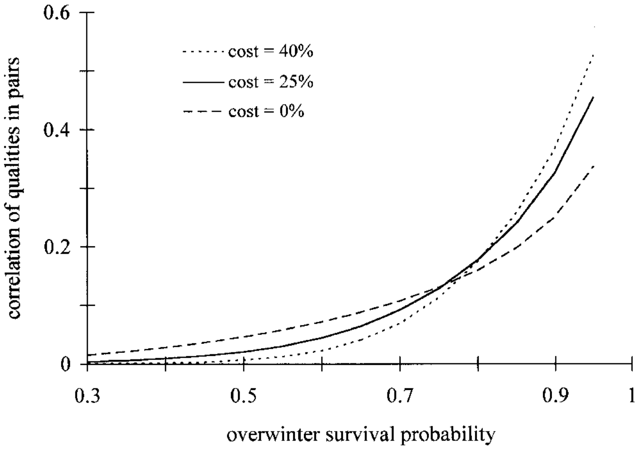

Figure 2. Correlation between male and female qualities in breeding pairs. Baseline model with $\sigma_m/2\mu = \sigma_f/2\mu = 0.2$ and random pairing ($\rho = 0$).

individuals of quality of 20 or above satisfy this criterion). Such individuals will only divorce if they initiate divorce. Individuals of intermediate quality will form stable pair bonds only with partners within a restricted range of qualities. For given male quality x let $\hat{y}(x)$ be the minimum value of y for which $x^*(y) > x$. Then a male of this quality will form a stable pair bond with his mate if and only if her quality, y, lies in the range $y^*(x) \leqslant y < \hat{y}(x)$. A similar result holds for females. Since $y^*(x)$ and $\hat{y}(x)$ are monotonic increasing functions of x there will be a positive correlation between the values for x and y of male and female qualities respectively for which stable pair bonds exists (figure 1*a*).

The region of the (x,y) plane where stable pair bonds occur takes the form of a block-like structure due to the acceptance thresholds being step-like functions of quality (figure 1*a*). The block-like structures occur for the same reason as the block structures obtained by McNamara & Collins (1990) for mutual mate choice, and can be understood as follows. A male of high quality is always accepted by all females. He can therefore be very choosy and accept only females of high quality. Females of high quality apply the same strategy. High-quality males and females therefore form stable pair bonds only with each other. If the quality of the male is somewhat lower, he will not be accepted by females of highest quality. However, he will be accepted by females of somewhat lower quality because these females cannot expect to be accepted by males of highest quality and, thus, have to suffice with males of lower quality. This forms the next 'step' in the acceptance threshold curve, and so on. The equivalent process applies to male acceptance thresholds, and the result is the formation of block structures within which stable pair bonds are formed. Males and females of lowest quality will, on the other hand, never be accepted as long-term mates and therefore always divorce (figure 1*a*). At present, it is not clear whether there is any biological relevance to the block structures.

When assortative pairing is introduced into the baseline model ($\rho > 0$), in all computations we have carried out, once acceptance thresholds are above zero they are strictly increasing functions of quality. Since acceptance thresholds are now much smoother than when $\rho = 0$ the block structure disappears (figure 1*b*).

(b) *The ESS strategy for other forms of* r_0 *and* r

In the baseline case r_0 and r are given by equations (1) and (2) respectively. The reproductive success of a male of quality x can then be decomposed into the sum of a component, x, due explicitly to his quality and which is independent of the male's divorce behaviour, and components y and c, which depend on mate quality and costs of repairings. Thus when $\rho = 0$, changes in the threshold $y^*(x)$ with male quality x are solely due to the fact that the divorce behaviour of females depends on the quality of their mates. When $\rho > 0$ in the baseline model, the male acceptance threshold also increases with male quality because quality of mates increases with male quality.

In general, however, one might not expect the reproductive success of a male to be decomposable into the sum of a component due solely to his own quality and a component due solely to mate quality and re-pairing costs. For example, if r is taken to be

$$r(x,y) = (x^{\frac{1}{2}} + y^{\frac{1}{2}})^2, \tag{8}$$

then $\partial^2 r/\partial x \partial y > 0$ for all x and y. Thus there is a positive interaction between qualities within a breeding pair, and a given increase in female quality y increases the reproductive success of a high-quality male more than that of a low-quality male. As a consequence, when $\rho = 0$ and $r_0(x,y) = r(x,y) - c$, males of high quality are more choosy than males of low quality. Thus $y^*(x)$ tends to always increase with male quality x. A similar remark holds for females. The resultant ESS still has a block structure but acceptance thresholds are smoother than in the baseline case with $\rho = 0$.

In contrast to the above case, when

$$r(x,y) = (x^2 + y^2)^{\frac{1}{2}}, \tag{9}$$

$\partial^2 r/\partial x \partial y < 0$ for all x and y. A given increase in female quality thus increases the reproductive success of a low-quality male more than a high-quality male. High-quality individuals are thus less choosy than low-quality individuals and this can result in a decrease in acceptance threshold with quality (figure 1*c*). One consequence is that a low-quality individual may be divorced by an intermediate quality mate but not by a high-quality mate.

Suppose we take r to be given by equation (2), but assume that

$$r_0(x,y) = \alpha(x + y), \tag{10}$$

where $\alpha < 1$. Then the cost of divorce to an individual increases with the quality of that individual. Computations show that at the ESS, acceptance thresholds may now decrease with quality over certain ranges of quality. This can again result in a low-quality individual being divorced by an intermediate quality partner but not by a high-quality partner.

(c) *Quality correlations in breeding pairs*

Because choosiness tends to increase with increasing quality in the baseline case, there is a positive correlation between male and female quality in those breeding pairs that form permanent pair bonds. Even in the absence of assortative pairing this leads to a positive correlation in the qualities of males and females in breeding pairs as a

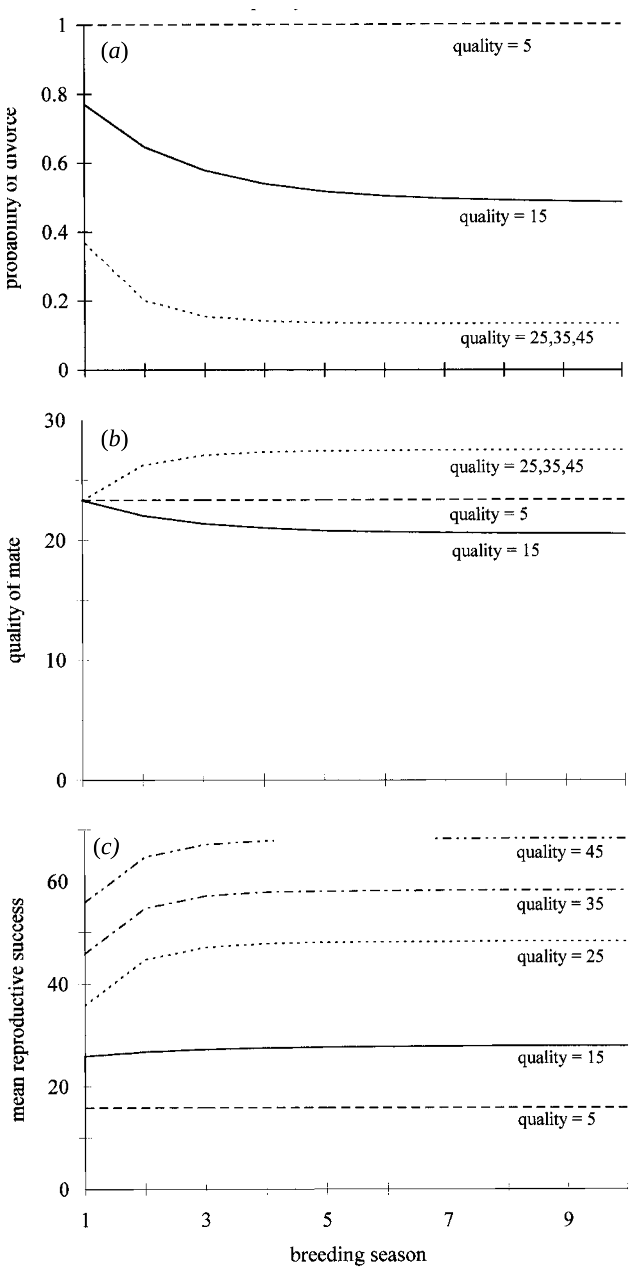

Figure 3. Dependence of various quantities on the number of times a bird has bred, shown for birds of different quality. (*a*) Probability of divorce after breeding. (*b*) Mean quality of mate. (*c*) Mean reproductive success. Baseline model with $s = 0.75$, cost = 25%, $\sigma_{\rm m}/2\mu = \sigma_{\rm f}/2\mu = 0.2$ and $\rho = 0$.

whole (figure 2). Increasing survival rates leads to greater choosiness (McNamara & Forslund, 1996) and hence to a higher correlation of qualities in pairs that form permanent bonds. It takes longer for choosy individuals to enter a stable pair bond, but this is more than offset by the fact that increased survivorship means the pairing lasts longer. The result is that the correlation of qualities in breeding pairs as a whole increases with survival rates (figure 2).

Under assortative pairing the correlation between qualities in breeding pairs increases as the degree of assortative pairing (ρ) increases. The difference between the breeding correlation and the pairing correlation ρ represents the effect of divorce and remating. As when there is random pairing this effect is strongest for long-lived species.

In some cases in which acceptance thresholds decrease with quality, one can obtain a negative correlation between qualities in breeding pairs. In particular, one can find cases of negative correlations when r is given by equation (9) and $r_0 = r - c$, or when r is given by equation (2) and r_0 by equation (10).

4. DYNAMICS OVER AN INDIVIDUAL'S LIFETIME

In our model, the qualities of the members of a breeding pair do not change with age. Since acceptance thresholds are also independent of age, a breeding pair either divorce after breeding for the first time or remain together until one partner dies.

Suppose that a male of quality x is single. The male will then pair and breed with a female from the mating pool. Let $Q_{\rm m}(x)$ be the probability that the pair divorce after breeding. Since either sex can initiate the divorce

$$Q_{\rm m}(x) = P(\Upsilon_x < y^*(x) \quad \text{or} \quad x < x^*(\Upsilon_x)) \qquad (11)$$

where the random variable Υ_x denotes the quality of the female that a male of quality x pairs with. Similarly define $Q_{\rm f}(y)$ as the probability a female of quality y divorces after first breeding.

Now consider an individual (of either sex) that has probability Q of divorce after first breeding with a new mate. The dynamics of divorce over the lifetime of this individual are as in McNamara & Forslund (1996). On average there are $Q/(1-Q)$ divorces before the individual forms a stable pair bond with its partner. The pair remain together until one of the pair members dies. If it is the partner who dies, the focal individual is in exactly the same situation as it was before first breeding and the process of finding a partner with whom to establish a stable pair bond starts all over again.

Averaging over what could happen to the above focal individual, McNamara & Forslund (1996) show that the probability of divorce after breeding for the nth time is

$$d_n = \left(\frac{1}{1-Qs}\right)[(1-Q)(Qs)^n + Q(1-s)]. \qquad (12)$$

Instead of interpreting d_n in terms of a single individual, it is perhaps more instructive to interpret it in population terms. Consider all males of quality x which are breeding for the nth time. Then the proportion of these individuals which divorce is given by d_n where Q is taken to be $Q_{\rm m}(x)$ in equation (12).

By equation (12) d_n is decreasing in n (provided $Q < 1$) and tends to a lower limit. Decreasing Q for given s increases the initial rate of decline as well as decreasing d_n for every n. As we discuss below it is a robust computational result that among members of a given sex, Q decreases with increasing quality. It follows that within a given sex in a population, the divorce rate among high-quality individuals declines faster with age and to a lower level than the divorce rate among lower quality individuals (figure 3*a*). The lowest quality individuals may divorce every year ($Q = 1$) (figure 3*a*).

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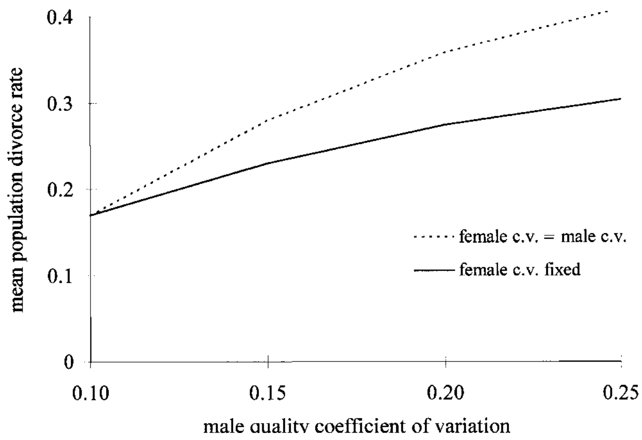

Figure 4. Mean population divorce rate as a function of quality variation within the population. Male coefficient of variation is $\sigma_m/2\mu$. The solid line is for female quality variation fixed ($\sigma_f/2\mu = 0.1$). The dashed line is for $\sigma_f/2\mu = \sigma_m/2\mu$.

(a) *Mate quality and reproductive success*

To analyse systematic changes in mate quality over an individual's lifetime, consider first an individual whose quality lies above the acceptance threshold of all members of the opposite sex. Such a high-quality individual will only divorce if he or she initiates the divorce, and will form a stable pair bond with the first partner whose quality exceeds his or her acceptance threshold. Thus, all partners divorced before the stable bond is formed have lower quality than the partner with whom the individual forms a stable bond. As a result of this process the mean quality of his or her partner increases over the lifetime of the focal individual (figure 3*b*). (See McNamara & Forslund (1996) for further illustration of this effect.) If the quality of an individual is so low that he or she always divorces, mean partner quality is independent of age and equals the mean quality of partners obtained from the pool.

Finally, consider an individual that is below average quality, but is acceptable to some partners. When there are costs, such an individual only initiates divorce with the very lowest-quality partners. The individual is, however, actively divorced by most partners from the pairing pool, and only forms a stable pair bond with a partner of similar quality. Thus, the individual will usually be actively divorced by a succession of partners until he or she obtains a partner of sufficiently low (but not too low) quality. The partner with which the stable bond is formed will tend to be of lower quality than previous partners who were divorced. Consequently, the mean quality of the partner of the focal individual will decrease over the lifetime of the focal individual (figure 3*b*).

Regardless of the trend in partner quality, if an individual can form any stable pair bond, his or her mean reproductive success on breeding must increase with age (figure 3*c*). This is because stable pair bonds are only formed if they increase mean reproductive success over the rest of the lifetime (see Appendix C for details).

When there are costs, the mean quality of partners of an individual of very low quality may be greater than the mean quality of partners of a slightly higher-quality individual (figure 3*b*). Despite this, the higher-quality individual has higher mean reproductive success over its lifetime, partly because of the contribution of its own quality to breeding success, but also because it tends to divorce, and hence pay the cost of divorce, less often (see below).

Table 1. *Comparison of mean population divorce rates for three scenarios: female-only choice and a fixed pool of unpaired males; female-only choice with the distribution of male qualities in the pool determined by female behaviour; the full ESS model with both male and female choice and the distribution of both male and female qualities in the pool generated by population behaviour*

(Baseline model with $\sigma_m/2\mu = \sigma_f/2\mu = 0.2$, $\rho = 0$.)

survival probability	cost	female only: fixed pool	female only: free pool	male and female
0.50	0	47.6	50.0	75.5
	10	31.5	33.7	56.0
	25	14.1	15.9	28.5
	50	2.0	2.4	4.7
0.75	0	43.4	50.0	74.6
	10	31.1	37.2	57.5
	25	18.6	23.6	35.7
	50	7.1	10.4	16.0
0.90	0	37.4	50.0	70.0
	10	28.9	39.9	53.3
	25	20.6	29.5	34.8
	50	12.2	19.2	20.0

5. POPULATION DIVORCE RATES

The mean divorce rate within a population is taken to be the proportion of breeding pairs that divorce immediately after breeding. The effect of longevity, costs of divorce and variation in quality among individuals on this mean population divorce rate are qualitatively the same in the present ESS model as in the optimization model of McNamara & Forslund (1996). With no costs of divorce, mean population divorce rates decrease with increasing longevity, although the decline is not always as marked as in the optimization model (table 1). Costs of divorce, in terms of reduced reproductive success at the first breeding of a pair, dramatically decrease mean divorce rates in short-lived species, but long-lived species are less affected (table 1). Mean population divorce rates increase with increasing variation (within the population) in quality among either males or females or both (figure 4).

Assortative pairing, i.e. a higher probability than random that a male and female of similar quality will form a new pair bond, leads to lower mean population divorce rates than random pairing. The higher the degree of assortative pairing, the lower the mean divorce rate (figure 5). As the correlation in quality among new pair bonds, ρ, is increased, the variation in mate quality experienced by an individual of given quality is reduced. The individual should thus become less choosy and hence less likely to divorce (cf. McNamara & Forslund 1996). The reduction in mean divorce rate with

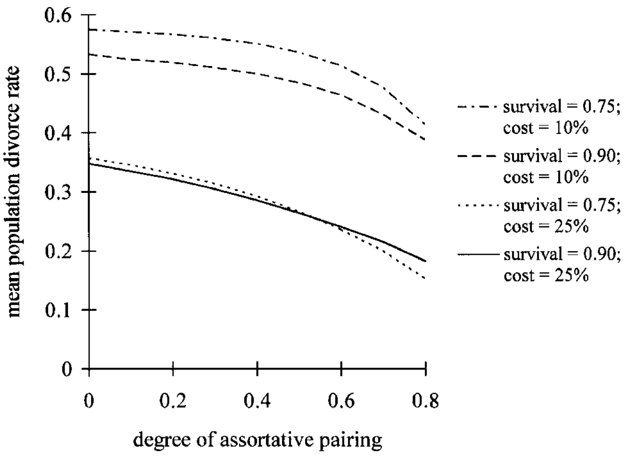

Figure 5. Mean population divorce rate as a function of the degree, ρ, to which pairing of single individuals is assortative in quality. Baseline model with $\sigma_m/2\mu = \sigma_f/2\mu = 0.2$.

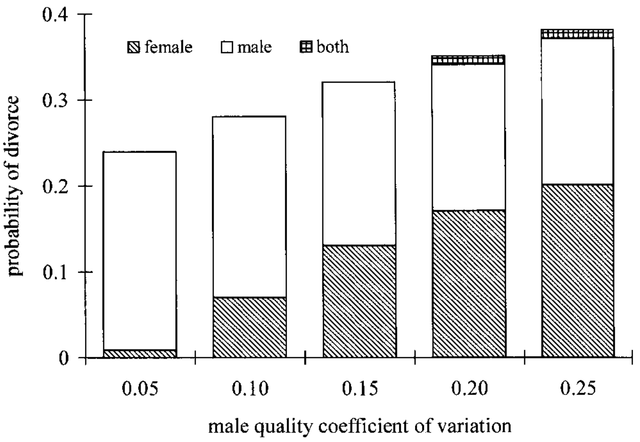

Figure 6. The probabilities that after breeding: both partners initiate divorce; the male alone initiates divorce; the female alone initiates divorce. The figure shows the effect of increasing the coefficient of variation in male quality $\sigma_m/2\mu$, while hold the coefficient of variation in female quality fixed at $\sigma_f/2\mu = 0.2$. Baseline model with $s = 0.75$, cost = 25%, $\rho = 0$.

increasing ρ is in good agreement with that obtained by reducing the quality variation in the population as a whole by the appropriate amount and assuming random pairing.

Although the present ESS model and the optimization model of McNamara & Forslund (1996) make similar qualitative predictions on the effects of parameters, mean population divorce rates are typically higher in the ESS model with random pairing than in the optimization model. To understand these differences we compare the results of three different models. In the present ESS model, both males and females can initiate divorce and the distribution of qualities of individuals in the pairing pool is generated by the behaviour of the whole population. One can also consider a game theoretical model in which males are not allowed to initiate divorce but the distribution of individuals in the pairing pool is generated by the behaviour of the whole population. This model is intermediate between the full ESS model and the optimization model of McNamara & Forslund in which males are not allowed to initiate divorce and the distribution of male qualities obtained by a female on re-pairing is taken to be fixed and equal to the distribution of male qualities in the population as a whole. As table 1 shows, when males are not allowed to initiate divorce, allowing the remating pool to be generated by the behaviour of the population results in a slight increase in the divorce rate.

When the pairing pool is generated by the behaviour of population members, the divorce rate is higher when both sexes can initiate divorce than when only one sex (females) initiate divorce (table 1). When both sexes can initiate divorce, one can break down the mean divorce rate as the sum of the proportion of breeding pairs where the female decides to divorce and the proportion of pairs where the female does not wish to divorce but the male does. There is therefore an additional source of divorce when males may also initiate divorce. However, the greater the probability that a female will be divorced by her mate, the less choosy the female should be (McNamara & Forslund 1996). This means that divorce of the male by the female is less common when both sexes make decisions than when only females initiate divorce. To give an example, at an annual survival of 0.75, a cost of divorce percentage of $100 \times c/2\mu = 25\%$ and a standard deviation in quality of $\sigma_m/2\mu = \sigma_f/2\mu = 0.2$, the divorce rate is 23.6% when only females initiate divorce (table 1). When both sexes can initiate divorce, the female divorces the male in 18.3% of breeding pairs. The mean divorce rate is nevertheless higher in this latter case since in 17.4% of breeding pairs the female does not want to divorce but the male does.

(a) *Initiator of divorce*

The previous optimization model (McNamara & Forslund 1996) and the present models show that the choosiness of individuals increases when the variation in quality of potential mates increases. In the case where both sexes make divorce decisions, the variation in quality of one sex may influence the degree to which members of both sexes initiate divorce or become the victim of divorce. We analysed this by varying the relative amount of variation in male quality, and looking at which sex initiated divorce. Figure 6 shows, as expected, that males initiate the majority of divorces when the variation in quality is larger in females than in males, and vice versa. The figure also shows that, as male quality variation increases and divorce initiated by the female becomes more frequent, males tend to initiate divorce less often (cf. McNamara & Forslund 1996).

The choosiness of an individual will also depend on the relative contribution of the individual's mate to the reproductive success of the pair. In the baseline model, the quality of each member of a pair contributes additively to the pair's reproductive success. Decreasing the relative importance of the male's quality in determining the reproductive success of a pair increases the choosiness of males in the population and decreases the choosiness of the females. When the quality of the male contributes little to the reproductive success of a pair, the majority of divorces are initiated by the male. Reducing male contribution to reproductive success is therefore similar in effect to decreasing male quality variation.

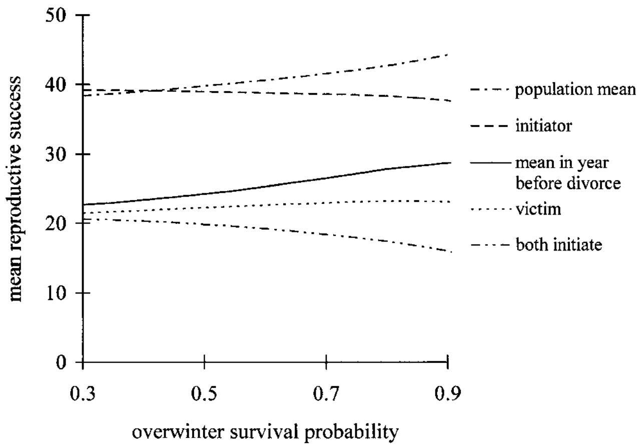

Figure 7. Reproductive success of divorcing birds before divorce and after divorce. Those birds that have divorced are broken down into those birds that alone initiated the divorce, those that did not initiate but were divorced by their partner (victims) and those where divorce was initiated by both partners. The mean population reproductive success is shown for comparison. Baseline model with $\sigma_{\mathrm{m}}/2\mu = \sigma_{\mathrm{f}}/2\mu = 0.2$, cost = 25%, $\rho = 0$.

(b) *Reproductive success following divorce*

Ens *et al.* (1993) predicted that initiators of divorce should increase their reproductive success after divorce, while victims should decrease their reproductive success. Figure 7 confirms this prediction; initiators of divorce will on average have a higher reproductive success the first year following a divorce as compared to before divorce, while victims on average will get lower reproductive success. An initiator will on average increase in reproductive success because its new mate is likely to be of higher quality, that is closer to average quality due to random pairing than the previous mate (the victim), which probably will be of lower-than-average quality. The reproductive success of a victim will decrease because its new mate is likely to be of lower quality, again closer to average quality, than the previous mate (the initiator), which probably is of higher-than-average quality. Individuals in pairs where both mates initiate divorce have the lowest reproductive success of all categories in the year following divorce (figure 7). The reason for this is that such individuals are of very low quality, which is evident from the fact that they are rejected by their low-quality mates. Although not shown in figure 7, these individuals will on average increase their reproductive success after divorce, since they are likely to get a new mate of higher quality, that is, closer to average quality (see above). The results reported on here are valid for all longevities investigated (figure 7).

6. DEPENDENCE OF DIVORCE RATE ON QUALITY

Let Q be the probability that an individual divorces after the first breeding (cf. equation (11)). We have already seen that Q determines how the probability of divorce depends on the number of times the individual has bred (equation (12)). Thus Q also determines the mean divorce rate of an individual over its lifetime. An increase in Q is equivalent to an increase in divorce probability at all ages and is equivalent to an increase in the mean lifetime divorce rate. Thus in analysing the dependence of divorce on quality, various equivalent measures are possible. We choose to use the mean annual divorce rate averaged across an individual's lifetime as our measure.

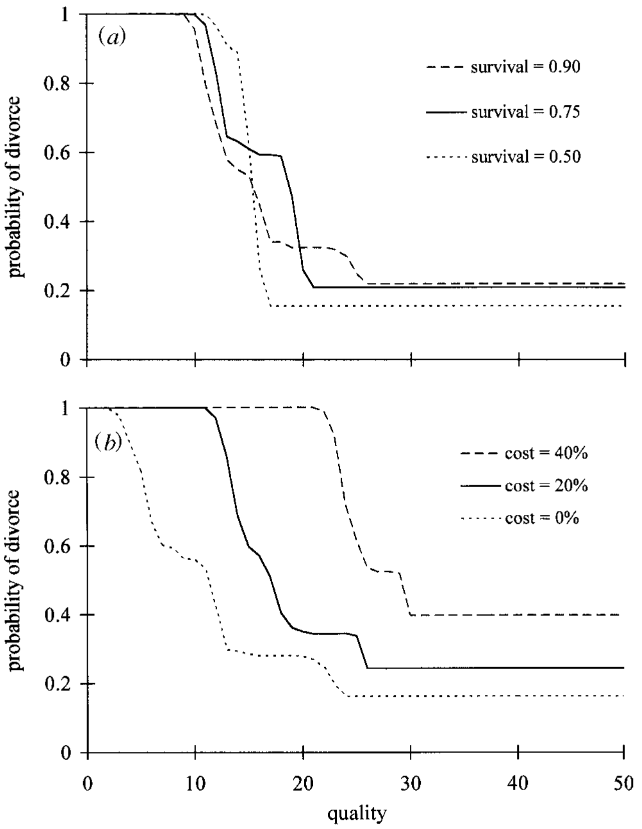

Figure 8. Mean annual probability of divorce as a function of quality. (*a*) Effect of survival probability, s (cost = 25%). (*b*) Effect of cost ($s = 0.9$). Baseline model with $\sigma_{\mathrm{m}}/2\mu = \sigma_{\mathrm{f}}/2\mu = 0.2$, $\rho = 0$.

(a) *Dependence on quality in the baseline model*

In the baseline model, an individual is more choosy than another individual of lower quality, but is itself divorced by less of the population. It is thus not *a priori* clear whether divorce rates should increase or decrease with increasing quality. Figure 8 shows an example in which divorce rate declines with increasing quality. Extensive computations suggest this is a robust conclusion, although we have not shown it analytically.

In short-lived species, acceptance thresholds are similar in all population members. Thus as quality increases within a sex, there is a sharp transition from individuals being rejected by all population members to individuals being accepted by all population members (figure 8*a*). The point of transition decreases rapidly as costs increase.

In long-lived species, there is a much greater increase of acceptance thresholds with increasing quality than in short-lived species. Consequently, the decline in divorce rate with quality is less abrupt (figure 8*a*). Increasing ρ leads to smoother acceptance thresholds and so the decline in divorce rate with quality is also smoother. An increase in divorce costs reduces the acceptance thresholds of high-quality individuals less than it reduces the accceptance thresholds of low-quality individuals. The resultant effects on the divorce rates of individuals is shown in figure 8*b*. Costs and survival have the same qualitative effects on divorce rates of individuals for all forms of r and r_0 investigated.

Reducing the quality variation of individuals in the population has a similar effect on the divorce rates of individuals as reducing survival. The transition from individuals being rejected by all members of the population to individuals being accepted by all members of the population is sharper when quality variation is low.

(b) *Qualities within the pairing pool*

Provided that the degree of assortative mating is not too high and costs are not extreme, individuals of very low quality are always divorced after breeding (e.g. figure 1*a*). They therefpre return to the pairing pool each year. Consequently, the distribution of qualities of each sex in the pairing pool is skewed towards low quality compared to the distribution of qualities of that sex in the population as a whole.

A second phenomenon adds to this skew. Among individuals of higher quality which do form stable pair bonds with a suitable partner, the mean time to find such a partner tends to decrease with increasing quality (see above). As a consequence, the mean proportion of a bird's life spent in the pairing pool decreases with increasing quality of the bird.

7. DISCUSSION

We investigated how individual divorce strategies and population divorce rates were affected by longevity, variation in quality among individuals, cost associated with finding a new mate, assortative pairing, and different interactions between males and females regarding their contributions to reproductive success. A basic assumption was that individuals make strategic decisions on whether or not to divorce a breeding partner. This decision problem is game theoretical. An individual's best decision depends on which members of the opposite sex would divorce it. It also depends on the availability of potential new partners. Since the composition of the pool of potential partners is itself dependent on the divorce decisions made by all individuals in the population, an individual's best divorce strategy is dependent on the strategies adopted by all individuals in the population. Our predictions are based on the assumption that the population follows the ESS for this game-theoretical problem.

In general, when both males and females made divorce decisions, individuals of high quality were more choosy about the quality of mates than were individuals of lower quality. Low-quality individuals were always divorced by their mates, whereas high quality individuals were always accepted by their mates. Individuals of intermediate quality would accept and were accepted by individuals of similar quality. These findings agree with those of McNamara & Collins (1990) and Johnstone *et al.* (1996), who investigated the related game-theoretical problem of mutual mate choice. There were, however, some deviations from the general pattern of assortative breeding found in the mate choice models, particularly for certain kinds of costs of divorce (relative costs rather than absolute costs) and when the qualities of the partners in a breeding pair did not contribute additively to the reproductive success of the pair.

(a) *Individual divorce strategies*

The tendency for pairs of males and females of similar quality to remain together resulted in a positive correlation between the quality of the male and the quality of the female within breeding pairs. This positive correlation occurred even when pairing of single individuals before breeding was at random, although the correlation was higher when there was assortative mate choice prior to breeding. A consequence of an increase in the correlation was an increase in the lifetime reproductive success of high-quality individuals, as they do not waste breeding opportunities breeding with low-quality individuals. On the other hand, low-quality individuals get lower lifetime reproductive success, because they seldom breed with high-quality individuals. These effects were most pronounced in long-lived species. It was also a robust conclusion of our baseline model that high-quality individuals divorce less often than low-quality individuals. This effect also increased the lifetime reproductive success of high-quality individuals relative to low-quality individuals as the latter paid the cost of divorce more often.

McNamara & Forslund (1996) found an increase of reproductive success with age. In the current model, apart from the lowest-quality individuals, which were always divorced by their partners, the probability an individual changed its mate after breeding decreased over its lifetime. Consequently, mean reproductive success increased with age in all but the lowest-quality individuals. This, therefore, supports the idea of McNamara & Forslund that divorce may be a new explanation for the age-related increase in reproductive success observed in many bird species (Clutton-Brock 1988; Newton 1989; Saether 1990; Forslund & Pärt 1995). However, this can only hold for species that repeatedly breed and divorce before forming a stable bond for several years (see the discussion in McNamara & Forslund (1996)).

As a baseline case, we assumed that the contributions of male and female qualities to reproductive success were additive. Introducing other interactions of male and female qualities could radically change divorce strategies. A positive interaction led to high-quality individuals being even more choosy. On the other hand, if the reproductive success of low-quality individuals was more dependent than that of high-quality individuals on the quality of their mates, high-quality individuals were expected to be less choosy than low-quality individuals. This led some individuals to be divorced by low-quality partners while they were not divorced by high-quality partners, and could lead to a negative correlation of qualities within breeding pairs.

The types of quality interactions we modelled may occur in nature. A positive interaction is suggested in cases where care by both parents is a prerequisite for successful breeding. For example, in penguins the male and female in a pair alternate incubation. While one is incubating, the other is out in the sea foraging. It is very important that the foraging individual returns in time, otherwise the incubating bird has to abandon the egg due to starvation. This leads to breeding failure (Williams 1996). A larger dependence among low-quality individuals than among high-quality individuals on mate quality may occur if the pair needs a resource that cannot be acquired or defended by a low-quality pair member. One example of this may be territory defence in some birds. However, the question in this case is whether there are mutual divorce decisions.

Our model results supported the prediction by Ens *et al*. (1993) that the reproductive success of initiators of divorce should increase after divorce, and that the success of victims should decrease after divorce.

We found that the sex with the least variation in quality was the choosiest sex. This is not surprising, as it agrees with predictions from classic sexual selection theory (Andersson 1994). But our model showed that there is a continuum between divorce decisions by just one sex and mutual divorce decisions by both sexes. As the quality variation in one sex decreased, the other sex became less and less choosy. Furthermore, a decrease in choosiness by one sex increased the choosiness of the other sex, as individuals of this latter sex had greater control over whether or not divorce occurred. It may seem unrealistic to assume that there should be no quality variation in one sex. However, the important thing is how individuals of one sex experience the quality of individuals of the opposite sex. For example, stochastic environmental variation may mask individual quality (McNamara & Forslund 1996), or environmental factors may be of overriding importance for reproductive success.

(b) *Population divorce rates*

The effect of survival, costs of divorce and variation in quality among individuals were qualitatively the same as those of the single female model of McNamara & Forslund (1996). Long-lived individuals divorced less frequently than short-lived individuals and introducing costs of divorce dramatically decreased divorce in short-lived individuals but had little effect on long-lived individuals. Increasing the variation in quality of one or both sexes resulted in an increase in the population divorce rate. Assortative pairing reduced the population divorce rate. Quantitatively, allowing both sexes to make divorce decisions increased the divorce rates. This resulted from an increase in divorce due to males choosing to divorce, despite a reduction in female choosiness as the likelihood of her being divorced increased. Further, if the divorce decision of an individual was dependent on the distribution of qualities among available mates, and hence on the strategies of other individuals in the population, higher population divorce rates resulted.

Our present model and our previous single female model (McNamara & Forslund 1996) predict a number of factors to be important for population divorce rates. The next step is undoubtedly to test the predictions empirically in comparative studies. Ens *et al*. (1996) attempted to investigate the relationship between survival rate and divorce rate among species, but failed to find any clear relationships. Accounting (if possible) for the factors we have found to be of theoretical importance may be needed if we are to do this kind of comparison.

(c) *Future models*

This model is more complex than the previous optimization model of McNamara & Forslund (1996) and has allowed us to investigate new areas of the divorce decision. In the current ESS model the divorce problem is treated as a game-theoretical problem, which is an improvement on the optimization model. However, there are more games inextricably linked with the divorce game. In our model, assortative pairing is a black box in which pairs of similar qualities mate. In reality, assortative pairing is itself likely to be a game of males and females searching for high-quality mates. Even assuming individuals can accurately assess quality, members of a pair will not necessarily be perfect quality matches. Single individuals may not have sufficient time to locate the perfect partner before the start of the breeding season. There may be a trade-off between searching for a new mate and reduced reproductive success due to a cost of delayed breeding. Also, an individual that spends a long time searching for a mate will have fewer, and possibly poorer quality, potential mates to choose from, since those potential mates that have already formed stable bonds are no longer available (Collins & McNamara 1993; Johnstone 1997). This ties in with the divorce game in that if you are a low-quality individual there may be little advantage in spending time looking for a high-quality mate if that mate will then divorce you in the following year. There are likely to be other links between the divorce game and the pairing game. For example, increasing quality variation not only changes divorce strategies but will also increase the choosiness of individuals during pairing and hence increase the degree of assortative pairing (Johnstone *et al*. 1996).

There is also likely to be an effort game between members of a pair (Burley 1988). If a low-quality individual mates with a higher-quality mate, should the low-quality individual increase its effort in an attempt to retain the mate or should it put in less effort knowing it will be divorced anyway? Also, what should the good quality individual do in this situation? In our model, mate change occurred after each breeding season. If, instead, it occurred throughout the year (Ens *et al*. 1993), there may be a cost to the current year's reproductive success due to time spent searching for a new mate or to having to prevent a mate being taken by a competitor. These costs may be higher if the current mate reduces his or her effort in response.

In addition to focusing on the divorce game, we have made several other simplifying assumptions. In our model we have assumed an equal sex ratio and that mortality is independent of both sex and quality. Only one cost was considered; that of reduced reproductive success in the year following divorce. Other costs were considered in the single female model of McNamara & Forslund (1996). As in that model, we have assumed that an individual's quality is fixed throughout his or her life and that there is no increase in reproductive success with pair duration. Despite these simplifications the model is a useful step towards understanding the divorce decisions of birds.

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APPENDIX A. THE ESS EQUATIONS

Since computations are based on a discrete set of quality values (Appendix B) we describe the ESS equations in this case.

Let $r(x,y)$ be the reproductive success of a pair (x,y) on breeding provided they have bred before. Let $R(y)$ be the mean annual reproductive success of a female (y). Then the analysis in Appendix A of McNamara & Forslund (1996) can be used to show that a female (y) should initiate divorce agains a male (x) if and only if $r(x,y) < R_{\mathrm{f}}(y)$. Thus if $D_{\mathrm{f}}(x,y)$ is the probability the female initiates divorce under the ESS strategy

$$D_{\mathrm{f}}(x,y) = \begin{cases} \mathrm{lll} & r(x,y) < R_{\mathrm{f}}(y) \\ 0 & r(x,y) \geqslant R_{\mathrm{f}}(y) \end{cases}. \tag{A1a}$$

(The value of $D_{\mathrm{f}}(x,y)$ when $r(x,y) = R_{\mathrm{f}}(y)$ is arbitrary and has been set by convention to 0.) Similarly the probability a male (x) initiates divorce against a female (y) under the ESS strategy is

$$D_{\mathrm{m}}(x,y) = \begin{cases} 1 & r(x,y) < R_{\mathrm{m}}(x) \\ 0 & r(x,y) \geqslant R_{\mathrm{m}}(x) \end{cases}, \tag{A1b}$$

where $R_{\mathrm{m}}(x)$ is the mean annual reproductive success of the male.

A female (y) in the pairing pool pairs with a male (x) with probability $P_{\mathrm{f}}(x|y)$. Her mean reproductive success on first pairing is thus

$$\bar{r}_{\mathrm{f}}(y) = \sum_{x} P_{\mathrm{f}}(x|y) r_0(x,y). \tag{A1c}$$

Generalizing the method used to obtain equation (A14) of McNamara & Forslund (1996) we have

$$R_{\mathrm{f}}(y) = \bar{r}_{\mathrm{f}}(y) + \sum_{x} H_{\mathrm{f}}(x,y) \max\{r(x,y) - R_{\mathrm{f}}(y), 0\}, \tag{A1d}$$

where

$$H_{\mathrm{f}}(x,y) = P_{\mathrm{f}}(x|y)\left[\frac{s^2(1 - D_{\mathrm{m}}(x,y))}{1 - s^2(1 - D_{\mathrm{m}}(x,y))}\right]. \tag{A1e}$$

Equation (A1d) uniquely determines R_{f} in terms of P_{f}. Similarly if $P_{\mathrm{m}}(y|x)$ is the probability the female obtained by a male (x) is quality y we have

$$R_{\mathrm{m}}(x) = \bar{r}_{\mathrm{m}}(x) + \sum_{y} H_{\mathrm{m}}(x,y) \max\{r(x,y) - R_{\mathrm{m}}(x), 0\}, \tag{A1f}$$

where

$$H_{\mathrm{m}}(x,y) = P_{\mathrm{m}}(y|x)\left[\frac{s^2(1 - D_{\mathrm{f}}(x,y))}{1 - s^2(1 - D_{\mathrm{f}}(x,y))}\right]. \tag{A1g}$$

For given functions P_{f} and P_{m} equations (A1a)–(A1g) determine the interdependence of the functions D_{f} and D_{m} on one another. They thus determine the ESS strategy for given repairing probabilities. The repairing probabilities P_{f} and P_{m} are determined by the composition of the pairing pool as follows. Let X denote the quality of a randomly selected male in the pairing pool. Similarly let Υ denote the quality of a randomly selected female. Let $g_{\mathrm{m}}(x) = P(X = x)$, $g_{\mathrm{f}}(y) = P(\Upsilon = y)$, $G_{\mathrm{m}}(x) = P(X \leqslant x)$ and $G_{\mathrm{f}}(y) = P(\Upsilon \leqslant y)$. Let Φ be the distribution function of a standard normal random variable and define random variables $\mathcal{Z}_1$ and $\mathcal{Z}_2$ by $\mathcal{Z}_1 = \Phi^{-1}(G_{\mathrm{m}}(X))$ and $\mathcal{Z}_2 = \Phi^{-1}(G_{\mathrm{f}}(\Upsilon))$. Then the marginal distributions of $\mathcal{Z}_1$ and $\mathcal{Z}_2$ are approximately standard normal (this is approximate because X and Υ are discrete). The joint distribution of $\mathcal{Z}_1$ and $\mathcal{Z}_2$ is taken to be (approximately) bivariate normal with correlation coefficient ρ. This then determines the joint probability mass function $\pi(x,y) = P(X = x, \Upsilon = y)$ for pairs (X,Υ) which are formed. The conditionals are then given by

$$P_{\mathrm{m}}(y|x) = \pi(x,y)/g_{\mathrm{m}}(x), \tag{A1h}$$

$$P_{\mathrm{f}}(x|y) = \pi(x,y)/g_{\mathrm{f}}(y). \tag{A1i}$$

To complete the ESS equations we specify how the composition of the pairing pool depends on the repairing probabilities P_{m} and P_{f} and the divorce strategies D_{m} and D_{f}. Let $Q_{\mathrm{m}}(x)$ be the probability that a male (x) in the pairing pool divorces after pairing and breeding. Then

$$1 - Q_{\mathrm{m}}(x) = \sum_{y} P_{\mathrm{m}}(y|x)(1 - D_{\mathrm{m}}(x,y))(1 - D_{\mathrm{f}}(x,y)).$$

Let $b_{\mathrm{m}}(x,n)$ be the probability that a male (x) is alive and in the pairing pool just prior to the nth breeding season. By definition $b_{\mathrm{m}}(x,1) = 1$. Since the male is alive just prior to the nth breeding season with probability s^{n-1} it is alive and not in the pool with probability $s^{n-1} - b_{\mathrm{m}}(x,n)$. Thus for $n \geqslant 2$

$$\begin{aligned} b_{\mathrm{m}}(x,n) =& b_{\mathrm{m}}(x,n-1)[Q_{\mathrm{m}}(x + (1 - Q_{\mathrm{m}}(x))s(1-s)] \\ &+ (s^{n-2} - b_{\mathrm{m}}(x,n-1)(1-s), \end{aligned}$$

which can be solved numerically by iterating on n. Let $h_{\mathrm{m}}(x)$ be the proportion of males in the population as a whole which have quality x. Set

$$\tilde{g}_{\mathrm{m}}(x) = h_{\mathrm{m}}(x) \sum_{n=1}^{\infty} b_{\mathrm{m}}(x,n).$$

Then the proportion of males in the pairing pool of quality x is

$$g_{\mathrm{m}}(x) = \tilde{g}_{\mathrm{m}}(x) \Big/ \left(\sum_{v} \tilde{g}_{\mathrm{m}}(v)\right).$$

A similar calculation gives $g_{\mathrm{f}}(y)$.

In summary the pairing probabilities P_{m} and P_{f} determine the divorce probabilities D_{m}, D_{f}. P_{m}, P_{f}, D_{m} and D_{f} determine the composition of the pairing pool g_{m} and g_{f}. In turn g_{m} and g_{f} determine P_{m} and P_{f}. An ESS requires a self-consistent solution in terms of all the above functions.

APPENDIX B. COMPUTATION OF THE ESS

Male quality is taken to be an integer in the range $x = 0,1,2,\ldots,50$. Similarly female quality is taken to be an integer in this range. Let $h_{\mathrm{m}}(x)$ be the proportion of males in the breeding population which have quality x. To give distribution of male qualities an approximate $N(\mu,\sigma^2)$ distribution define

$$\tilde{h}_{\mathrm{m}}(x) = \exp\left\{-\frac{1}{2\sigma^2}(x-\mu)^2\right\} \quad \text{for } x = 0,1,\ldots,50,$$

and

$$\text{norm} = \sum_{x=0}^{50} \tilde{\mathrm{h}}_{\mathrm{m}}(x).$$

Then $h_{\mathrm{m}}(x) = \tilde{\mathrm{h}}_{\mathrm{m}}(x)/\text{norm}$ for $x = 0,1,\ldots,50$. Calculation of $h_{\mathrm{f}}(y)$ is analogous.

To find an ESS we start with some distribution of qualities in the pairing pool given by functions $g_{\mathrm{m}}^{(0)}$ and $g_{\mathrm{f}}^{(0)}$. A sequence $(g_{\mathrm{m}}^{(0)},g_{\mathrm{f}}^{(0)}),(g_{\mathrm{m}}^{(1)},g_{\mathrm{f}}^{(1)}),\cdots$ are computed iteratively as follows.

Given $g_{\mathrm{m}}^{(n)}$ and $g_{\mathrm{f}}^{(n)}$, the functions $P_{\mathrm{m}}^{(n)}$ and $P_{\mathrm{f}}^{(n)}$ can be computed by the method outlined in Appendix A.

Given $P_{\mathrm{m}}^{(n)}$ and $P_{\mathrm{f}}^{(n)}$, we compute $D_{\mathrm{m}}^{(n)}$ and $D_{\mathrm{f}}^{(n)}$ iteratively as follows. We start with some function $D_{\mathrm{m}}^{(n,0)}$. This then determines $D_{\mathrm{f}}^{(n,0)}$ via equations (A1*e*), (A1*c*), (A1*d*) and (A1*a*). $D_{\mathrm{f}}^{(n,0)}$ in turn determines $D_{\mathrm{m}}^{(n,1)}$ via equation (A1*g*), the analogy of (A1*c*), (A1*f*) and (A1*b*). $D_{\mathrm{m}}^{(n,1)}$ then determines $D_{\mathrm{f}}^{(n,1)}$, and so on. The sequence $D_{\mathrm{m}}^{(n,0)}, D_{\mathrm{m}}^{(n,1)}, D_{\mathrm{m}}^{(n,2)},\ldots$ has always been found to converge (to $D_{\mathrm{m}}^{(n)}$ say). Similarly, for the sequence $D_{\mathrm{f}}^{(n,0}, D_{\mathrm{f}}^{(n,1)}, D_{\mathrm{f}}^{(n,2)},\ldots$.

Given $P_{\mathrm{m}}^{(n)}$, $P_{\mathrm{f}}^{(n)}$, $D_{\mathrm{m}}^{(n)}$, $D_{\mathrm{f}}^{(n)}$, we calculate $g_{\mathrm{m}}^{(n+1)}$, $g_{\mathrm{f}}^{(n+1)}$ using the method described in Appendix A.

The iteration is stopped once

$$\max_x |g_{\mathrm{m}}^{(n-1)}(x) - g_{\mathrm{m}}^{(n)}(x)| + \max_y |g_{\mathrm{f}}^{(n-1)}(y) - g_{\mathrm{f}}^{(n)}(y)|,$$

is less than some specified tolerance.

For given y let $x^*(y)$ satisfy $r(x^*(y),y) = R_{\mathrm{f}}(y)$. Then a female of quality y should reject a male (x) if and only if $x < x^*(y)$. Since x takes only integer values, a slight change in $x^*(y)$ can produce a discontinuous change in measures such as the population divorce rate. Thus as parameters such as longevity are varied one can get irregular behaviour of the divorce rate due to grid effects. To smooth out these grid effects, computational results presented here are based on the following modification to equation (A1*a*). Let $x_I(y)$ be the largest integer satisfying $x_I(y) \leqslant x^*(y)$ and let $p = x^*(y) - x_I(y)$, then

$$D_{\mathrm{f}}(x,y) = \begin{cases} 1 & x \leqslant x_I(y) - 1 \\ \frac{1}{2} + \frac{1}{2}p & x = x_I(y) \\ \frac{1}{2}p & x = x_I(y) + 1 \\ 0 & x \geqslant x_I(y) + 2. \end{cases}.$$

The formula for $D_{\mathrm{m}}(x,y)$ is modified in an analogous manner.

APPENDIX C. DEPENDENCE OF MEAN REPRODUCTIVE SUCCESS ON AGE

Let V_n denote the reproductive success of an individual during its nth breeding season (conditional on survival till this time). Define $I_1 = 0$, and for $n \geqslant 2$ set $I_n = 0$ if the individual breeds with a new partner during the nth season and $I_n = 1$ otherwise. Then $P(I_n = 1) = (1 - d_{n-1})s$ where $d_0 = 1$ and d_n is the probability of divorce after breeding for the nth time $(n \geqslant 1)$ given by equation (12). Thus,

$$\begin{aligned} E(V_n) &= E(V_n|I_n = 0)P(I_n = 0) + E(V_n|I_n = 1)P(I_n = 1) \\ &= R_0 + (R - R_0)(1 - d_{n-1})s, \end{aligned} \tag{A3a}$$

where $R_0 = E(V_n|I_n = 0)$ and $R = E(V_n|I_n = 1)$. The mean total lifetime reproductive success of the individual is therefore

$$\sum_{n=1}^{\infty} E(V_n)s^{n-1} = R_0(1-s)^{-1} + (R - R_0)\sum_{n=1}^{\infty}(1 - d_{n-1})s^n. \tag{A3b}$$

First suppose that under an optimal strategy the individual always divorces. Then $d_n = 1$ for $n \geqslant 0$ and $E(V_n) = R_0$ for all $n \geqslant 1$.

In contrast, suppose that under the optimal strategy, the individual does not divorce all partners, and that this strategy is strictly superior to the strategy of always divorcing all partners. Then the mean lifetime success must exceed $R_0(1-s)^{-1}$ and hence by equation (A3*b*) $R > R_0$. By equation (12) d_n is a strictly decreasing function of n. Thus by equation (A3*a*) $E(V_n)$ is a strictly increasing function of n.

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