



Fitness consequences of divorce in the oystercatcher, *Haematopus ostralegus*

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(Received 30 October 2001; initial acceptance 7 December 2001;
final acceptance 3 December 2002; MS. number 7113R)

We investigated the fitness consequences of divorce in oystercatchers. We made a distinction between two types of divorce: in desertions the disruption of the pair bond is initiated by one of the pair members, and in usurpations by a conspecific individual. Survival and reproduction prospects for oystercatchers are largely determined by their social status (nonbreeder or breeding bird at a site of a specific quality). Changes in social status in relation to divorce showed that birds taking the initiative to leave their mate increased in fitness, relative to birds that were forced to leave their partner. Status of individuals that remained in their territory after divorce was unaffected if their mate was expelled, but declined if their mate deserted. Survival after divorce was significantly lower for birds that were expelled than for those deserting. Divorce rate, and especially desertion rate, was higher among occupants of low- than high-quality territories. In general, divorce rate increased following elevated mortality. In high-quality territories usurpations increased with increasing breeder mortality, but at low-quality territories this relation was absent. Desertion rates were similarly related to mortality in both territory types. Divorce participants thus differed strongly in their fitness prospects, depending on the type of divorce, the role played in the divorce and the quality of the territory where divorce took place. Studies that do not observe the birds during divorce cannot determine the type of divorce and the role played by the individuals, and this may lead to misleading conclusions on the costs and benefits of divorce.

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Mate fidelity and divorce in monogamous bird species have been studied empirically for several decades (reviewed first in Rowley 1983). The degree of divorce in bird populations ranges from 0.0% in the wandering albatross, *Diomedea exulans* (Tickel 1968, cited in Dubois et al. 1998) to 99% in the greater flamingo, *Phoenicopterus ruber roseus* (Cézilly & Johnson 1995). Part of this variance can be explained by the type of partnership and migratory behaviour: species with high divorce rates tend to have part-time partnerships and be migratory more often than species with low divorce rates (Ens et al. 1996). In an analysis of all species for which data were available,

Ens et al. (1996) did not find an effect of site fidelity on divorce rate, but Cézilly et al. (2000a) observed that divorce rates were positively correlated with site faithfulness in Ciconiiformes.

Theoretical models (McNamara & Forslund 1996; McNamara et al. 1998) have only recently been developed, and a number of hypotheses to explain divorce have been put forward (reviewed in Choudhury 1995; Black 1996). The hypotheses can be grouped into four categories based on the ultimate causes of divorce.

(1) According to the 'incompatibility hypothesis' (Coulson 1966), some pairs have reduced success because they consist of incompatible partners. Both members of such pairs might initiate the events that lead to divorce and both are predicted to experience an increase in fitness after the divorce.

(2) According to the 'better option hypothesis' (Ens et al. 1993), an individual should initiate a divorce when the net expected benefits of breeding with a new mate outweigh the costs of pursuing the old pair bond and the costs of divorce itself. Only the individual initiating

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This paper is dedicated to the memory of our friend Jean-Paul Ongenae, young Dutch ornithologist.

the divorce is expected to benefit in terms of fitness. McNamara & Forslund (1996) modelled the optimal divorce strategy of females under such circumstances, assuming that only females initiate divorce and McNamara et al. (1998) derived the evolutionarily stable strategy when both males and female can initiate a divorce in favour of a better option.

Finally, it is possible that neither pair member initiates the divorce or enjoys fitness benefits. (3) According to the 'forced divorce hypothesis' (Ens et al. 1993; Taborsky & Taborsky 1999), an outsider usurps the breeding position of one of the pair members and only the usurper is expected to benefit. (4) According to the 'habitat-mediated hypothesis', an external event other than usurpation destroys the basis of the partnership leading to divorce (we prefer this name proposed by Desrochers & Magrath 1993 to the 'accidental loss hypothesis' from Owen 1988, cited in Choudhury 1995).

Other hypotheses can all be considered as proximate variations of these four ultimate explanations. For example, the musical chair hypothesis (Dhondt & Adriaensen 1994), expensive fat storage hypothesis (Olsson 1998), asynchronous arrival hypothesis (González-Solís et al. 1999) and bet-hedging hypothesis (Handel & Gill 2000) should not be confused with the ultimate costs and benefits of divorce. For instance, the asynchronous arrival hypothesis might be a variant of the incompatibility hypothesis (early- and late-arriving individuals reproduce equally well, but pair members arriving at different times on the breeding grounds do worse) or the better option hypothesis (early arrivers do best; late arrivers are in poorer condition and are less fit; early-arriving birds can better pair with birds that also arrive early).

Studying the actual process resulting in a divorce and the behaviour of the participants is time consuming and difficult. However, as the previously described hypotheses make clear, the study of this process is crucial, because the cause of a divorce, whether the initiative arises within the pair or comes from an outsider, can have major consequences for the participants. An individual that deserts its mate in favour of a better option is expected to enjoy a fitness gain, whereas an individual that is ousted by a usurper is expected to suffer a loss in fitness. In a territorial species such as the oystercatcher, an individual can do nothing to prevent its mate from deserting the territory. However, a bystander can decide whether to assist its mate against potential usurpers (Ens 1992). If desertions and usurpations both occur in the population, the overall fitness consequences of divorce in general may be blurred by the averaged opposite fitness effects.

Divorce has been studied in a population of individually marked oystercatchers breeding on the Dutch island of Schiermonnikoog (53°29'N, 6°14'E) since 1985. We used this data set to examine whether the consequences of a pair breakup are strongly related to the type of divorce. Ens et al. (1993) predicted improved fitness prospects for individuals that 'voluntarily' changed mate, as in desertions, particularly for birds deserting low-quality territories. Ens et al. (1993) also predicted decreased fitness prospects for individuals that

were forced to change mate, as in usurpations; this decrease should be particularly large for birds from high-quality territories. Individuals whose mate was expelled were predicted to have better fitness prospects than those whose partner left voluntarily. Birds in poor-quality territories can improve by switching to (1) a better-quality mate or (2) a mate with a territory of higher quality. There would be less scope for improvement through option 2 for birds in high-quality territories. We therefore predicted that divorces in low-quality territories would comprise mainly desertions, whereas in high-quality territories we expected mostly usurpations. Furthermore, we predicted desertion rate to increase and evictions by nonbreeders to decrease after high breeder mortality, allowing breeders to desert their mates to join widows in the population, and allowing nonbreeders to occupy the more easily available vacant sites instead of usurping established breeders.

METHODS

Study Population

We studied the Schiermonnikoog oystercatchers from 1985 to 2000. For a detailed description of the area and the methods see Heg et al. (2000). Colour ringing of unmarked breeders and fledglings started in 1983, and nearly all breeders in the study area were individually marked from 1984 onwards. Divorces could be determined from 1985 onwards. During the study, an increasing number of new settlers were already colour marked because of recruitment of birds born in the study area and large-scale catching and marking of nonbreeders.

In general, oystercatchers are long lived and site faithful. The semiprecocial young are fed by both parents, which rear only one brood to fledging per breeding season. Pair members cooperatively defend their territories in easily visible and noisy displays with their neighbours. This territorial and courtship behaviour starts in March, when the birds reoccupy their territories, having spent the winter feeding on more distant mud flats. Egg laying starts 2 months later. Territory ownership, pair bond and mates were determined in the main study area on a weekly basis from March to August by observations from hides. We defined two oystercatchers as a pair and their activities as a breeding attempt, when male and female cooperatively defended a nesting territory, roosted in close proximity and frequently copulated in their nesting territory. This was usually followed by egg laying, shared incubation and shared chick-feeding duties. Chicks were caught by hand at the age of 25 days and marked with plastic leg rings, under licence of the Animal Ethics Committee (DEC) of the University of Groningen.

Oystercatchers occupy breeding territories of different quality, depending on the spatial orientation of the nesting and feeding territories (Ens et al. 1992). We distinguish two types: residents and leapfrogs. Residents occupy a nesting territory close to the shoreline with an adjacent feeding territory on the mudflats. The feeding territory is accessible only during low tide, and the

Table 1. Characterization of the individuals involved in desertion and usurpation and whether they changed to a new territory or remained in the same territory during the divorce

Participant	Description of role	Change in territory
Desertion		
Victim of desertion	Abandoned by partner	Remains
Deserter	Abandons mate	Moves to another
Usurpation		
Victim of usurpation	Forced to abandon mate	Forced to leave
Bystander	Loses old mate, gains new mate	Remains

The participants might be unsuccessful in keeping their breeding territory and/or mate after the divorce.

semiprecocial chicks follow the parents to the mudflats to feed. Leapfrogs occupy a nesting territory further inland and a spatially segregated feeding territory further offshore. Their chicks do not follow them to the mudflats, but wait in the nesting territory to be fed. [Ens et al. \(1995\)](#) estimated that residents fledge 0.67 chicks whereas leapfrogs fledge only 0.19 chicks per pair annually. Although feeding territories may differ strikingly in size and food density, so far this variation has not been linked to fledgling production ([Heg 1999](#)). Early-laying females fledge more chicks than late-laying females, regardless of territory quality, and early-laying females are in significantly better body condition than late-laying females ([Heg 1999](#)). This suggests that there is variation in individual quality, independent of variation in territory quality, which might affect the probability of divorce. However, we restricted the analyses to the different types of divorce in the population in relation to territory quality and annual survival, and ignored the potential effects of individual quality on divorce rate. We categorized oystercatchers into three social classes (henceforth 'social status'): residents, leapfrogs and nonbreeders ([Ens et al. 1992, 1995; Heg et al. 2000](#)). Nonbreeders were birds not in possession of a nesting territory, but observed on communal high-tide roosts and intruding into nesting territories.

Desertion and Usurpation

[Choudhury \(1995\)](#) defined divorce as a pair breakup at any time of the year when both partners are still alive and where the subsequent breeding attempt, if any, of at least one bird is with another bird. [Ens et al. \(1993\)](#) described how oystercatchers divorce. Two basic types of divorce can be distinguished: desertion and usurpation ([Table 1](#)).

In desertion, the pair bond is disrupted by one of the focal pair members (also called mate desertion). One pair member (the 'deserter') takes the initiative to disrupt the pair bond, and leaves the territory and its mate (the 'victim of desertion'). Desertions are characterized by three successive events. First, a breeder switches back-and-forth between the old and the new mate for a certain time. Next, the deserter is no longer associated with the old mate, which usually remains unpaired for a couple of days up to several weeks. Lastly, the victim of desertion (the old mate) may obtain a new mate.

In usurpations, a conspecific outsider, that is, not one of the focal pair members, disrupts the pair bond. First, an individual repeatedly intrudes into a territory and challenges a pair member of the same sex. Next, the usurper engages in severe fights with the pair member, which might last a couple of days up to several weeks. Finally, the pair member is evicted from the territory. The focal breeder that is forced to leave the territory is labelled the 'victim of usurpation', and the ex-mate of a victim of usurpation is called a 'bystander' ([Ens et al. 1993](#)). The role of the bystander seems passive, but repeated intrusions are common in oystercatchers and a cooperative pair can easily displace a single intruder. When the usurper successfully evicted a pair member, the bystander did not assist its mate in a joint effort to deter the intruder. In this sense bystanders have a decisive role. Usurpations always include an outsider, breeder or non-breeder. We never observed a bird evict its own mate.

We observed 13 cases of individuals engaging in sequential divorces within one breeding season, or divorces of new pairs within the season of settlement, or pairs chased from their territory leading to divorce (see also [Heg et al. 2000](#)). These cases were omitted from all analyses, as were all divorces within polygynous pairs ([Heg & van Treuren 1998](#)). Divorce rate was calculated as the number of divorced pairs in a year, divided by the total number of reuniting and divorced pairs in our study site for that year. When we refer to divorce rate, we refer to the sum of desertion rate and usurpation rate.

Fitness Estimates

We documented the social status for each individual annually. Social status largely determines reproductive output in oystercatchers ([Ens et al. 1992; Heg 1999](#)). To analyse the fitness consequences of divorce, we compared the status of an individual before and after divorce (within a year). Social status changes were investigated in relation to the type of divorce and the participation in the divorce (whether birds moved to another territory or remained in their original territory immediately after divorce). In the next step, year-to-year status changes in the 4 years after the divorce were calculated. These estimates were not corrected for resighting rates, because the resighting rate for adult breeders and ex-breeders equals 1 in our main study area. Survival probability is highly

Table 2. The social status of males and females before and after divorce broken down by type of divorce and participant

Social status before divorce, sex	Social status after divorce			
	Resident	Leapfrog	Nonbreeder	Total
Desertion				
Victims of desertion				
Resident, ♂♂	4	1	5	10
Resident, ♀♀	0	0	0	0
Leapfrog, ♂♂	2	22	10	34
Leapfrog, ♀♀	0	5	7	12
Total	6	28	22	56
Deserters				
Resident, ♂♂	0	0	0	0
Resident, ♀♀	5	4	1	10
Leapfrog, ♂♂	4	6	2	12
Leapfrog, ♀♀	10	17	7	34
Total	19	27	10	56
Usurpation				
Victims of usurpation				
Resident, ♂♂	0	0	5	5
Resident, ♀♀	1	3	9	13
Leapfrog, ♂♂	0	0	7	7
Leapfrog, ♀♀	0	5	26	31
Total	1	8	47	56
Bystanders				
Resident, ♂♂	13	0	0	13
Resident, ♀♀	5	0	0	5
Leapfrog, ♂♂	0	30	1	31
Leapfrog, ♀♀	0	7	0	7
Total	18	37	1	56

dependent on winter severity (Camphuysen et al. 1996), and hence we corrected survival for this effect (the winters following 1985, 1995 and 1996 were very severe; see Results). Second, we calculated the expected future lifetime reproductive success, based on these social status changes, using the value of 9.2 expected lifetime fledglings for residents, 5.2 fledglings for leapfrogs and 4.4 fledglings for nonbreeders (Ens et al. 1995). These estimates are based on the annual survival probability per social status (assuming survival is independent of age), the probability of acquiring or maintaining a certain social status, and annual reproductive success per social status. We show in the Results that the social status obtained just after divorce suffices to estimate the future probabilities of acquiring a certain social status (i.e. the type of participant has a significant effect on the social status just after divorce, year t , but no effect on the social status in year $t+n$ when corrected for the social status obtained just after divorce). Hence, the expected future lifetime reproductive success for each participant is the weighted average of the expected lifetime reproductive success of the individuals becoming resident, leapfrog and nonbreeder in the year of divorce, respectively. Assuming that survival is independent of age crucially affects the quantitative results, but the qualitative results will essentially be unaltered. Third, we compared the fledgling production of divorce participants in the 3 years before divorce until 4 years after divorce. In this analysis we corrected for the variation between years and social status.

RESULTS

Divorce Rate

We observed 112 cases of divorce (Table 2), with similar numbers of desertions and usurpations. The identical sample sizes are a coincidence. Average annual divorce rate in our population was 7.9%, annual desertion rate was 3.8% and annual usurpation rate 4.1%. Local survival of breeding birds was high on average (92.9%, range 71.0–99.0%, $N=16$) and only after severe winters did we observe substantially lowered survival (3 years with survival rates of 71, 86 and 78%, respectively). After moderate or mild winters survival was on average 96% (range 92–99.0%, $N=13$). Survival of residents and leapfrogs were correlated over the years (Spearman rank correlation: $r_s=0.65$, $N=16$, $P<0.01$) and did not differ significantly (Wilcoxon signed-ranks test: $Z=-0.91$, $N=16$, $P=0.4$). Divorce rate in general increased with increasing mortality of the breeding birds in the population (logistic regression: $W_1=12.49$, $P<0.001$) and was higher for leapfrogs ($W_1=17.90$, $P<0.0001$); the relation with mortality differed between residents and leapfrogs ($W_1=3.96$, $P<0.05$).

We also split the total divorce rate into its two components, usurpation rate and desertion rate, and analysed them separately. Usurpation rates increased with breeder mortality ($W_1=16.90$, $P<0.001$), depended on social status ($W_1=4.64$, $P<0.05$), and their interaction was highly significant ($W_1=10.65$, $P<0.001$). Usurpations increased in residents after high breeder mortality

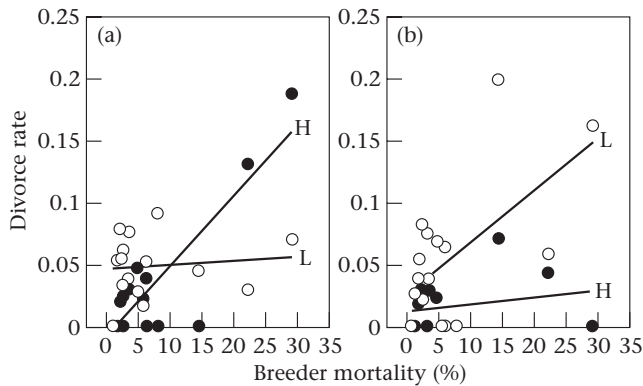


Figure 1. (a) Annual usurpation rate and (b) desertion rate as a function of mortality among breeders in the preceding winter, for birds in high-quality territories (residents; ●, lines labelled H) and in low-quality territories (leapfrogs; ○, lines labelled L).

($W_1=26.46$, $P<0.001$), but were unaffected by mortality in leapfrogs ($W_1=0.701$, $P=0.4$; Fig. 1a). The average annual usurpation rate was 3.3% for residents and 4.8% for leapfrogs.

Desertion rates also increased after elevated breeder mortality ($W_1=18.53$, $P<0.001$) and were more common in low-quality territories ($W_1=14.836$, $P<0.001$), but here the interaction was not significant ($W_1=0.209$, $P=0.6$). Desertion rate increased similarly in both territory types after breeder mortality (Fig. 1b). The average annual desertion rate was 1.6% for residents and 5.6% for leapfrogs.

Divorce and Status Change

Table 2 summarizes all divorce cases and the associated changes in social status. Females that divorced changed social status more often than males (79 and 21%, binomial test: $P<0.001$). This was independent of whether they deserted or were evicted (log-linear model: desertion or eviction \times sex: $\chi^2_1=0$, $P=1.0$) and of the type of territory where the divorce took place (resident or leapfrog \times sex: $\chi^2_1=0.3$, $P=0.58$).

To depict the positive and negative changes in social status, we gave birds in high-quality positions one point, birds in low-quality territories two points and birds without a breeding territory three points. A change in status was calculated as the old status minus the new status. Positive changes in social status indicated birds promoted to a social category with higher fitness perspectives (range -2 to 2 ; Fig. 2). We investigated these changes in social status with respect to the social status before the divorce, sex, the type of divorce and movement (i.e. deserting or forced to leave the old territory, that is, deserters and usurped individuals, versus remaining in the same territory, that is, victims of desertion and bystanders). This distinction is based on the territory movements of divorce participants during the divorce, but victims of desertions and bystanders may lose their territory a few days later if they do not acquire a mate in time. Multinomial logistic regression ($R^2=0.51$, $\chi^2_{12}=157.6$,

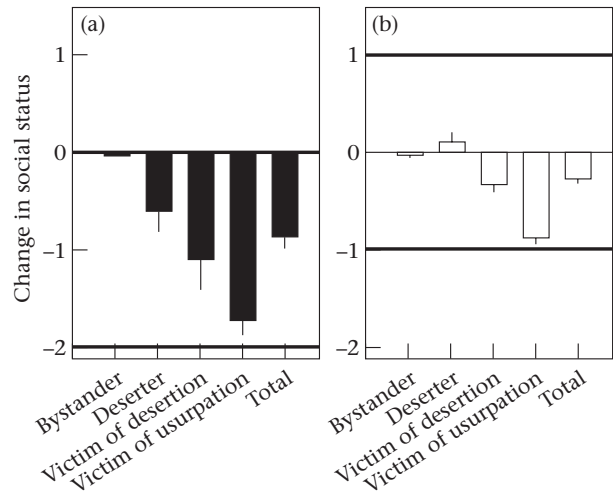


Figure 2. Change in social status ($\bar{x}\pm SE$) for all participants in divorce. The participants in the divorce are separated according to their status prior to the divorce: (a) high-quality territories (residents) and (b) low-quality territories (leapfrogs). Social status in a high-quality territory was given the value 1, low-quality territory 2 and nonbreeder 3; status change is status prior to divorce minus new status. Per definition the scope for a change in status is different for the two categories: the horizontal lines represent the maximum and minimum change attainable for both.

$P<0.001$) showed that all four factors affected the change in status: social status before divorce ($\chi^2_3=74.2$, $P<0.001$), sex ($\chi^2_3=10.7$, $P<0.05$), type of divorce ($\chi^2_3=21.5$, $P<0.001$) and movement ($\chi^2_3=44.4$, $P<0.001$). The model explaining most of the variance ($R^2=0.63$, $\chi^2_{12}=220.5$, $P<0.001$) included only the status before divorce ($\chi^2_3=73.00$, $P<0.001$) and a significant interaction of the type of divorce and movement (deserters and usurped individuals versus victims of desertion and bystanders: $\chi^2_3=133.09$, $P<0.001$). These results imply that breeders on average lost more status in usurpations than in desertions, and birds changing territory lost more status than those remaining in the former territory immediately after divorce (Table 2). Furthermore, the victims of desertion lost status compared to deserters (the 'movers'). As predicted, this effect of movement was opposite in usurpations: the victims of usurpation (the 'movers') lost status, but bystanders were unaffected.

All consequences of divorce were dependent on the status before divorce. In other words, residents lost more status (and had more to lose) from a divorce than did leapfrogs (Fig. 2). A comparison of the status change between all participants in a divorce for a given territory (Fig. 2) showed that in high-quality territories (residents), deserters and victims of desertion did not differ in status change (Mann–Whitney U test: $U=35.5$, $N_1=N_2=10$, $P=0.2$) and that victims of usurpation did not differ from victims of desertion ($U=59.5$, $N_1=18$, $N_2=10$, $P=0.1$). All other participants differed significantly from each other (all $P<0.005$, or $P<0.03$ after Bonferroni correction). In low-quality territories, only deserters did not differ from bystanders (Mann–Whitney U test: $Z=-1.26$, $N_1=46$, $N_2=38$, $P=0.2$) and all other participants differed

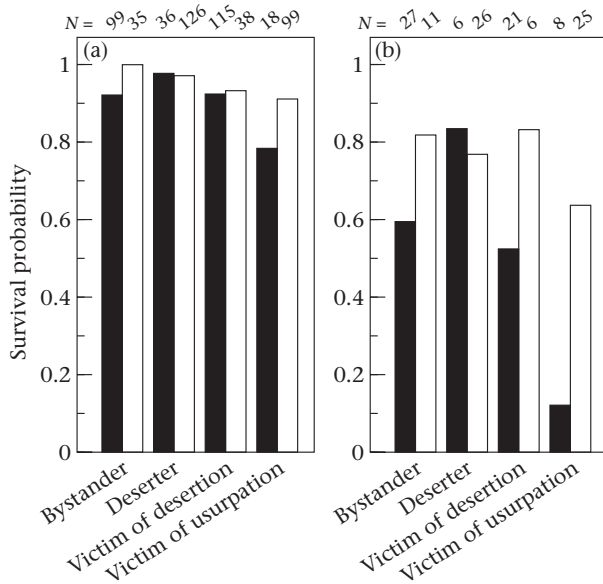


Figure 3. Annual survival probability for all participants in divorce depending on sex and winter severity. (a) Mild and (b) severe winters. Data for 1–4 years post divorce. ■: Males; □: females. Sample sizes are indicated above the bars.

significantly (all $P < 0.005$, or $P < 0.03$ after Bonferroni correction).

Divorce and Fitness

Survival and transition probabilities

Survival was analysed for all participants in divorce (Fig. 3). A categorical logistic regression model of survival, depending on sex, participant (bystander, deserter, victim of desertion or usurpation), status before divorce (resident or leapfrog), years since divorce (1–4) and winter severity (mild or severe), showed a significant effect of sex, participant, winter severity and an interaction between sex and participant (model likelihood ratio: $\chi^2_8 = 95.0$, $P < 0.0001$; coefficient \pm SE of the constant = 0.74 ± 0.58 ; sex: $\chi^2_1 = 6.2$, $P = 0.013$; coefficient for males = -4.87 ± 0.61 ; participant: $\chi^2_3 = 13.7$, $P = 0.003$; coefficient for deserter = 0.51 ± 0.65 , bystander = 1.19 ± 0.93 , victim of usurpation = -0.39 ± 0.62 , victim of desertion is the reference category; winter severity: $\chi^2_1 = 85.5$, $P < 0.0001$; coefficient for mild winter = 2.12 ± 0.26 ; sex \times participant: $\chi^2_3 = 26.4$, $P < 0.001$; coefficient for deserter male = 0.76 ± 1.03 , bystander male = -1.10 ± 1.00 , victim of usurpation male = -1.01 ± 0.81).

The social status 1 year after divorce (for individuals surviving) was, as predicted, dependent on the status just after divorce (loglinear model: status just after divorce \times status 1 year after divorce: $\chi^2_6 = 53.3$, $P < 0.001$) and was not affected by the role played in the past divorce (participant \times status 1 year after divorce: $\chi^2_6 = 7.6$, $P = 0.3$). Similar results were found for the status 2 ($\chi^2_6 = 5.1$, $P = 0.5$), 3 ($\chi^2_6 = 2.0$, $P = 0.9$) and 4 years after divorce ($\chi^2_6 = 4.43$, $P = 0.6$). Thus the part played in the divorce strongly influenced the social status obtained just after the

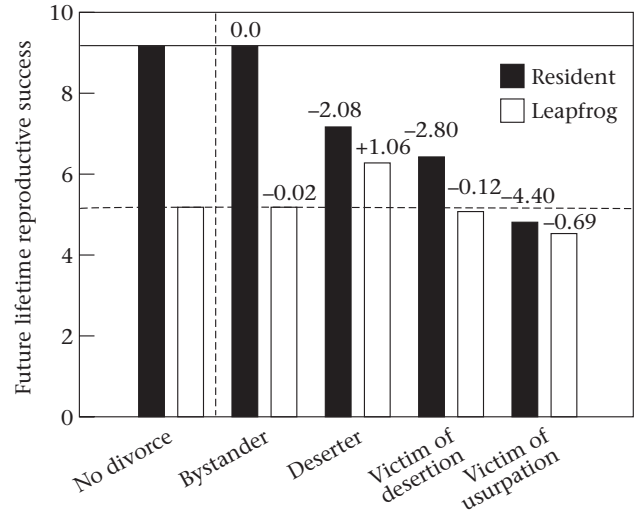


Figure 4. Expected future lifetime reproductive success (i.e. number of fledglings produced) of the participants in the divorce, depending on their status before the divorce occurred (resident or leapfrog). Control values for residents (solid line) and leapfrogs that do not divorce (dashed line) are indicated, and the changes from these values are given above the bars.

divorce, and knowing this status just after divorce sufficed to predict the long-term fitness effects of divorce for each participant.

Future lifetime reproductive success

For leapfrogs, the predicted future lifetime reproductive success (FLRS) increased for deserters, and decreased for the victims of desertion and usurpation (Fig. 4). For residents, however, all participants (except bystanders) decreased in FLRS, including the deserters (Fig. 4). This reflects the low scope for improvement in mate and territory quality for residents deserting their mate.

This raises the question why residents should desert their mates and territory at all. We observed a considerable proportion of resident deserters leaving their mate and territory for a leapfrog territory (40%) or no nesting territory at all (10%, Table 2). In addition, 20% of the leapfrog deserters chose to become nonbreeders, instead of continuing breeding with the old mate (Table 2). Some resident and leapfrog deserters tried to obtain a new breeding territory, but failed to acquire one. So why should both residents and leapfrogs desert their mates for a nesting territory of lower quality and take the risk of getting no breeding territory at all? Deserters had a significantly lower reproductive success in their old territory preceding divorce, and quickly improved their reproductive success after the divorce (one-way ANOVAs with years around divorce as fixed effect and polynomial contrasts: $F_{7,354} = 2.2$, $P = 0.04$, with significant quadratic term $P = 0.014$; intercept $F_{1,354} = 2.9$, $P = 0.09$; Fig. 5). No such relation was found for bystanders ($F_{7,280} = 1.1$, $P = 0.38$; intercept $F_{1,280} = 1.0$, $P = 0.33$) and victims of usurpation ($F_{7,182} = 0.9$, $P = 0.49$; intercept $F_{1,182} = 1.3$, $P = 0.26$; Fig. 5). The relation for victims of desertion was different from the deserters, because these victims did not

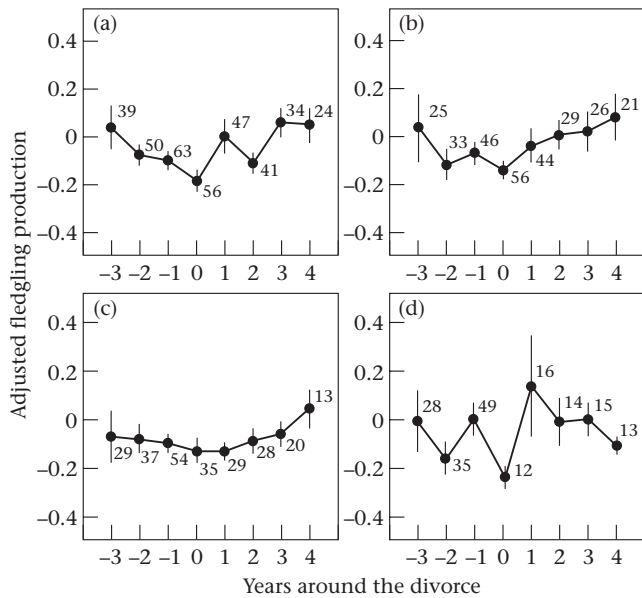


Figure 5. Adjusted fledgling production \pm SE for the participants in divorce, in the 3 years before to the 4 years after divorce. (a) Deserter, (b) bystander, (c) victim of desertion and (d) victim of usurpation. Divorce occurred at year 0. Sample sizes (the number of breeding individuals) are indicated. Adjusted fledgling production is the fledgling production minus the average fledgling production for that particular year and territory quality (resident or leapfrog).

recover their reproductive success after the divorce as quickly as deserters did ($F_{7,245}=0.5$, $P=0.48$; intercept $F_{1,245}=11.8$, $P=0.001$; Fig. 5). Using mixed model ANOVAs with years around divorce as a fixed effect and individual as a random factor gave essentially the same results (P values for the intercept and fixed effect, respectively, deserters: 0.039, 0.049; bystanders: 0.48, 0.41; victims of usurpation 0.27, 0.52; victims of desertion: 0.70, 0.002). If we assume that the deserters continue breeding with their old mates with such low success (ca. -20% compared to the control population), the FLRS of deserting is very similar to the FLRS of nondeserting.

DISCUSSION

The most important conclusion from our results is the large difference in fitness consequences between desertions and usurpations, and between the different participants in divorce. To our knowledge this is the first study systematically investigating these two types of divorce and its effects on the different participants. Territory quality and sex also appeared to be crucial for explaining the incidence of divorce.

Desertions and Usurpations

Both kinds of divorce were equally common in the population, but unevenly spread over high- and low-quality territories, and the sexes played different roles. As predicted, desertions were more common in low-quality territories, where individuals had more scope for improvement. In contrast, usurpations were slightly more

abundant in high-quality territories, where usurpers might have been more willing to engage in escalated fights, since they had more to gain compared to fighting for a low-quality territory (Heg et al. 2000). High incidences of mate separation in inferior habitats have been reported for blackbirds, *Turdus merula* (Desrochers & Magrath 1993, 1996), sparrowhawks, *Accipiter nisus* (Newton & Wyllie 1996), and blue tits, *Parus caeruleus* (Blondel et al. 2000). If it is generally true that desertions are more common in low-quality habitat and usurpations more common in high-quality habitat, it would suggest that for these species a large proportion of pair breakups involve desertions.

Divorce rate in oystercatchers was correlated with breeder mortality as reported by Ens et al. (1993). In barnacle geese, *Branta leucopsis* (Black et al. 1996), and kittiwakes, *Rissa tridactyla* (Coulson & Thomas 1985), both long-lived species, a similar relation was found. As predicted, desertions increased when the threshold to change mate was lowered by vacant breeding positions in the population. In contrast to expectation, the usurpation rate also increased in response to an elevated mortality, but only in high-quality territories. Widowed residents evicting other residents did not cause this, since they accounted for only 10% of the usurpations. The majority of usurpers originated from the nonbreeder pool (75%; see also Heg et al. 2000). The most likely explanation is that residents surviving the previous severe winter were handicapped the following breeding season and that nonbreeders took advantage of this. This explanation is supported by the fact that evicted breeders had lower survival after divorce. Bystanders in turn may favour these local familiar nonbreeders as replacement mates, therefore choosing not to assist their mates in repelling the intruder (Heg et al. 1993, 2000). Although bystanders will clearly profit if they let a partner in poor health be ousted by a healthy nonbreeder, the bystanding strategy also carries risks. Sometimes neither female succeeds in winning the contest and a polygynous trio develops (Heg & van Treuren 1998). For oystercatchers, polygyny does not lead to an increased reproductive success for males, and success is reduced for females (Heg & van Treuren 1998).

The divorce rate in our population (7.9%) is strikingly similar to that of 8.0% reported for oystercatchers breeding on the island of Skokholm, Wales, U.K. (Harris et al. 1987). Since mortality is low as well, this means that the majority of the pairs reunite each year, making divorcing a minority 'strategy'. Reuniting makes sense, because there is evidence that reproductive success increases with duration of the pair bond (Ens et al. 1993; Heg 1999). These ideas await experimental testing.

In the majority of cases, females were the initiators of divorce, either as deserter or as usurper. Black-capped chickadee, *Poecile atricapillus*, females deserted their territory for nearby experimentally created high-quality vacancies (Otter & Ratcliffe 1996). Indirect evidence that females are often the initiating sex in divorce exists for many species (reviewed by Cézilly et al. 2000b). It is usually females that move between territories, and males are usually site faithful; the moving sex is usually also the

sex with the most extensive natal dispersal. For species that show male-biased dispersal, there is evidence that males are also the moving sex in divorces (Aebischer et al. 1995; Williams & McKinney 1996).

Divorce Hypotheses

The long-term effects of divorce were in the predicted direction: all victims lost fitness, and deserters from low-quality territories gained fitness compared to the population average. This was in large part due to changes in social status, since in our population they have a profound effect on lifetime fitness. Victims of divorce from high-quality territories lost more fitness than those from low-quality sites. These facts fit the better option hypothesis and are not in agreement with the incompatibility hypothesis. Many studies have found indirect evidence for the better option hypothesis (Bradley et al. 1990; Dhondt & Adriaensen 1994; Orell et al. 1994; Ens et al. 1996; Otter & Ratcliffe 1996; Catry et al. 1997; Bried et al. 1999; Blondel et al. 2000; Mougin et al. 2000; Streif & Rasa 2001). In black-capped chickadees, females abandoned low-ranking males for high-quality mates; the cost of mating with low-ranking males was overcome by soliciting for extrapair matings (Ramsay et al. 2000). In oystercatchers it seems that extrapair partners may become social partners through divorce (Heg et al. 1993). This phenomenon, which can be considered a proximate filling in of the better option hypothesis, is also known as the mate sampling hypothesis (Colwell & Oring 1989; Heg et al. 1993). This hypothesis may explain the positive relation between the divorce rate and extrapair paternity in bird species generally (Cézilly & Nager 1995). Although desertions can be explained by the better option hypothesis, the equally common usurpations can be explained only by the forced divorce hypothesis. Finally, we observed one divorce case that is best explained by the habitat-mediated hypothesis (L. W. Bruinzeel, unpublished data). This rarity of this type of divorce can be easily understood from the stability of the oystercatcher's breeding habitat.

Our most important conclusion is that divorce in oystercatchers cannot be explained by a single ultimate hypothesis, but requires at least two. We do not think that the oystercatcher is peculiar in this respect. Divorce as a result of both usurpations and desertions has also been reported for blue ducks, *Hymenolaimus malacorhynchus* (Williams & McKinney 1996), great tits, *Parus major* (Dhondt et al. 1996), house wrens, *Troglodytes aedon* (Freed 1987), and great skuas, *Catharacta skua* (Catry et al. 1997). That it has not been reported for more studies on divorce can be explained by the difficulty of collecting detailed behavioural observations on most species (Ens et al. 1996).

The Need for Experiments

The general picture to emerge from our study is that participants pay a variable price, related to the type of divorce, the role in the divorce and the territory type

where the divorce took place. We have presented evidence to suggest that divorce entails costs. Breeders deserted their mate to fill a vacancy instead of usurping a mate, and in many cases divorce participants did not breed in the year of divorce. The only prediction not supported by the data is related to deserters from high-quality territories, since they did not improve in fitness. This shows that deserters trying to acquire another mate and territory might be unsuccessful and lose their breeding position altogether. However, since our analyses are only correlational, our fitness estimates should be treated with caution. Without experimental manipulation, we cannot compare our fitness estimates to an appropriate control population. The decline in reproductive success of deserters in the years before the divorce suggests deserters might leave a 'sinking ship': they might face a below-average reproductive success if they continue breeding with their current mate. In future experiments and analyses, the cost of reproduction should also be taken into account. Experimental manipulation of pair performance is one logical next step. Lindén (1991) has performed brood size manipulations, where reduced broods induced more divorces. However, Orell et al. (1994), Blondel et al. (2000) and S. Verhulst (personal communication) found opposite results (all in *Parus* species). Lifjeld & Slagsvold (1988) and Bried & Jouventin (1999) experimentally decreased the breeding success of pied flycatchers, *Ficedula hypoleuca*, and white-chinned petrels, *Procellaria aequinoctialis*, respectively, and thereby induced more divorces than in control pairs. Creating experimental vacancies in low- and high-quality sites (Otter & Ratcliffe 1996), or manipulating mate or territory quality (Slagsvold & Lifjeld 1986), and studying the usurpation and desertion rates might be another way forward.

Acknowledgments

This study has been, and still is, relying on many enthusiastic students and coworkers, and we thank them all for their support and companionship. Jan Hulscher, Marcel Kersten, Alex Brenninkmeijer, Kees van Oers, Martijn van de Pol, Kees Oosterbeek and Simon Verhulst deserve special mention. The long-term study on the oystercatcher population and the field station facilities were made possible through the continuous input of Rudi Drent and Joost Tinbergen. Jan Koenes and crew, Jan Nijboer and Ger Veltman gave practical support. D.H. was supported by a fellowship from the Alexander von Humboldt Stiftung (Bonn, Germany) and is grateful to Anna Rasa for her support. B.E., D.H. and I.B. were supported by consecutive grants of the Dutch Science Foundation (NWO, grants NR: 811430163, 80530164 and 80536124). Comments by Jacob González-Solís and especially Henk van der Jeugd markedly improved the manuscript.

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