Behavioral Ecology
doi:10.1093/beheco/arl109
Advance Access publication 19 January 2007

How partnerships end in guillemots *Uria aalge*: chance events, adaptive change, or forced divorce?

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Divorce in socially monogamous species can result from different mechanisms, for example, chance events, active desertion of the partner, or the intrusion of a third individual ousting the partner. We compared the predictions associated with such mechanisms with data from common guillemots (*Uria aalge*) breeding on the Isle of May, Scotland. The data cover the years 1982–2005 and show a yearly divorce rate of 10.2%. In most divorces (86%), one of the original partners moved to another breeding site, whereas the other bird stayed and bred with a new partner. On average, movers had a significantly lower breeding success after divorce, stayers were largely unaffected, whereas the incoming birds benefited significantly from the change. This pattern fits best the predictions of the "forced-divorce" hypothesis, suggesting that many divorces were caused by incoming birds rather than the original partners or chance events. Although we are unable to document the precise behavioral sequence that led to divorces, our interpretation is supported by observations of frequent fights over breeding-site ownership. Our data also indicate within-population diversity of divorce mechanisms: some divorces were apparently accidental, others desertion of partners and sites if the latter were of low quality. Our study finally illustrates that a negative correlation between breeding success and probability of divorce (which our data show) need not indicate the adaptiveness of divorce for the original partners. Because such a connection has often been made, adaptive divorce may in general be less common than usually assumed. *Key words:* auks (Alcidae), common guillemots, common murres, forced divorce, pair-bonds, reunification rate. *[Behav Ecol 18:460–466 (2007)]*

Most bird species are socially monogamous with males and females forming bonds either continuously or during the breeding season. Knowledge of how such partnerships begin and end gives insight into a variety of evolutionary topics including mate choice (for a review, see Black 1996a). Death of the partner inevitably ends a pair-bond, but so does divorce where both birds are alive but no longer paired with each other (Black 1996b). The reported frequency of divorce varies from 0% (e.g., in waved albatrosses *Diomedea irrorata*, Harris 1973) to 100% (e.g., in great blue herons *Ardea herodias*, Simpson et al. 1987; see also reviews by Ens et al. 1996 and Dubois et al. 1998), and it is still true what Catry et al. (1997, p. 1475) wrote a decade ago: "there is no theoretical framework capable of predicting, to any reasonable degree of accuracy, the interspecific variation in divorce rates in birds [...]. Our lack of understanding is partly the result of the scarcity of empirical studies attempting to assess the causes and consequences of divorce."

The causes of divorce can be categorized into adaptive and nonadaptive ones (Table 1). As a null model, chance events may separate members of a pair so that they accidentally lose contact (Choudhury 1995; Black 1996b). Similarly, one member may arrive at its usual breeding site late in the prebreeding period to find its place occupied by another individual, just as in the game "musical chairs" (Dhondt and Adriaensen 1994; Gunnarsson et al. 2004; Naves et al. 2006). Adaptive explanations for divorce include 1) responses to incompatibility where both members benefit from terminating the partnership (Coulson 1972), 2) correcting errors of mate choice where the initial mate choice was associated with low success (Johnston and Ryder 1987), and 3) the "better option" hypothesis where one of the birds initiates divorce when it has the option to pair with a better partner (Ens et al. 1993; Dubois et al. 2004). Finally, divorce may be nonadaptive for the pair members if it is brought about by an intruder ousting one of the partners (Taborsky B and Taborsky M 1999). These different hypothetical causes of divorce predict different observable phenomena, for example, in terms of the change in breeding success before versus after divorce or with respect to timing of divorce, that is, whether divorces should be more common early or late in partnerships or in certain age classes (Table 1). Comparing these predictions with empirical data allows insights into the causes of divorce in a population.

We used this approach to investigate divorce patterns in common guillemots (also known as common murres; *Uria aalge* Pontoppidan; hereafter termed guillemots) breeding on the Isle of May, Scotland, a colony that has been studied intensively since 1982. The data set contains over 500 individually identifiable birds whose breeding sites and success had been recorded over many years. During these years, the number of breeding pairs increased considerably, and there is evidence for site-dependent population regulation and a shortage of high-quality sites (Harris and Wanless 1988; Harris et al. 2003; Kokko et al. 2004). These conditions differ from the ones under which Moody et al. (2005) investigated patterns of divorce in guillemots. They directly observed 30 pairs in Newfoundland, finding that "chooser" individuals opportunistically left their mates if a better option was available, thereby improving their breeding success. We show that this pattern cannot be generalized: data from the Isle of May do not support the "better option" mechanism but are in line with the predictions of the "forced-divorce" hypothesis.

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Received 4 September 2006; revised 6 December 2006; accepted 17 December 2006.

Table 1
Predictions of major hypotheses on the causes of divorce

Hypothesis	Predictions Breeding success before/after divorce	Timing of divorce
Accidental loss[a]	May decrease for both	No specific prediction
Musical chairs[b]	May decrease for late-coming bird	No specific prediction
Better option	Increases for chooser and may decrease for victim	No specific prediction
Incompatibility, correcting errors of mate choice	Increases for one or both partners	Early in partnership and more frequent among young birds
Forced divorce	Does not increase for bystander, may decrease for victim, and increases for intruder	Possibly more frequent among young birds

Further existing hypotheses can be considered as proximate variations of the given ones (Heg et al. 2003). Sources: Coulson (1972), Johnston and Ryder (1987), Ens et al. (1993), Dhondt and Adriaensen (1994), Choudhury (1995), Black (1996b), Taborsky B and Taborsky M (1999), Heg et al. (2003), Dubois et al. (2004).

[a] Also called "habitat-mediated hypothesis"; additionally predicts a very high frequency of reuniting pairs.

[b] Also predicts a very high divorce rate.

MATERIAL AND METHODS

Common guillemots are abundant seabirds with an average adult body mass of about 1 kg that inhabit temperate and colder parts of the northern hemisphere. They breed on cliffs from the age of 5 or 6 years, can live 30 years or longer, and have a single-egg clutch (for general information, see Harris and Birkhead 1985; Gaston and Jones 1998; Harris and Wanless 2004). Males and females are morphologically similar and form monogamous partnerships during the breeding season but, as far as is known, are not associated for the remainder of the year. At the beginning of each breeding season, a pair usually reunites on the same site; we term such birds "faithful." Divorce occurs but at a low rate (Moody et al. 2005). Following Black (1996b), we define divorce as the case where both birds from a pair are known to be alive in the following year but do not occupy a common breeding site any more.

Data were collected at the long-established colony on the Isle of May, Firth of Forth, Scotland (56°11′N, 2°33′W). The number of guillemots on this island has increased for at least 50 years; the population was estimated at 11 250 pairs in 1981 and 18 858 pairs in 2005 and may be close to its carrying capacity now, given that the population increase leveled off in the late 1990s. There is considerable variation in breeding-site quality, and most high-quality sites are occupied, so birds without a site either have to fight for a good site or occupy a low-quality one (Kokko et al. 2004).

Our data cover the period from 1982 to 2005 and contain details of 540 color-ringed birds (273 males, 267 females, sexed by repeated observations of copulations) plus 16 males and 7 females of the bridled morph (about 5% of the population, Harris et al. 2003) that allowed their discrimination from neighboring birds. If a ringed bird bred with a bridled bird in consecutive years, we assumed that the bridled bird was the same in each year. If, in the next year, the ringed bird bred with an unbridled guillemot, we did not count this incidence as a divorce because we could not be sure whether the bridled original partner was still alive.

A breeding site refers to the site of one nesting pair, usually a small ledge on a cliff with several close neighbors. Its quality Q was defined as the total number of young reared between 1985 and 2005 (the period over which the study area remained constant) divided by the number of these years it was used for breeding (cf., Kokko et al. 2004). An alternative measure of breeding-site quality was developed by Kokko et al. (2004) who used physical characteristics of each breeding site to predict breeding success. Because using this latter measure did not change any of the conclusions of Kokko et al. (2004) compared with using Q and because their analysis focused on the same guillemot population as our analysis, we only used Q here.

The availability of breeding sites changed through time due to fluctuations in population size. We used an index developed by Kokko et al. (2004) to represent this availability: Q_{50} is the quality of breeding sites that have a 50% probability of being occupied in a given year in a logistic regression. This site-availability index declines in more crowded conditions (for further details, see Kokko et al. 2004). We defined high-quality breeding sites as those whose Q exceeded Q_{50}, whereas low-quality sites had a Q smaller than or equal to Q_{50}.

Additional variables included in the study are relative lay date, which is the difference in days between the date an egg was laid and the mean laying date for all pairs in the local area and year, based on at least daily checks of the sites; breeding success, which is either 0 (no young fledged) or 1 (a young fledged); and minimum age, which is the number of years elapsed since a bird was ringed (birds were normally ringed as adults rather than as chicks).

For statistical analyses, we used MATLAB R2006a and SPSS 12.0.1. In order to avoid pseudoreplication, we did not compare cases of faithfulness and divorce on a yearly basis. For example, we did not compare the breeding success for the observed cases of faithfulness with the breeding success for the cases of divorce because pairs staying together for a number of years would be included multiple times in the faithful sample. We prevented such pseudoreplication by defining and comparing different categories of partnerships: one category includes divorcing pairs, the second one includes pairs that stayed together until the end of the study period, and the third one includes pair-bonds that ended with the disappearance of a partner, usually by death although the possibility that it had moved out of the study area cannot be ruled out for every case. When comparing these different categories, we expected that the results for pairs that are faithful until the end of the study period will be intermediate between divorcing pairs and truly faithful pairs (where the bond ended with the death/disappearance of a partner).

RESULTS

We recorded 202 cases of divorce and 1787 cases where the partners stayed together in consecutive seasons, giving an

Table 2

Change in breeding site (moved away or stayed) and partner (divorce or no divorce)

Male	Female	Divorce?	Number of cases ($\Sigma = 1989$)
Moved	Moved	Divorce	27
Moved	Moved	No divorce	6
Moved	Stayed	Divorce	81
Stayed	Moved	Divorce	94
Stayed	Stayed	No divorce	1781[a]

[a] Includes 11 cases where the pair slightly adjusted (<10 cm) the position of the breeding site when a neighboring site was unoccupied.

overall divorce rate of 10.2% per year. These records are further categorized in Table 2, showing that change in partner and change in breeding site happened simultaneously in most cases. There were no significant differences between the 2 sexes regarding who moved away from partner and site and who remained: the male moved in 81 cases (46%) and the female in 94 cases (54%, $P = 0.364$, 2-tailed exact test), so we pooled the 2 sexes in the subsequent analyses.

There were 194 pair-bonds that ended in divorce, 70 faithful pairs still in the data set at the end of the study period, and 179 pair-bonds that ended with the death/disappearance of a partner (Table 3). Of the 194 divorcing pairs, 26 (13%) reunited again in a subsequent year. The subsequent fates of the birds that "interrupted" these pairings were generally unknown because only 6 were ringed; of these, 1 was breeding in the year the original pair reunified, 2 were floating (i.e., did not breed that season), and 3 were not resighted and therefore presumably dead. The number of divorcing pairs (194) is lower than the number of cases of divorce (202, see above) because a few of the reunited pairs divorced for a second time. In the analysis of such pairs, only the first divorce was included.

Faithful pairs occupied higher quality breeding sites than pairs that divorced and had a higher breeding success (Table 3). These differences were statistically significant with the effect being larger for breeding success. As expected, site quality and breeding success of faithful pairs that reached the end of the study period were intermediate between those of divorcing pairs and of pair-bonds that ended with the death/disappearance of a partner. This was not true for relative lay date, however, which was earliest for partnerships reaching the end of the study period. Faithful pairs that ended with the death/disappearance of a partner laid slightly earlier than divorcing pairs and were formed by slightly older birds, but these differences were not significant and the effect sizes small.

Divorces where one partner moved

In the majority of divorces, one bird moved away from the original breeding site and the other one stayed. In 174 (99%) out of these 175 cases, the bird that moved away was replaced; in the remaining case, the bird had no mate that season. Of the incoming birds that could be identified, 29 were breeding in the previous year and 18 were floating.

The different roles in a divorce (mover, stayer, incoming bird) were associated with marked differences in change in breeding success before versus after the divorce. The breeding success of movers was significantly lower after the divorce, the breeding success of stayers was largely unaffected, and the breeding success of the incoming birds was significantly higher (pairwise comparisons in Figure 1 and Table 4). The patterns became less marked with time after the divorce.

The results presented above describe the average effect of a divorce. However, there may be individual birds benefiting from moving away from partner and site, and in the 175 divorces where one partner moved away from the original site and the other partner stayed, we found a highly significant correlation between the change in breeding-site quality and the original site quality ($r = -0.56$, $P < 0.001$, 1-tailed Pearson correlation test). In other words, it can be beneficial for a bird to move if it is currently occupying a low-quality breeding site. We therefore compared the change in breeding success before versus after divorce separately for high- and low-quality breeding sites (Figure 2, Table 5). For high-quality sites, we found a similar pattern as for all sites combined: divorce was detrimental for movers, neutral for birds that stayed at the original site, and beneficial for the replacers. In contrast, birds that moved away from low-quality sites had no detectable disadvantage.

Divorces where both partners moved

Figures 1 and 2 show the more typical context of divorce at this colony where one of the partners left the original breeding

Table 3

Average differences between divorcing pairs and faithful pairs (means ± standard errors)

	Site quality Q	Relative lay date	Breeding success	Minimum age[a]
Divorcing pairs ($N = 194$)	0.68 ± 0.017	−0.29 ± 0.451	0.67 ± 0.035	8.84 ± 0.514
Faithful pairs, 2005 reached ($N = 70$)[b]	0.72 ± 0.023	−1.25 ± 0.338	0.73 ± 0.025	N/A[c]
Faithful pairs, partner died ($N = 179$)	0.74 ± 0.013	−0.97 ± 0.300	0.82 ± 0.022	9.65 ± 0.548
Statistics, comparing divorcing pairs with faithful pairs where the partner died	$P < 0.01$[d], $d = -0.29$[e]	$P = 0.21$[d], $d = 0.13$	$P < 0.01$[f], $d = -0.38$	$P = 0.29$[g], $d = -0.11$

[a] Minimum age of the pair (sum of male's and female's minimum age) when the partnership was formed.

[b] These pairs did not divorce until 2005, that is, the end of the study period.

[c] Not applicable because partnerships reaching the end of the study period were formed later, so the birds were relatively older than the birds in the 2 other categories of pair-bonds.

[d] Two-tailed t-test for unequal variances.

[e] Effect size d (Gurevitch and Hedges 2001), for example, the effect size for site quality Q was calculated as (mean Q of divorcing pairs − mean Q of faithful pairs where the partner died) $\times J$/pooled standard deviation of Q of divorcing pairs and faithful pairs where the partner died, where $J = 1 - 3/(4(N_{\text{all pairs}} - 2) - 1)$, a correction factor for small sample sizes.

[f] Two-tailed exact test.

[g] Two-tailed t-test.

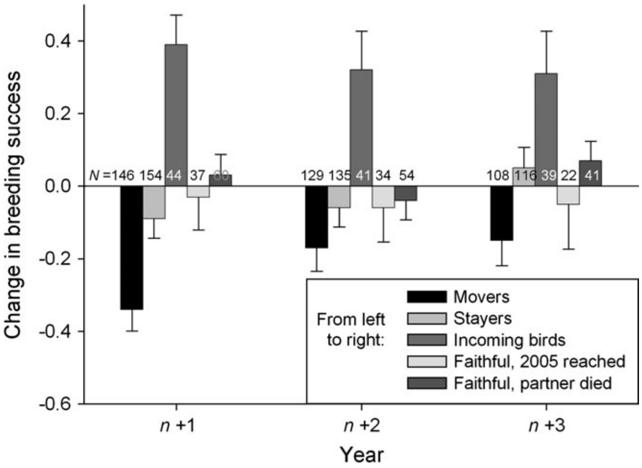

Figure 1
Average change in breeding success (±standard error) between year *n* and years *n* + 1, *n* + 2, *n* + 3, respectively, where year *n* is the year before divorce ("movers," "stayers," "incoming birds"—for divorces where one partner moved away from the original site and the other partner stayed, breeding with a new partner, the "incoming bird"), is the year before the partner died ("faithful, partner died"), or is year 4 in a faithful pair-bond that reached 2005, that is, the end of the study period; year 4 was chosen because divorces happen on average after a pair was breeding together for 3.9 consecutive years. The graph is based on pairwise comparisons. Each change in breeding success relates to the year before divorce, death/disappearance of the partner, or year 4, respectively. For example, the given change in breeding success for movers at year *n* + 3 is the average change in breeding success 3 years after a divorce compared with the year before the divorce. The given sample sizes indicate the number of pairs for which information was available in each case. The differences among the 5 different scenarios are significant (years *n* + 1, *n* + 2, $P \leq 0.001$; year *n* + 3, $P < 0.01$; Kruskal–Wallis tests; see Table 4 for post hoc tests).

site and the other partner stayed. However, there were an additional 27 cases where both partners moved away from the original site (Table 2). In 18 of these cases, the original site remained unoccupied. Not surprisingly, these breeding sites were of low quality ($Q = 0.50 \pm 0.070$, mean ± standard error, $N = 17$), so birds likely benefited from leaving them and their original partner. In the other 9 cases, the original sites were of significantly higher quality ($Q = 0.73 \pm 0.036$, $N = 9$; $P < 0.01$, 2-tailed *t*-test for unequal variances with $N = 26$) and were all occupied by other pairs the following year. These divorces were possibly caused by the new pairs ousting the original site-holding pairs, either as a unit or individually. Support for this mechanism was provided by observations of intense fights prior to divorce at 5 of the 9 sites involved.

Familiarity with the partner

If familiarity with the partner was important, there should have been a difference between the 2 different categories of faithful pairs because birds in pairs that stayed together until the end of the study period never had to become familiar with a new partner, in contrast to birds that bred with a new partner after their original mate had died/disappeared. There was no significant difference in change in breeding success between these 2 scenarios (Figures 1 and 2; Tables 4 and 5), suggesting that familiarity with the partner either was not very important or its effect was masked by other factors.

DISCUSSION

Forced divorce

When comparing our results to predictions of the different divorce hypotheses (Table 1), we find that they best match those of the forced-divorce scenario. In the majority of cases, divorce was not beneficial for either of the original partners, leading to a decrease in breeding success for the birds that left their partner and site and having no effect on breeding success for the birds that stayed at the original site. This pattern contradicts all hypotheses that assume an adaptive choice by either partner, that is, incompatibility of the 2 partners, correcting errors of mate choice, and the better option hypothesis, all of which predict that the breeding success of at least one of the original partners should increase after divorce

Table 4
Results of post hoc tests (years *n* + 1, *n* + 2, *n* + 3; 2-tailed *P* values, *U*-tests) on change in breeding success for all breeding sites (cf., Figure 1)

	Stayers	Incoming birds	Faithful, 2005 reached	Faithful, partner died
Movers	*n* + 1: 0.001* *n* + 2: 0.134 *n* + 3: 0.024	*n* + 1: <0.001* *n* + 2: <0.001* *n* + 3: 0.001*	*n* + 1: 0.005* *n* + 2: 0.313 *n* + 3: 0.462	*n* + 1: <0.001* *n* + 2: 0.117 *n* + 3: 0.041
Stayers		*n* + 1: <0.001* *n* + 2: 0.001* *n* + 3: 0.026	*n* + 1: 0.547 *n* + 2: 0.978 *n* + 3: 0.487	*n* + 1: 0.155 *n* + 2: 0.744 *n* + 3: 0.901
Incoming birds			*n* + 1: 0.002* *n* + 2: 0.009 *n* + 3: 0.041	*n* + 1: <0.001* *n* + 2: 0.001* *n* + 3: 0.031
Faithful, 2005 reached				*n* + 1: 0.559 *n* + 2: 0.798 *n* + 3: 0.322

The results were obtained by comparing the group of birds given in the leftmost column with the group of birds given in the top row. For example, comparing movers with stayers in year *n* + 1 (the first year after divorce) yielded a *P* value of 0.001 that is a significant difference between these 2 groups even after Bonferroni–Holm correction. By contrast, in year *n* + 2, there was no significant difference between these groups: $P = 0.134$.

[*] Significant after Bonferroni–Holm correction ($\alpha = 0.05$).

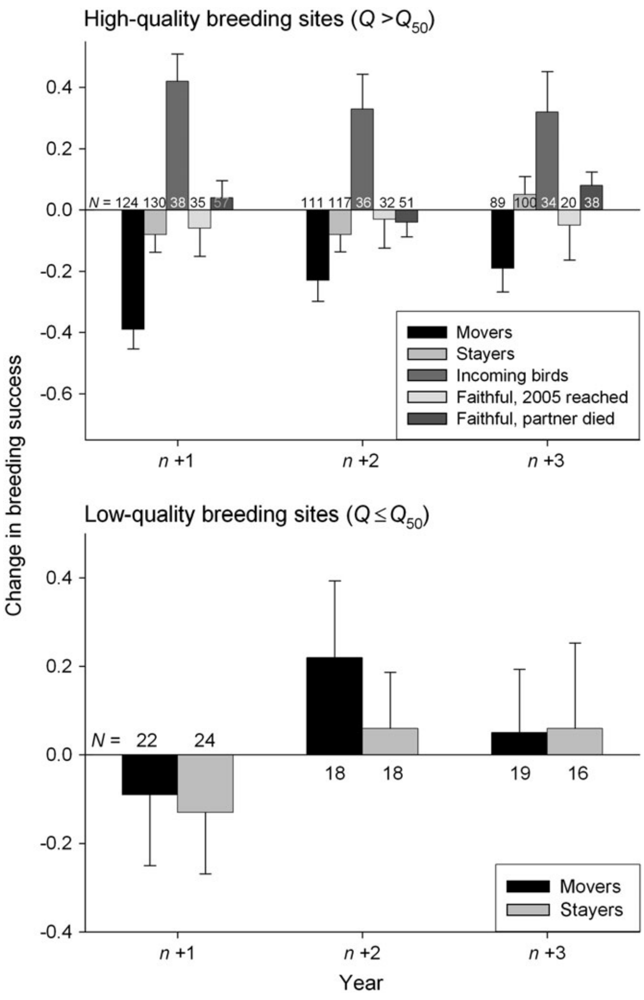

Figure 2
As Figure 1, but separated for high- (top) and low-quality (bottom) sites. For high-quality sites, differences are significant in all years ($n + 1$, $n + 2$, $P < 0.001$; $n + 3$, $P < 0.01$; Kruskal–Wallis tests; see Table 5 for post hoc tests). For low-quality sites, results for incoming birds and faithful pairs are not given due to very small sample sizes. For these sites, there were no significant differences between movers and stayers ($P = 0.90$, 0.38, 0.94, respectively; *U*-tests).

(Table 1). It could be argued that the better option hypothesis applies in an unusual sense, as the staying bird may obtain a higher quality mate (who is able to oust the previous mate). However, the better option hypothesis then predicts that stayers improve their breeding success that is contradicted by our data. What about chance events? If partners lose contact with each other accidentally, breeding success of both may decrease, but there should be no systematic difference in the change in breeding success between movers and stayers, and reunification rate should be very high. Our results disagree with these predictions. In the musical-chairs hypothesis, a very high divorce rate is predicted, and breeding sites should be occupied according to the sequence in which birds arrive at the colony. In our study, divorce rate was relatively low (10%) and fights were common, particularly in the prelaying period: for our focal population in 1982–1987, Kokko et al. (2004) recorded that 23 (32%) of 72 changes in breeding site involved fighting for the cases where the site left by a bird was occupied by another one. The real figure must be even higher because Kokko et al. (2004) were only making observations during part of the prebreeding period. Forced divorce may be more frequent among young birds than among older birds because young birds are presumably easier to oust (Table 1). Although our results are in line with this expectation, they do not offer clear-cut evidence, perhaps because information on bird age was limited to minimum age based on the year a bird was ringed. In general, in our correlational data set, it is difficult to reach firm conclusions, particularly as the precise behavioral sequence of events that led to divorce remains unknown for most cases. Despite these limitations, the forced-divorce scenario is the only one in line with the data.

Guillemots typically defend a small breeding site (100–150 cm^2) on a cliff ledge year after year, and a consequence of this constancy is that divorce and change in breeding site are strongly linked. A previous study found evidence for adaptive site changes in this population, in which "voluntarily" moving birds improved the quality of their breeding site but also caused "involuntary" changes (takeovers) that typically reduced the victim's subsequent breeding success (Kokko et al. 2004). This pattern was reflected in the current study with many individuals apparently causing a divorce by ousting a site holder and thereby improving their own breeding success, whereas the ousted bird's breeding success decreased. To our knowledge, no previous study has investigated changes in the breeding success of incoming birds.

Many of the incoming birds had bred before but did not breed the previous year. Such floaters can play a complicated role in population regulation. Recent theory (López-Sepulcre and Kokko 2005) highlights how their role is not restricted to forming a passive "buffer" against population fluctuations (Durell and Clarke 2004). Their active site-acquisition tactics can also hamper population growth. For example, they may harass breeders and disrupt established pair-bonds, thus reducing population growth.

Although scattered reports of pair-bonds ended by intruders have existed for decades (Minton 1968; Ball et al. 1978), the importance of this phenomenon was only recognized in the 1990s when Taborsky B and Taborsky M (personal communication with Choudhury 1995) introduced a precise term for it, "forced divorce." We are aware of only 3 previous studies with evidence that forced divorce can be a major cause of partnership terminations: Taborsky B and Taborsky M (1999) on brown kiwi (*Apteryx mantelli*), Heg et al. (2003) on oystercatchers (*Haematopus ostralegus*), and Williams and McKinney (1996) on blue ducks (*Hymenolaimus malacorhynchos*). Our study adds further evidence. Additional incidences of forced divorce have been reported (Freed 1987; Ens et al. 1993; Dhondt et al. 1996; Catry et al. 1997), suggesting that it may be more common than thought. Williams and McKinney (1996), Taborsky B and Taborsky M (1999), Heg et al. (2003), and the current study all suggest that forced divorce may be associated with populations that are at, or near, their carrying capacity and limited by the availability of high-quality breeding sites. This conclusion is further supported by comparison with the study of guillemots by Moody et al. (2005) in Newfoundland where breeding sites were of high quality and competition for sites was apparently less intense than on the Isle of May. Although the divorce rate was similar to that reported here (8.2% cf., 10.2%), Moody et al. (2005) found no evidence of forced divorce. Instead, the "better option" mechanism (Table 1) dominated at their study site.

Other causes of divorce

Our data suggest that there were also other mechanisms that ended partnerships in guillemots on the Isle of May. Birds that bred on low-quality sites often benefited from leaving their partner and site, so they may have actively deserted them. Additionally, 13% of the divorcing pairs reunified in a consecutive

Table 5

Results of post hoc tests (years $n + 1$, $n + 2$, $n + 3$; 2-tailed P values, U-tests) on change in breeding success for high-quality breeding sites (cf., Figure 2)

	Stayers	Incoming birds	Faithful, 2005 reached	Faithful, partner died
Movers	$n + 1$: <0.001* $n + 2$: 0.054 $n + 3$: 0.011	$n + 1$: <0.001* $n + 2$: <0.001* $n + 3$: <0.001*	$n + 1$: 0.004* $n + 2$: 0.091 $n + 3$: 0.318	$n + 1$: <0.001* $n + 2$: 0.026 $n + 3$: 0.016
Stayers		$n + 1$: <0.001* $n + 2$: 0.001* $n + 3$: 0.022	$n + 1$: 0.773 $n + 2$: 0.678 $n + 3$: 0.473	$n + 1$: 0.181 $n + 2$: 0.604 $n + 3$: 0.843
Incoming birds			$n + 1$: 0.001* $n + 2$: 0.013 $n + 3$: 0.036	$n + 1$: <0.001* $n + 2$: 0.001* $n + 3$: 0.026
Faithful, 2005 reached				$n + 1$: 0.360 $n + 2$: 0.961 $n + 3$: 0.224

* Significant after Bonferroni–Holm correction ($\alpha = 0.05$).

year. Some of these divorces were probably again caused by an incoming bird, and its death or other circumstances allowed the original pair to reunite. It is very likely, however, that accidental loss caused many of these divorces, a mechanism that is associated with a high reunification rate (Table 1).

Although it is highly plausible that divorce occurs for different reasons within a population, only few previous studies have demonstrated this empirically (Ens et al. 1993; Cockburn et al. 2003; Heg et al. 2003). In even fewer cases is information available for a given species under different demographic conditions. The contrasting results for guillemots in Scotland (this study) and Newfoundland (Moody et al. 2005) indicate that the main cause of divorce can differ between populations of a single species. These findings also highlight the importance of the inevitable link between divorce, mate choice, and breeding-site choice in territorial birds (Blondel et al. 2000; Morton et al. 2000; Heg et al. 2003). Because site-change rules should be sensitive to site availability, spatial or temporal variation in the latter factor can create large differences in divorce patterns. Because causes of divorce can differ between and within colonies, we should avoid the question "What is the reason for divorce in species *x*?" and rather ask: "What is the main reason for divorce in population *y* of species *x* under a particular set of conditions?" while also remembering that the constraints and possibilities for different individuals can differ within a population.

Familiarity with the partner

Our analysis did not show an influence of familiarity with the partner on breeding success. At first sight, this seems to contradict with Lewis et al. (2006) who found that, after controlling for bird age, breeding success in this population increased with the number of years a pair successfully bred together. However, this increase was only up to a certain value of successful experience beyond which the relationship reversed to a decrease. In other words, the relationship between breeding success and previous successful experience was dome shaped. When Lewis et al. (2006) looked at the number of years a pair bred together independently of the success of these breeding attempts, they found no significant effect of familiarity on breeding success; hence, their results do not contradict our findings.

There are a number of other previous studies that looked at the influence of familiarity with the partner on breeding success. Although many studies have shown a positive correlation between breeding success and pair duration, this should not be taken as evidence for a mate familiarity effect because such a correlation can be caused by a positive influence of bird age on breeding success (Black 1996b). Of the studies that did present evidence for or against the mate familiarity effect, some found such an effect, whereas others did not (e.g., Coulson 1972; Emslie et al. 1992; Ens et al. 1996; Catry et al. 1997; Blondel et al. 2000; Naves et al. 2006). At present, these discrepancies between different species cannot be explained.

Moody et al. (2005) found in Newfoundland that guillemots whose partner died had a lower breeding success after this event than before. Their study does not allow for testing the mate familiarity effect, but this related finding is worth discussing because it disagrees with our results. Similarly to other, above mentioned, differences between Newfoundland and Scotland, the reduction in breeding success after the partner's death in Newfoundland suggests that it was difficult there for guillemots to find high-quality partners. In Scotland, however, widowed birds apparently had no problem finding a new partner. Here, the key to successful reproduction was mainly to own a high-quality breeding site.

Breeding success and the probability of divorce

The final point of this study is that a negative correlation between breeding success and probability of divorce need not indicate the adaptiveness of divorce. Such a connection has often been made, quoting Ens et al. (1993, p. 1200): "The evidence that divorce in monogamous bird species is adaptive derives primarily from the correlation between reproductive failure and increased probability of divorce" (see also Dubois and Cézilly 2002). Our results show such a correlation (Table 3) but also the nonadaptiveness of divorce for either partner. A potential reason for such a pattern is that the highest quality birds can best resist takeover attempts and also have the highest breeding success. Thus, correlations between breeding success and probability of divorce must be interpreted with caution. Another important implication of our finding, that a correlation between breeding failure and probability of divorce need not indicate the adaptiveness of divorce, is that adaptive divorce may in general be less common than usually assumed.

We thank the many people who helped with the fieldwork over many years and the Scottish Natural Heritage for permitting this work. Comments on the manuscript were provided by Katja Bargum, Mark Hauber, Katja Heubel, Jan Heuschele, Sue Lewis, Andrés López-Sepulcre, Irja Ratikainen, Perttu Seppä, Lotta Sundström, Cédric Tentelier, Emma Vitikainen, and 2 anonymous reviewers. Finally, we appreciate financial support from the Academy of Finland and the UK Joint Nature Conservation Committee.

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