Better to Divorce than Be Widowed: The Role of Mortality and Environmental Heterogeneity in the Evolution of Divorce

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ABSTRACT: Despite widespread interest in the evolution and implications of monogamy across taxa, less attention—especially theoretical—has been paid toward understanding the evolution of divorce (ending a socially monogamous pairing to find a new partner). Here, we develop a model of the evolution of divorce by females in a heterogeneous environment, where females assess territory quality as a result of their breeding success. Divorce results in females leaving poor territories disproportionally more often than good territories, while death of a partner occurs independent of territory quality, giving an advantage to divorce. Increasing environmental heterogeneity, a decreasing benefit of pair experience, and moderate survival rates favor the evolution of higher divorce rates, even in the absence of variance in individual quality and knowledge of available territories. Imperfect information about territory quality constrains the evolution of divorce, typically favoring divorce strategies that remain faithful to one's partner whenever successful reproduction occurs. Our model shows how feedbacks between divorce, widowhood, and the availability of territories are intricately linked in determining the evolutionary advantage of divorce. We detail testable predictions about populations that should be expected to divorce at high rates.

Keywords: better options hypothesis, divorce, mate fidelity, monogamy, pair bond, territoriality.

Introduction

Whenever monogamous pairs form, divorce may follow. In birds, social monogamy associated with the pair raising the brood is common (Bennett and Owens 2002), but still divorce varies from absent in some species to annual partner turnover in others (Jeschke and Kokko 2008). Understanding this variation has largely been the provenance of empirical correlative studies. First, long-lived species seem to be less likely to get divorced between seasons (Jeschke and Kokko 2008; Botero and Rubenstein 2012; fig. S1). Some striking exceptions (e.g., high divorce rates in long-lived species) have been linked to variable breeding opportunities (e.g., in France, breeding possibilities for the flamingo *Phoenicopterus ruber* depend on degree of flooding; Cézilly and Johnson 1995). Second, species with female-biased adult sex ratios tend to have higher divorce rates (Liker et al. 2014). Female-biased sex ratios are often associated with polygamy, and secondary females may leave their partner to seek out improved opportunities (Wheelwright and Teplitsky 2017). Finally, more ornamented species (Botero and Rubenstein 2012) and species often engaging in extrapair paternity (Cézilly and Nager 1995) are more likely to get divorced, attributed to the importance of choosing a high-quality partner in species with strong sexual selection.

These comparisons among species have been complemented by studies within populations that confirm that divorce is likely adaptive (Diamond 1987; Choudhury 1995; Culina et al. 2015). Building on an earlier meta-analysis by Dubois and Cézilly (2002), Culina et al. (2015) evaluated studies of 64 socially monogamous bird species. Within species, females that divorced typically did so if they had low breeding success. Divorcing females showed a large increase in reproductive success in the year following, yet their reproductive success was still lower than that of faithful pairs. These findings suggest that divorce comes with benefits (increased reproductive success) and costs (notably, cooperation between familiar birds is more efficient; Dhondt and Adriaensen 1994; Sánchez-Macouzet et al. 2014); both of these forces are likely important drivers in divorce evolution. The increase in reproductive success following divorce is often used as evidence that divorce is adaptive. However, this need not always be the case, and alternative explanations for divorce exist, such as few benefits

from fidelity and forced evictions (Sandercock et al. 2000; Jeschke et al. 2007; Wheelwright and Teplitsky 2017).

Despite correlates to divorce identified by these studies, less attention has been paid to developing a mechanistic underpinning for how life history and environmental features influence the evolution of divorce. Impacts of longevity have been most often considered. Some verbal arguments predict that short-lived species should have low divorce rates because temporary costs associated with entering into a new partnership would outweigh benefits that persist for only one or two breeding seasons (Rowley 1983; Diamond 1987; Johnston and Ryder 1987). Others have argued that short-lived species should divorce more frequently (Linden 1991; Bried et al. 2003; Jeschke and Kokko 2008), claiming that short-lived species face intense pressure to find the best mate and/or territory quickly, that the benefits of mate fidelity compound given a longer life span, or that breeding opportunities are reduced when individuals live longer and widows/widowers are not created (Ens et al. 1993; Lloyd 2007). These competing verbal hypotheses along with the logistical challenges of manipulative work highlight the need for theory to elucidate causal explanations.

There have been a number of theoretical insights regarding the evolution of divorce. Dubois et al. (2004) considered alternative mate assessment strategies in the evolution of divorce, finding that divorce can sometimes be favored when females pay search costs to assess quality prior to breeding (as in sexual selection models). Other approaches have assumed that quality is instead assessed during breeding. McNamara and Forslund (1996) assumed a normal distribution of the quality of available males and that females assessed male quality after breeding but could then do so perfectly. In their model, a threshold in male quality appears: once paired with a male above the threshold, females should not divorce, whereas when a female is paired to a male below the threshold, on average divorce is beneficial (although the female may subsequently pair with a lower-quality male by chance). They found that divorce rates decrease with age, as females find and stay with high-quality partners. In the model, a high-quality partner is especially valuable in a long-lived species, as he will generally live for a long time. On average, this leads to lower divorce rates in long-lived species. However, when costs to divorce are added to the model, McNamara and Forslund (1996) found that short-lived species also have low divorce rates, as females cannot afford to pay these costs, given their few opportunities to reproduce. This model was extended by McNamara et al. (1999) to allow both males and females to initiate divorce and to vary in quality. They found that survival had little effect on divorce rate in the absence of costs, but in the face of costs higher survival (at least up to an annual survival rate of 0.9) typically led to higher di-

vorce rates (McNamara et al. 1999, their table 1). A key advance of this study was the computation of the distribution of available qualities that result from different divorce rates, recognizing that if divorce is a more likely outcome when mates are of low quality, then the distribution of available mates will be skewed to be worse than average whenever divorce occurs in the population. Divorce thus creates conditions that are less favorable to the evolution of further divorce. Though divorce must overcome these feedbacks in order to evolve in McNamara et al.'s (1999) model, the way in which this occurs was not stressed: elucidating the importance of divorce altering the distribution of available reproductive opportunities is thus one goal of our study.

Here, we build on past findings, using a model that (1) explicitly incorporates the way divorce alters the distribution of available reproductive opportunities, (2) treats divorce as a response to nest failure (predation) to consider the importance of territory quality, and (3) imposes incomplete knowledge of territory quality even after breeding. We focus on birds to guide our model development, but our findings should be general to any species that forms social pair bonds over multiple breeding attempts. We model nest failures as the main source of environmental heterogeneity, with nest predation in mind. While it has been difficult to empirically link predation to subsequent divorce (e.g., Harvey et al. 1979), divorce correlates with relatively low reproductive success across species (Culina et al. 2015), and in many small birds, nest predation is the primary cause of nest failure (Martin 1995). In some cases, females may assess the likelihood of predation directly and divorce if they observe an opportunity to trade up (e.g., Pärt 2001). In other cases, as we model here, females may infer territory quality on the basis of their reproductive success. This means that females have imperfect information when settling and that females may mistakenly assess their territory as poor when they are on a good territory (if their nest fails because of bad luck) or good when they are on a poor territory (if they are lucky and their nest succeeds in spite of poor territory quality), a feature not considered in previous models. We find that divorce skews the distribution of available territories in a way that vitally affects the costs and benefits of divorce. Overall, intermediate mortality, high variation in territory quality, and a low cost to being in a new pair favors the evolution of divorce.

Model

We develop a game-theoretic model assuming haploid genetics in a population of fixed size N with overlapping generations and female-controlled divorce. In this paragraph, we present the essential features. We assume that the environment consists of $N/2$ territories (a proportion p_g of which are of good quality and $p_p = 1 - p_g$ of poor

quality). Considering two territory types rather than continuous territory quality allows for analytical tractability and straightforward interpretations of associations between divorce alleles and territory quality, and it simplifies the measurement of skew in territories that become available for females by divorce. At the time of reproduction, there is exactly one male and one female on each territory. Individuals of the same sex are equivalent except for divorce strategy determined at an autosomal V locus. We assume that females control divorce (Harris et al. 1987; Ens et al. 1993; Dhondt and Adriaensen 1994; Orell et al. 1994; Otter and Ratcliffe 1996; Blondel et al. 2000). Reproductive success in a given time step is independent of an individual's divorce strategy but is controlled by territory quality and whether the pair is in their first year together. Successful reproduction occurs on a proportion r_g of good territories and r_p of poor territories ($r_g > r_p$), and new pairs produce $1 - c$ offspring relative to experienced pairs. Below we will see that the influence of divorce strategies on the amount of time females spend on good/poor territories in new/experienced pairs determines the fitness consequences of divorce. Specifically, following a nest failure, females carrying the V_i allele divorce with probability v_i; this probability, conditioned on nest failure, is the propensity to divorce and can take any value from 0 to 1. We assume that a female cannot determine a territory's quality a priori or with certainty. Instead, she relies on imperfect information she acquires about her territory through her reproductive success. We assume that the population is (nearly) monomorphic for divorce propensity (with resident value v_1) and consider the invasion of a rare mutant (with divorce propensity v_2) in the limit of an infinite population. In appendix S1, we also develop a population genetic model that explicitly tracks two genotypes competing through time and show that our results are not sensitive to the assumptions of the invasion analysis.

Model Formulation

We now provide a detailed description of the model with parameters summarized in table 1. We set the reproductive output of an experienced pair on a territory that never suffers from nest failure to 1. Then, the (relative) reproductive output of a pair with experience l on a territory of quality k is

$$F_{kl} = \begin{cases} r_k, & l = e, \\ r_k(1 - c), & l = n. \end{cases} \tag{1}$$

Again, r_k is the probability of successful reproduction on good ($k = g$) or poor ($k = p$) territories and c is the relative cost of reproduction of being in a new pair (so that the subscript e corresponds to an experienced pair and n corresponds to a new pair).

Following reproduction, females may divorce. Because divorce often follows low reproductive success (Coulson 1966; Rowley 1983; Harris et al. 1987; Bradley et al. 1990; Dhondt and Adriaensen 1994; Ens et al. 1996; Dubois and Cézilly 2002; Culina et al. 2015), we start with the simplifying assumption that divorce never occurs after a nest success but sometimes occurs following a nest failure, although we consider other divorce strategies later. The probability a female with divorce propensity v_i on a territory of quality k divorces is

$$\delta_{ik} = v_i(1 - r_k). \tag{2}$$

Single males remain on their territory regardless of whether they are divorcees or widowers, whereas female divorcees and widows move territories and find a new mate during the next breeding season. Individuals survive to the next breeding season with probability s, regardless of their sex, territory, breeding success, and pair age. Since death and divorce are independent and death rate does not depend on territory quality, the relative order of these two events is irrelevant.

Next, territories refill and individuals that lost a partner as a result of death or divorce re-pair. Because we assume that males do not divorce, selection does not act on males, and our assumption that each territory has one male at the time of reproduction means that males need not be explicitly tracked. In the population genetic version of the model (app. S1), we allow for changes in

Table 1: Summary of parameters and their role in evolution of divorce propensity

Parameter	Meaning	Values that favor high divorce propensities
v	Divorce propensity	Not applicable
s	Survival rate	Intermediate
p_g	Proportion of territories that are good	Intermediate
r_g	Probability of nest success on good territories	High
r_p	Probability of nest success on poor territories	Low
c	Cost of being in a new pair	Low
a	Bias against leaving experienced pair	High

allele frequency in male offspring on different territory types to contribute to the correlations between divorce and both territory quality and pair experience; this does not have notable effects on the results. Next, single females (new recruits, widows, and divorcees) acquire a new territory. There must be $N(1-s)/2$ new females recruited into the population to keep its size fixed. Divorce results in a proportion of good and poor territories available for females that differs from p_g and p_p, respectively. The number of territories A_k of quality $k \in \{g, p\}$ available for females in a population with divorce propensity v_1 is

$$A_k = \frac{p_k N}{2}[1 - s^2(1 - \delta_{1k})]. \qquad (3)$$

The term outside the square brackets is the total number of territories of quality k (the proportion p_k times the total number of territories $N/2$), and the term inside the square brackets is the proportion of territories of quality k that are available to females (measured as 1 minus the proportion that are unavailable to females, i.e., territories where both individuals survive and divorce did not occur). Then, a single female obtains a good territory with probability $A_g/(A_g + A_p)$ and a poor territory with probability $A_p/(A_g + A_p)$. Now, every individual is on a territory with a partner and the time step ends.

Frequency dependence and environmental feedbacks complicate whether and why divorce evolves. As such, we first determine how the divorce strategy affects the proportion of time females spend on good-quality territories and in experienced pairs, which jointly determine the costs and benefits of divorce and mate fidelity that emerge from our model. We then use an invasion analysis to find the evolutionarily stable strategy (ESS) divorce propensity v^* across the possible range of parameter values to determine conditions favoring divorce. Since we are dealing with a fixed population size with survival independent of trait values, expected lifetime reproductive success is a reliable proxy to use in the fitness gradient

$$\left.\frac{dR_0}{dv_2}\right|_{v_2 = v_1}$$

(Lehmann et al. 2016). The sign of the fitness gradient gives the expected direction of evolution at the resident strategy, and resident strategies at which it is zero are potential ESSs.

We model a single female with divorce propensity v_2 in a fixed environment determined by a nearly monomorphic resident divorce propensity v_1. The female can be in one of five states: in a new pair on a poor territory (pn), in an experienced pair on a poor territory (pe), in a new pair on a good territory (gn), in an experienced pair on a good territory (ge), or dead ($\emptyset$). We will show how to calculate the expected number of times that the female visits each state as a function of her (and the resident) divorce propensity, which ultimately determines expected lifetime reproductive success. The female's state is a discrete-time Markov process. We define M to be the transition matrix for the Markov chain describing the female's state such that $M(i, j)$ is the probability that a female in state i at time t is in state j at time $t + 1$. On the basis of our underlying biological assumptions, we can explicitly write down M. Females die with probability $1 - s$ in each time step, so starting from any living state i at time t, we find that the probability of the female dying by the next time step is

$$M(i, \emptyset) = 1 - s. \qquad (4)$$

Of course, females are always dead in the next time step once they have died, so transitions out of the death state do not occur (i.e., $M(\emptyset, j) = 0$ for all $j \in \{pn, pe, gn, ge\}$ and $M(\emptyset, \emptyset) = 1$). The female can enter a new pair in a territory of quality k only if three things occur: (1) she survives, (2) she leaves her territory (through either partner death or divorce), and (3) she obtains a new territory of quality k. Together this means that the probability that this v_2 female is in a new pair on a territory with quality k at time $t + 1$, starting in any living state i at time t, is

$$M(i, kn) = s(1 - s(1 - \delta_{2q}))\frac{A_k}{A_g + A_p}, \qquad (5)$$

where q is the quality of her current territory, s out front accounts for female survival, the term in the outer parentheses is the probability that the surviving female will leave her territory (recall that this is a function of her divorce propensity v_2), and the final term accounts for the probability that she obtains a territory of quality k given that she leaves (recall that this is a function of the resident divorce propensity v_1). Finally, the female enters (or remains in) an experienced pair if (1) she survives, (2) her partner survives, and (3) she does not divorce. Together this means that for all $i \in \{n, e\}$ and $k \in \{p, g\}$, a transition from state ki at time t into an experienced pair state ke at time $t + 1$ occurs with probability

$$M(ki, ke) = s^2(1 - \delta_{2k}) \qquad (6)$$

and $M(qi, ke) = 0$ if $q \neq k$. Here, s^2 accounts for both individuals surviving, and the term in parentheses accounts for the female not divorcing. With the transition matrix M fully specified by equations (4)–(6), we can compute the number of times the female is expected to visit each state before her death (app. S2), which determines her expected

lifetime reproductive success. We can then obtain analytical expressions for the fitness gradient and ESS (app. S2). All analyses were carried out using Mathematica (Wolfram Research 2020) using code deposited in Zenodo (https://doi.org/10.5281/zenodo.6506637; Lerch et al. 2022).

Since increasing the probability of successful reproduction on good territories r_g has analogous effects on relative fitness to decreasing the probability of successful reproduction on poor territories r_p, we are concerned with four qualitatively distinct parameters (the survival rate s, the cost to being in a new pair c, the proportion of territories that are good p_g, and the probability of successful reproduction on either good territories r_g or poor territories r_p). We also consider an extension to the model where females are biased against leaving experienced pairs (as observed empirically; Coulson 1966; Harris et al. 1987; Bradley et al. 1990) in appendix S3.

Finally, note that the usual empirical measure of divorce rate D is the proportion of individuals in new pairs given that both partners survived the previous breeding season. This measure captures an emergent, population-level metric of divorce, which is not the target of selection. In our model, this is given by $D = v_1(p_g(1 - r_g) + p_p(1 - r_p))$. In general, with polymorphism for divorce propensity (as in the population genetic model), mean divorce propensity is not necessarily linearly related to divorce rate. We use D to illustrate some outcomes of our model.

Alternative Divorce Strategy: Always Divorce after a Nest Failure

In the model as described above, females never divorce after a successful reproduction event. In reality, divorce happens following both successful and failed attempts but occurs more frequently following low success (Culina et al. 2015). Allowing variation in divorce associated with both successful and nonsuccessful reproductive outputs substantially complicates the model and is not pursued here. Instead, we consider an extreme alternative: to always divorce following nest failure and sometimes divorce following successful reproduction. With this strategy, the probability that a female with divorce propensity v_i divorces off of a territory with quality k becomes $\delta_{ik} = 1 - r_k(1 - v_i)$ (females do not divorce only if they both successfully reproduce (r_k) and do not divorce after success ($1 - v_i$); cf. eq. [2]). We consider the evolution of divorce propensity with this strategy (referred to as divorce upon failure) and compete it against the strategy from the main model section (referred to as faithful upon success) in the population genetic framework of appendix S1. This alternative strategy provides additional insights into the importance of feedbacks between the environment and evolution.
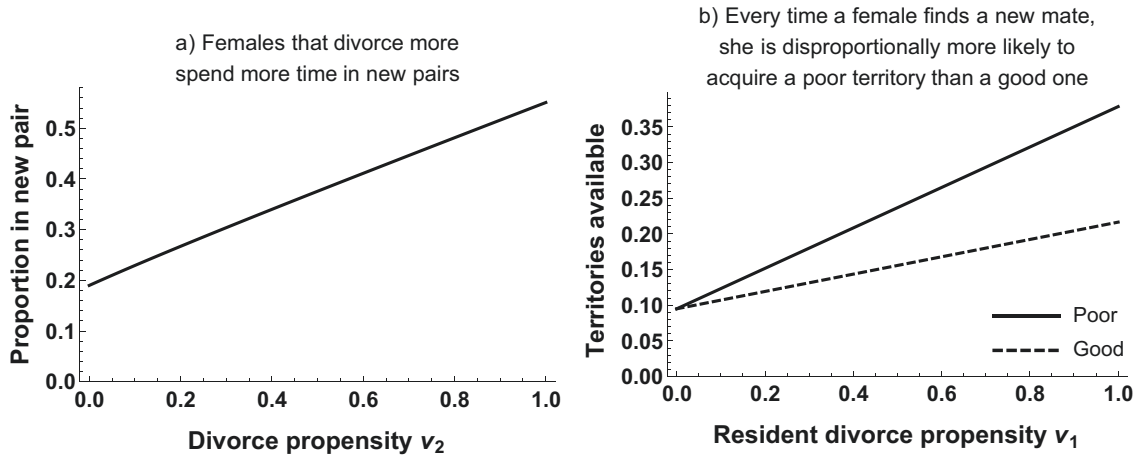
Results

Costs and Benefits to Divorce and Mate Fidelity

We first outline the costs and benefits of divorce that emerge from the model. Females that divorce more frequently spend more time in new pairs (fig. 1a). Because new pairs are assumed to have lower fitness than experienced pairs (c), this constitutes a cost to divorce. The influence of divorce on the distribution of available territories also disfavors the evolution of further divorce because females are more likely to divorce off of poor territories than good territories. In appendix S4, we prove that this increases the frequency of available poor territories over their frequency in the environment as a whole (i.e., we prove that $A_p/(A_p + A_g) > p_p$; see also fig. 1b). Consequently, whenever a female must find a new mate in a population where there is divorce, she is disproportionately likely to obtain a poor territory than a good territory relative to the overall frequencies of these territories. Thus, selection for divorce is negatively frequency dependent: females that divorce more must find a new territory more often, but high divorce rates raise the frequency of available territories that are poor.

Divorce is often considered to be beneficial because it allows individuals to acquire high-quality reproductive opportunities. In our model, this would correspond to being more likely to obtain a good territory rather than a poor one. However, divorce itself disproportionately makes available poor territories. This begs the question, how could divorce ever be favored if divorcees are in new pairs more often and divorce itself causes poor territories to be prevalent?

The key to solving this apparent paradox is considering whether females are more likely to leave a poor territory or a good territory through divorce or death of their partner. Females that never divorce will leave good and poor territories equally when their mate dies (fig. 1c at divorce propensity $v_2 = 0$). When divorce is present ($v_1 > 0$), more poor territories are available than good territories (fig. 1b), so females that leave territories when their partner dies obtain worse territories on average. In contrast, as we prove in appendix S5, females that divorce more leave poor territories more frequently than good territories (see also fig. 1c). Relative to females that are less likely to divorce, females that divorce with higher propensity improve their situation. Consequently, when territories are also freed up by death, females that are more likely to divorce spend more time on good territories (fig. 1d): the benefit of divorce. Note that the association between a higher divorce propensity and good territories builds not because females that divorce are likely to acquire good territories on leaving: most available territories are poor. They are, however, likely to improve their lot (trade up):

Leaving a pair bond is costly:

a) Females that divorce more spend more time in new pairs

b) Every time a female finds a new mate, she is disproportionally more likely to acquire a poor territory than a good one

Leaving due to divorce, rather than widowhood, is preferable:

c) Females that divorce more leave poor territories disproportionally more often than good territories

d) The lines in c) result in a positive association between divorce and territory quality

Figure 1: Outline of general features of model that give rise to costs and benefits of divorce and mate fidelity by competing a resident nondivorcing strategy ($v_1 = 0$) with a successfully invading mutant strategy v_2. Note that the qualitative conclusions remain even if the resident also divorces (fig. S2). *a*, Females that divorce more spend more time in new pairs (which have lower fitness than experienced pairs), calculated as the expected number of time steps in a new pair divided by expected life span (see eq. [S6]). *b*, As resident divorce propensity v_1 increases, there are increasingly more poor than good territories available (eq. [3]) over what is expected on the basis of the proportion of good territories p_g, because divorce is more likely to occur off of poor territories than good territories. The effects in both *a* and *b* contribute to the cost of divorce. *c* and *d* demonstrate the benefits of divorce. *c*, Probability that a surviving V_2 female leaves poor and good territories at various divorce propensities (eq. [S13]). Increasing divorce propensity increases the proportion of leaving V_2 females that come off of poor territories (y-axis value) relative to all leaving V_2 females (sum of solid and dashed lines) to be greater than the proportion of poor territories p_p (app. S4; with a zero divorce propensity, a proportion p_p of individuals that leave come off of poor territories and a proportion p_g come off of good territories because of partner death). *d*, Females with a divorcing genotype spend more time on good territories than a nondivorcing genotype (>0.5 on y-axis; calculated as expected number of time steps on a good territory divided by expected life span; see eq. [S6]), and this increases with divorce propensity. The overall benefit to divorce results from the interaction between these costs and benefits. Parameters: $v_1 = 0$, $p_g = 0.5$, $s = 0.9$, $r_g = 0.7$, $r_p = 0.3$, $c = 0.2$.

we prove in appendix S6 that the probability a divorcing female will be on a poor territory in the next breeding season is less than it would be if they stayed with their mate after nest failure. The effect of each parameter in our model on the ESS divorce propensity (discussed in detail below) can be understood through the costs and benefits of divorce and mate fidelity described above and shown in figure 1.

ESS Divorce Propensity

We find that the ESS divorce propensity v^* varies from 0 to 1 depending on parameter values, although never di-

vorcing is a frequent outcome. All qualitatively distinct parameters (s, r_g, p_g, and c) influence the ESS divorce propensity (fig. 2). Survival rate has a nonlinear effect on the ESS divorce propensity whereby in relatively short-lived
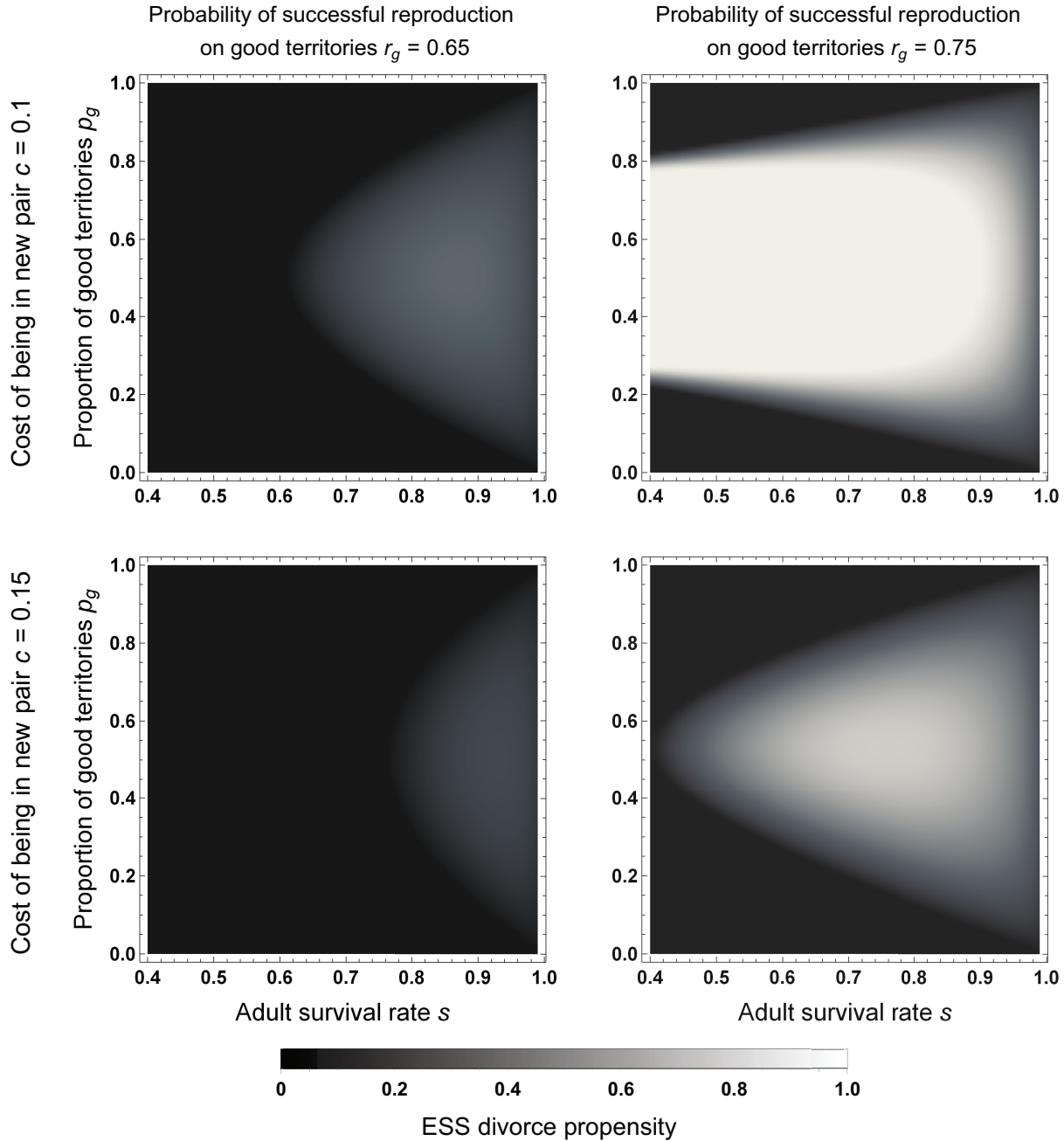

Figure 2: ESS divorce propensity v^* as a function of survival rate s (horizontal axis) and proportion of good territories p_g (vertical axis), with probability of successful reproduction on good territories r_g defining columns and cost to being in a new pair c defining rows. Lighter colors indicate higher divorce propensities (white = divorce every nest failure; black = never divorce). In all cases, intermediate survival rates and intermediate proportion of good territories favor the evolution of higher divorce propensities. A high probability of successful reproduction on good territories tends to increase the amount of parameter space where divorce evolves, whereas high cost to being in a new pair decreases it. Other parameters: $r_p = 0.4$.

species (low to moderate *s*) higher adult survival favors divorce, but in long-lived species (high *s*) higher adult survival favors mate fidelity. A large variance in territory quality (i.e., environmental heterogeneity)—resulting from more equal numbers of good and poor territories (p_g closer to 0.5) and greater difference in probability of success between different territory qualities (higher r_g and lower r_p, the latter not shown)—favors higher divorce propensities. High costs to being in a new pair (higher *c*) favors lower divorce propensities, as is expected. In appendix S3, we show that a bias against leaving experienced pairs also increases the ESS divorce propensity. We consider the role of each parameter below (summarized in table 1).

Effect of Survival Rate. Survivorship has two intertwined but conflicting effects on the evolution of divorce, with in-creasing survivorship favoring divorce in short-lived species and fidelity in long-lived species (fig. 3*a*). The point where the maximum divorce propensity evolves (the transition between these regimes) depends on specific parameter values but tends to occur in species that live between 5 and 10 years (*s* between 0.8 and 0.9).

The first effect of survivorship is that, from the perspective of the female, death of her mate means that she cannot freely choose between staying on their territory and leaving it, since females are assumed not to hold a territory after the death of their partner. While partner death causes females to leave good and poor territories in proportion to the frequency with which they are occupied (following divorce), divorce biases females toward leaving poor territories. Therefore, the ability of females to leave poor territories disproportionately more often than good
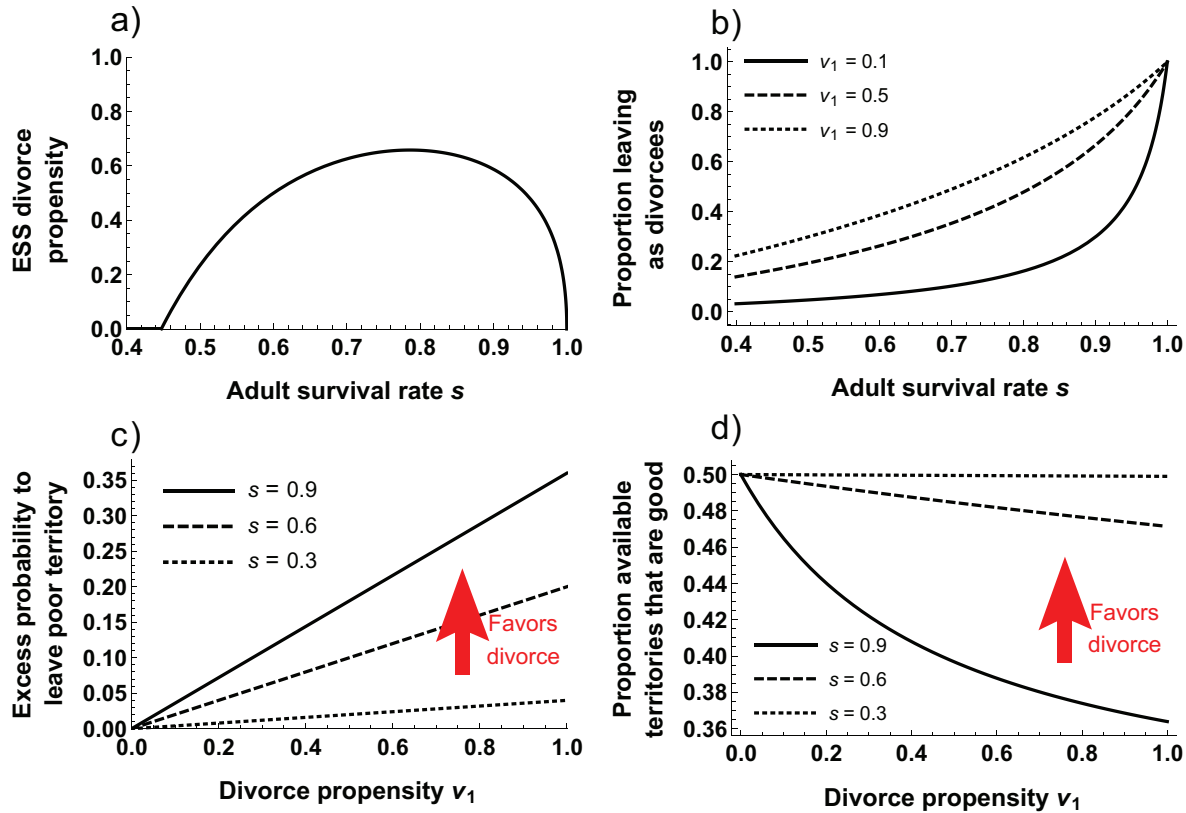

Figure 3: *a*, ESS divorce propensity v^* is a function of survival rate *s*. As in figure 2, intermediate survival rates favor the evolution of high divorce propensities. *b–d* explain the origin of this nonlinearity. *b*, Probability that a female leaves her territory as a divorcee (rather than a widow) as a function of survival rate *s* at three different divorce propensities (see legend). High survival rates and divorce propensities result in a larger proportion of females leaving their territory as divorcees. *c*, Probability a female leaves a poor territory minus the probability a female leaves a good territory (which we call excess probability to leave poor territory). *d*, Proportion of available territories that are good. As survival rate *s* increases, females gain control over whether they leave their partner (*b*), meaning that the probability they leave a poor territory increases relative to the probability they leave a good territory (*c*). This results in higher survivorship favoring divorce. At the same time, however, increasing survival rate *s* means fewer good territories become available (*d*), resulting in higher survivorship favoring fidelity. Together, these result in an intermediate survival rate favoring the highest ESS divorce propensities (*a*). Parameters: $p_g = 0.5$, $s = 0.9$, $r_g = 0.7$, $r_p = 0.3$, $c = 0.2$.

territories (the driver of divorce; fig. 1*c*) increases with survival rate (fig. 3*c*; proven in app. S5). So, in this way, high survivorship favors divorce. However, low survival (high mortality) results in an increased availability of good territories (fig. 3*d*; proven in app. S7). So, in this way, low survivorship favors divorce. Put differently, increasing survival rates make divorce more beneficial for mutants (fig. 3*c*) but make the social environment less favorable for divorce (fig. 3*d*).

It is not obvious how these conflicting effects are resolved to generate the overall influence of longevity on the ESS divorce propensity. As shown in figure 3*b* and proven in appendix S8, for a given divorce rate, in short-lived species a higher proportion of territories become available for females as a result of death rather than divorce (the proportion leaving as divorcees is less than 0.5), whereas in long-lived species a higher proportion of territories become available for females as a result of divorce rather than death. This means that females of short-lived species less frequently have the opportunity to choose between staying on a territory or leaving it, so the gain in control from increasing survival rate dominates, favoring divorce (seen in fig. 3*a* as a result of the effect in fig. 3*c*). In contrast, females of long-lived species are frequently able to choose between staying on their territory and leaving it (fig. 3*b*), so the fact that relatively few territories are available each year (with survivorship restricting the availability of good territories) dominates, favoring fidelity (seen in fig. 3*a* as a result of the effect in fig. 3*d*). In "Discussion," we consider how predicted trends relate to empirical data.

Effect of Habitat Heterogeneity. Divorce most often evolves when the number of good and poor territories is approximately equal (fig. 2). An equal number of good and poor territories maximizes a female's ability to spend more time on good territories than poor territories relative to other females when she divorces more (fig. S3) because this is the point of maximum variance. If the proportion of good territories p_g becomes high or low, then most individuals that must find a new territory will obtain a good or poor territory, respectively.

As the probability of successful reproduction on good territories r_g increases (i.e., environmental heterogeneity increases), higher divorce propensities evolve (fig. 2). A relatively high value of good territories relative to poor territories means that the positive association of divorce propensity with good territories (fig. 1*d*) is more beneficial. In addition, if reproduction is more often successful on good territories, females are less likely to mistakenly divorce away from them. Likewise, decreasing the probability of successful reproduction on poor territories r_p makes it more likely that females are able to identify and leave

poor territories quickly. In other words, increasing environmental heterogeneity means that a female's (imperfect) information about her territory becomes a better indicator of its quality.

Cost of Being in a New Pair. A low cost of being in a new pair c favors the evolution of higher divorce propensities (fig. 2). As the cost increases, individuals that divorce more frequently suffer a greater cost from being in a new pair more often (fig. 1*a*). Hence, mean population fitness declines with increasing divorce propensity (fig. S4).

Alternative Divorce Strategy: Always Divorce after a Nest Failure

Previous results were derived assuming that females never divorce after nest success and facultatively divorce after a failure (the faithful upon success strategy). We now consider an alternative extreme, where females always divorce after nest failures and facultatively divorce after successful reproduction (the divorce upon failure strategy). In this case, the ESS is the unconditional strategy of never divorcing after a nest success ($v^* = 0$). Under these assumptions, more poor territories than good territories are available (fig. 4*a*) and variation in divorce strategy results in individuals with higher divorce propensities increasingly likely to leave good territories relative to poor territories (until they do so at an equal rate when $v = 1$; fig. 4*b*; in contrast to the faithful upon success strategy in fig. 1*c*). This leads to females that divorce less spending more time on good territories (fig. 4*c*), eliminating the benefit to higher divorce propensity seen previously (fig. 1*d*). This demonstrates the extent to which it can be detrimental to mistakenly leave good territories, highlighting how imperfect information about one's territory limits the evolution of divorce.

To see which of these two strategies was more likely to evolve, we redefined our variables to compete the faithful upon success strategy (now v_1) against the divorce upon failure strategy (now v_2) in 10,000 random parameter combinations from the population genetic model in appendix S1. For 98.5% of the evaluated parameter combinations, faithful upon success outcompetes divorce upon failure. Divorce upon failure is more likely to win given three conditions (table S1; fig. 4*d*). The first condition is if both divorce propensities are low. Low divorce propensities mean the divorce upon failure strategy results in better discrimination between good and poor territories (cf. fig. 4*b*, fig. 1*c*). The second condition is that the cost to being in a new pair is low. High costs to being in a new pair disfavor the divorce upon failure strategy because females using this strategy are more frequently in new pairs. The third condition is that the probability of successful reproduction on poor
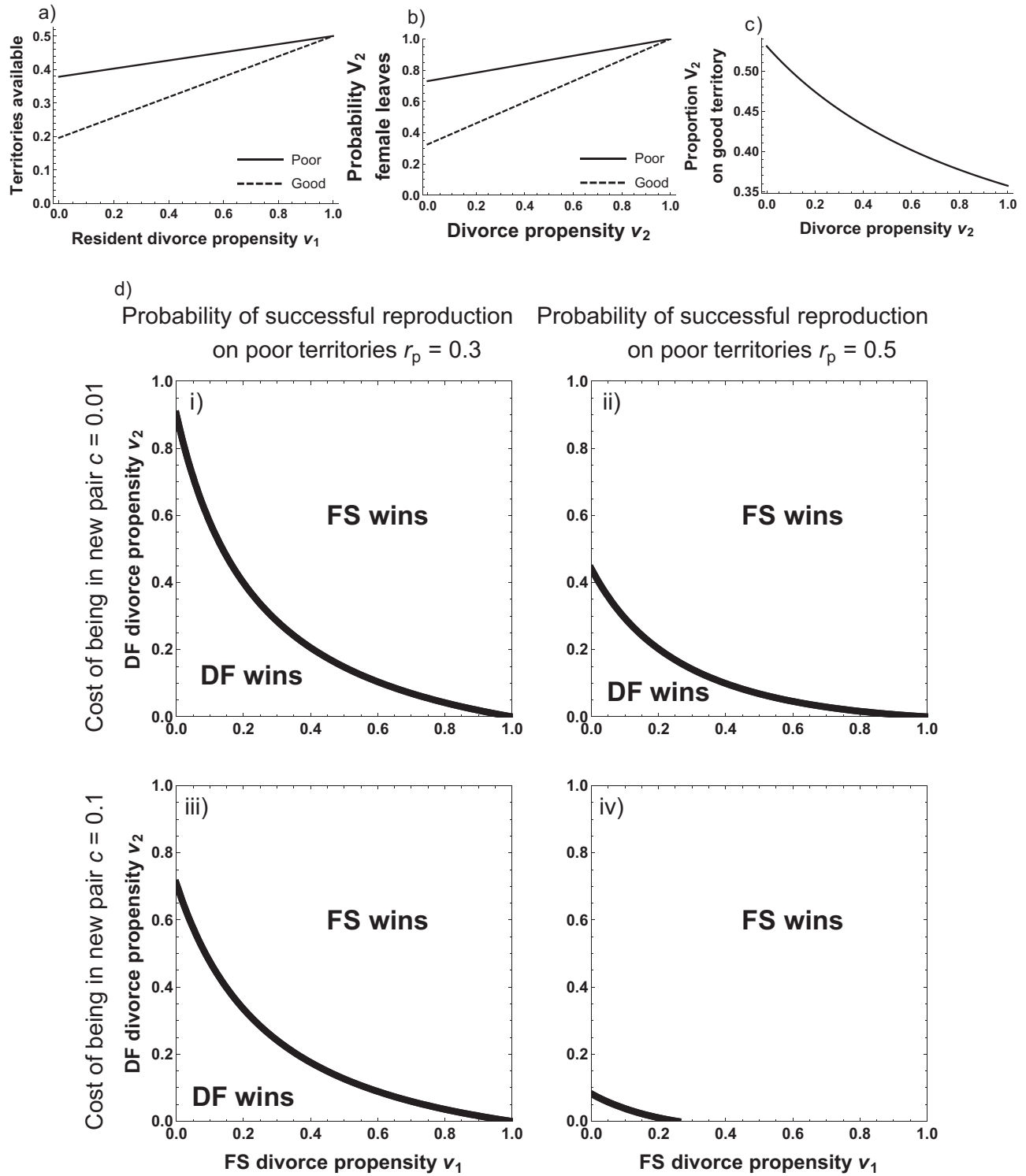
Figure 4: Analysis of divorce strategy where females always leave failed nests and sometimes leave successful nests using parameter values that are expected to be highly favorable for divorce and the divorce upon failure strategy. For a–c, a resident strategy with $v_1 = 0$ is invaded by a mutant strategy v_2. a, In this model variant, still more poor territories are available for females than good territories, as in figure 1b. b, Increasing divorce propensity leads to individuals with higher divorce propensities increasingly leaving good territories. In other words, the difference between leaving poor territories and leaving good territories decreases with increasing divorce propensity, while this increased in the initial model. c, The result of this is that a positive association forms between individuals that never divorce after nest success and good territories. As a result, females evolve to lower their divorce propensity. d, Competition between divorce upon failure (DF) and faithful upon success (FS) strategies, with DF divorce propensity v_1 on y-axis and FS divorce propensity v_2 on x-axis. i–iv show the winner of the pairwise competition. Parameters (unless otherwise noted in figure): $s = 0.9$, $p_g = 0.5$, $r_g = 0.75$, $r_p = 0.3$, $c = 0.2$.

territories is low. A low probability of successful repro-
duction on poor territories (and high probability on good
territories) implies that nest failures are informative about
territory quality, disfavoring the faithful upon success
strategy with low divorce propensities that often remain
on poor territories following nest failures. The overall re-
sult is that the constraints placed upon females by having
imperfect information about their territory quality often
favor a more conservative strategy of never divorcing after
a successful nesting attempt.

Discussion

We introduce a model of divorce that explicitly tracks the
distribution of available territories to show how divorce
itself alters the environment in which it must evolve. Fo-
cusing on feedbacks between the evolution of divorce and
the social environment (i.e., the distribution of available
territories) sheds new light on the benefits of divorce
(fig. 5). In particular, the interplay between death and di-
vorce on the distribution of available territories provides a
benefit to divorce whereby individuals with high divorce
propensities leave poor territories at a greater rate than
individuals with low divorce propensities. This results
in a positive association between individuals that divorce
more and good territories. Elucidating these costs and
benefits provides a mechanistic explanation of how envi-
ronmental heterogeneity (in particular, nest predation)
and mortality influence the evolution of divorce, showing
that high environmental heterogeneity and intermediate
mortality are most favorable for divorce to evolve. Impor-
tantly, the benefit to divorce is valid even if a female can-
not precisely assess the quality of her own territory and
has no information about other territories. More broadly,
this perspective connects the evolution of divorce to a
broader theoretical literature on the influence of environ-
mental feedbacks on evolutionary outcomes (Kokko and
Lundberg 2001; Ravigné et al. 2009).

We also find that a strategy of always divorcing after
nest failure as well as sometimes after success rarely out-
competes a strategy of always remaining faithful following
a successful nest but sometimes divorcing after the nest
fails. Under the former strategy, females with higher di-
vorce propensities increasingly leave good territories; thus,
the fact that females cannot accurately assess their territory
quality influences divorce, in this case driving the evolution
of greater fidelity. Though we cannot assess which divorce
strategy is more often found in nature (both predict divorce
being more common after low reproductive success), they
bracket the range of possibilities and show an important
feature of an evolutionarily stable divorce strategy that al-
lows females to trade up: namely, females are increasingly
more likely to leave poor (rather than good) territories with
increasing divorce propensity.

Divorce in our model evolves via the better options hy-
pothesis (Ens et al. 1993), wherein individuals divorce to
obtain a higher-quality breeding scenario (in our model a
territory, or in other models a mate). Much empirical sup-
port suggests that this often explains divorce (Dhondt and
Adriaensen 1994; Orell et al. 1994; Otter and Ratcliffe 1996;
Blondel et al. 2000; Moody et al. 2005; Streif and Rasa 2008;
Culina et al. 2015). Our model shows that the better op-
tions hypothesis is valid even if females cannot gain infor-
mation about other territories and mates (much like Mc-
Namara and Forslund 1996) and also even if females can
never perfectly assess the quality of their territory/mate.
In this case, divorce evolves because it provides a mecha-
nism to preferentially leave poor territories, giving a better
option than staying (app. S6). This is the crux of the feed-
back between the social environment and the evolutionary
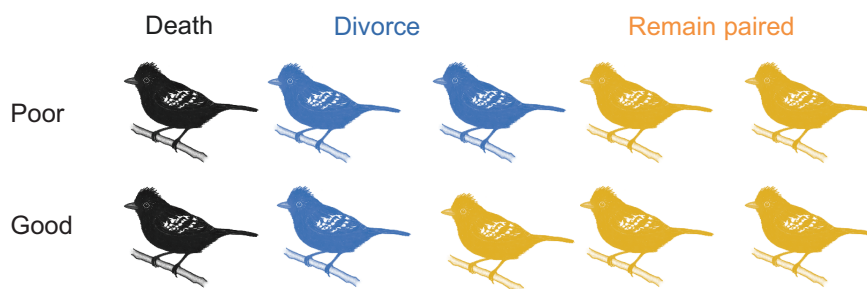dynamics. The complexity of how females that divorce

Figure 5: Why divorce results in trading up. In this example, there are an equal number of poor and good territories. Because divorce
occurs more often from poor territories, after death and divorce, 40% of available territories (two out of the five freed by these processes)
are good. Since death occurs randomly, females vacate good territories 50% of the time that they lose their partner and trade down on av-
erage. In divorce, females vacate good territories only 33% of the time and hence trade up on average. Note that if death did not occur, only
33% of available territories would be good (from divorce alone), so divorce would not result in trading up. Thus, the fact that some terri-
tories are vacated by death is necessary for there to be a benefit to divorce.

more spend more time in high-quality reproductive opportunities is an aspect of the better options hypothesis that has been previously underdeveloped.

Our model identifies two regimes for how mortality mechanistically influences the evolution of divorce, suggesting a way to generalize its impact by examining frequency-dependent feedbacks between divorce and the distribution of available territories. First, death works against a female's ability to leave a poor territory more often than a good territory by divorcing (fig. 3c), disfavoring its evolution. Second, at the same time, death makes good territories available for females, enhancing the potential benefit of divorce (fig. 3d). This leads to the feedback between divorce and the social environment that we have stressed previously. The key is that individuals that divorce can leave poor territories disproportionately more often than good territories, not that divorce allows individuals to be any more likely to acquire a good territory than a widow (fig. 5). Because widows do not leave poor territories disproportionately often, the cost to becoming widowed is, on average, greater than the cost to divorce.

As noted above and elsewhere (Choudhury 1995; McNamara and Forslund 1996), mortality can have conflicting impacts on the evolution of divorce. However, in the model of McNamara et al. (1999), divorce typically increases monotonically with survival, at least between the 50% and 90% annual survival rates that they examined (their table 1). In their model, females assess (fixed) male quality after one season of breeding with him. Hence, in their model, divorce is favored because a long-lived female has more to gain from finding a partner of above average quality. Our results are similar, predicting divorce propensities to maximize at intermediate survival rates, often beyond 90% for the parameters explored. In our model, females assess territory quality every breeding episode, and whenever breeding fails, a female is more likely to divorce. Consequently, species with high survivorship may still experience high divorce rates. Contrasting with these theoretical studies, empirically, divorce rates monotonically decline with increasing adult survival over the 50%–90% range (fig. S1). We see two explanations for the discrepancy. First, intermediate survival may indeed favor the highest divorce rates, but changing multiple parameters between the species obscures this signal. Second, features not included in the present models may be required. That is, the evolution of divorce may be highly contingent on biological details, as suggested by some model results. For example, McNamara and Forslund (1996) noted that cost of pairing with a new partner (increasing c) reduces the divorce rate in short-lived species but not long-lived species (a result mirrored by fig. 2). However, a fidelity cost of waiting for a deceased partner to return (e.g., in migratory species) dramatically increases the divorce rate of short-lived but not long-lived species. Finally, patterns of mortality may also change as a result of divorce (as shown in Brent geese *Branta bernicla*; Leach et al. 2020), which could alter conclusions.

Earlier models focused on male quality (McNamara and Forslund 1996; McNamara et al. 1999; Dubois et al. 2004) rather than environmental heterogeneity, a feature we consider with three parameters (probability of successful reproduction on good territories r_g, probability of successful reproduction on poor territories r_p, and proportion of all territories that are good p_g). The resulting predictions are similar when comparing the roles of individual and territory quality. In both cases, increasing the variance in benefits accruing to females (whether territory or mate quality) increases the divorce rate. Thus, comparing between these models shows that environmental and individual heterogeneity provide two analogous paths for influencing divorce that are mechanistically equivalent despite being biologically distinct.

Given that most work on the evolution of divorce is observational, better understanding the drivers of divorce provides an exciting opportunity for future work. Because all of the models for the evolution of divorce developed so far have included either male quality or environmental heterogeneity but not both, it would be interesting to consider both of these features simultaneously. If associations develop between individual and territory quality, then these two aspects could interact synergistically, although dynamics may not be so straightforward if low-quality individuals or territories have higher mortality rates. Additional realism—such as female-biased adult sex ratios (suggested to increase divorce rates; Liker et al. 2014), variance among females in the costs and benefits of divorce (Wheelwright and Teplitsky 2017), or age-dependent mortality—could also be included in the model. Age-dependent mortality, in particular, may alter some of our conclusions regarding intermediate survival rates favoring divorce. This is possible if individuals pair assortatively with respect to age, in which case relatively fewer widows may be created (because females may die at the same time as their mate), potentially complicating the way that increased survival can decrease the ESS divorce propensity. However, senescence in wild birds contributes only a very small fraction to annual mortality (e.g., Bouwhuis et al. 2009). Further, although ecology plays a central role in our model (through environmental heterogeneity and the associated feedbacks), we make many simplifying assumptions about the ecology of the system (such as fixed population size). Given the potential for mate search and Allee effects to constrain the evolution of divorce (Berec and Boukal 2004), incorporating realistic ecological features may influence our results in important ways. For example, divorce is capable of driving population cycles (Maxin and Berec 2010), so interesting

eco-evolutionary dynamics might arise if divorce rate was allowed to evolve with changing population sizes. Additionally, since space is important for mate fidelity through extrapair copulations (Lerch et al. 2020) and mate choice (Berec and Boukal 2004), this could be another factor affecting the evolution of divorce (as suggested in Catry et al. 1997; Moody et al. 2005; Botero and Rubenstein 2012).

In addition to theoretical extensions, this model suggests multiple empirical directions. The role of environmental heterogeneity in divorce has largely been neglected in empirical studies, but assessing this would test our prediction that populations with high levels of environmental heterogeneity have high divorce rates. Indeed, a recent study has documented the importance of temporal environmental heterogeneity for divorce in albatross (*Thalassarche melanophris*; Ventura et al. 2021). Our prediction that populations that divorce more are expected to have lower mean fitness (fig. S4) is an example of a tragedy of the commons (Rankin et al. 2007) that could also be tested empirically. The environmental, ecological, and life history factors that influence the costs and benefits of divorce along with the opportunities for more theoretical and manipulative work make this an exciting direction for the evolution of reproductive behavior.

Acknowledgments

Statement of Authorship

T.D.P. and M.R.S. developed the initial (now population genetic) model and assumptions; B.A.L. finalized the model, developed the game-theoretic version of the model, and led the development of the model variants. B.A.L. led the analysis of the model with input from M.R.S. B.A.L. wrote the first draft of the manuscript with substantial edits made by all authors.

Data and Code Availability

Code replicating results have been deposited in Zenodo (https://doi.org/10.5281/zenodo.6506637; Lerch et al. 2022).

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