

Breeding performance, mate fidelity, and nest site fidelity in a long-lived seabird: behaving against the current?

Liliana C. Naves, Jean Yves Monnat and Emmanuelle Cam

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There is evidence that breeding failure is associated with divorce and dispersal in many bird species. However, deviations from the general pattern “success-stay/failure-leave” seem to be common, suggesting that factors other than breeding performance may importantly influence mate and habitat selection. Moreover, variability in response to performance suggests coexistence of different evolutionary strategies of mate and site selection within a population. In this study, we assessed how individuals conform to the success-stay/failure-leave pattern in kittiwakes (*Rissa tridactyla*), and aimed to identify categories of individuals presenting different behavioural patterns. We considered individual attributes (experience, prior residence at the nest site, performance in multiple breeding attempts), pair attributes (arrival asynchrony, timing of failure, pair duration), and productivity in habitat patches. Timing of failure was an important factor. Pair reunion probability was close to 0.5 in failed pairs, but it was consistently higher in early failed than in late failed pairs. Prior residence better explained variability in probability of reunion in failed pairs than pair duration. However, the positive influence of prior residence on the probability of reunion was perceptible only in early failed pairs. Divorce probability in successful pairs increased with arrival asynchrony, and was higher in first-time than in experienced breeders. Local productivity positively influenced site fidelity probability in early failed birds, but not in late failed ones. Using memory models, we found that dispersal decisions integrate information on individual breeding performance in a temporal scale longer than one year. This study contributed to the identification of relevant states to be considered when addressing mate and nest site choice. Natural selection may operate on slight fitness differences that cannot be detected without high levels of stratification according to the appropriate individual and habitat attributes.

L. C. Naves (*liliananaves@yahoo.com*), Univ. Pierre et Marie Curie, Laboratoire d'Écologie, Bât A7 case 237. 7, quai St Bernard, FR-75252 Paris cedex 05, France. – J. Y. Monnat, Penn ar Run Izella, FR-29770 Goulien, France. – E. Cam, Univ. Paul Sabatier, Laboratoire Évolution et Diversité Biologique, Bât 4R3 salle 209. 118, route de Narbonne, FR-31062 Toulouse cedex 04, France.

In behavioural ecology, understanding habitat and mate selection requires assessment of fitness prospects associated to the different possible decisions (Choudhury 1995, McNamara and Forslund 1996). Generally, successful breeding attempts lead to mate and nest site fidelity, while failure is often followed by divorce and dispersal (Mills 1973, Coulson and Thomas 1983,

Johnston and Ryder 1987, Bradley et al. 1990, reviewed by Dubois and Cézilly 2002). This led to a general pattern “success-stay/failure-leave” (Schmidt 2004), which has been used as an assumption in models of population dynamics incorporating individual behaviour. From an evolutionary perspective, divorce and dispersal can be viewed as strategies preventing

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repetition of poor performance (Rowley 1983, Johnston and Ryder 1987, Choudhury 1995, Ens et al. 1996).

However, a number of studies failed to find evidence of an influence of previous breeding performance on mate and habitat choice (Penney 1968, Harris 1979, Reilly and Cullen 1981, Gratto et al. 1985, Wiens and Cuthbert 1988, Murphy 1996, Murray and McKinney 1996). Several hypotheses have been put forward to explain the occurrence of divorce and dispersal in this circumstance (Johnston and Ryder 1987, Choudhury 1995, Bried and Jouventin 2002). From an optimisation viewpoint (Seger and Stubblefield 1996), divorce and dispersal are assumed to be favoured when their advantages outweigh their costs. Empirical studies have suggested the existence of such costs, i.e. that re-mating and dispersal are generally followed by increased occurrence of non-breeding or poor performance (Coulson 1966, Chardine 1987, Bradley et al. 1990, Ens et al. 1996, Cam 1997, Catry et al. 1997, Hall 1999). There may be circumstances in which mate and site change are not cost-effective even when a previous breeding failure would suggest higher fitness prospects associated with changes.

Despite general behavioural patterns such as the success-stay/failure-leave, one should not expect all individuals in populations to react to breeding outcome in the same way. Indeed, even in species where this general pattern is observed (as in kittiwakes), there is evidence that pair reunion is common in failed pairs and that divorce occurs in successful ones (Table 1). Moreover, such atypical cases seem not to represent an insubstantial minority. The strength of the relationships involving breeding success and mate fidelity is likely to

vary according to life history traits (Dubois and Cézilly 2002). Variability in the response to breeding performance suggests the coexistence of antagonistic or complementary strategies of mate and nest site selection within a population. Such strategies may reflect variability in fitness associated to individual condition-dependant decisions (Ronce et al. 2001). In this paper we addressed hypotheses on how individual attributes (experience, prior residence at a nest site, performance in multiple breeding attempts), pair attributes (pair duration, timing of failure, arrival asynchrony), and habitat quality may affect cost-effectiveness of the general relationship between breeding performance and habitat and mate choice. Our objective was to assess the extent to which individuals conform to the success-stay/failure-leave pattern in a population of kittiwakes (*Rissa tridactyla*), a long-lived colonial seabird species, and to identify categories of individuals exhibiting different behavioural patterns.

Biological hypotheses and predictions

Timing of failure

Breeding failure may be caused by external factors (predation, meteorological conditions) or by intrinsic pair attributes (poor parental quality) (Bried and Jouventin 1999). Here we put forward that timing of failure reflects different causes of failure, which in turn may influence nest site and mate choice. First, predation on eggs by carrion crow (*Corvus corone*) accounts for massive failure at the egg stage in the studied colonies

Table 1. Percentage (%) of divorce in successful birds and of mate fidelity in failed birds. In parentheses are sample sizes (number of pair-years in which both mates survived between two consecutive years).

Species	Divorce rate	Divorce after success	Pair reunion after failure
Atlantic fulmar <i>Fulmarus glacialis</i> (Ollason and Dunnet 1988)	<5 (696)	4	93
Cassin's auklet <i>Ptycorhampus aleuticus</i> (Sydeman et al. 1996)	7 (220)	6	89
Manx shearwater <i>Puffinus puffinus</i> (Brooke 1978)	10 (175)	5	73
oystercatcher <i>Haematopus ostralegus</i> (Harris et al. 1987)	12 (487)	7	86
short-tailed shearwater <i>Puffinus tenuirostris</i> (results for males, Wooller and Bradley 1996)	17 (1911)	33	45
red-billed gull <i>Larus novaehollandiae</i> (Mills 1973)	<18 (148)	18	–
kittiwake <i>Rissa tridactyla</i> (present study)	26 (1004)	13	53
fork-tailed storm-petrel <i>Oceanodroma furcata</i> (Boersma et al. 1980)	≤29 (38)	≥18	≤19
least auklet <i>Aethia pusilla</i> (Jones and Montgomerie 1991)	36 (55)	36	57

Note: here we present only the species for which there is evidence that previous breeding performance influences the occurrence of divorce. Species are listed in crescent order of divorce rate. The information necessary to build this table (i.e. raw data, proportions or rates) is no longer found in the literature after the second half of the 1990s because by this time, authors adopted the use of linear models and estimated probabilities

(Cam et al. 2004). Such predation events are unambiguous and generally occur in consecutive years. In contrast, causes of failure at the chick stage are diverse (disturbance by intruders, death of a mate, diseases, ectoparasites, predation by seagulls) and do not involve massive failure. Early failure may provide information on a predictable component of habitat quality associated to consistent failures, whereas the information held in late failure may not necessarily (but see Boulinier et al. 1996b). An early failure may indicate low fitness prospects associated to site fidelity. If so, higher dispersal probability might be expected after early failure than after late failure.

Second, pairs that almost managed to raise a chick to independence are unlikely to have failed because of a major insufficiency in breeding skills in either mate. In contrast, early failure may indicate low mate quality. As above, early failure may provide information on a component of mate quality that might be associated to consistent failures (i.e. low individual quality), whereas the information held in late failure may not necessarily. Accordingly, we might expect higher divorce probability in early failed than in late failed birds.

Third, costs of re-mating and establishing a new territory may be lower after an early failure than after a late failure. That is because, especially in case of early failure, divorce and dispersal may be initiated before the end of the season (Fetterolf 1984, Williams and Rodwell 1992, Williams 1996). Early failed birds are free to undertake prospecting activities when the presence of full-grown chicks seems to provide reliable information on habitat quality (Cadiou et al. 1994, Boulinier et al. 1996a). This may facilitate the onset of breeding in the following year. We might expect higher divorce and dispersal probability in early failed individuals if they experience lower costs of divorce and dispersal. In addition, early failed birds may progressively loose their pair bond because of reduced within-pair interactions while undertaking prospecting activities. Similarly, inconsistency in nest site attendance may result in territory loss to prospecting birds. Higher divorce and dispersal probability in early failed than in late failed individuals may result from a passive process.

Pair duration and prior residence

Long pair duration and prior residence may be associated to high costs of divorce and dispersal (Schjørring et al. 2000). Several studies have reported a positive relationship between pair duration and breeding performance (Brooke 1978, Coulson and Thomas 1983, Ollason and Dunnet 1988, Bradley et al. 1990). One explanation for this relationship is that increased familiarity with the mate leads to higher success probability because of progressive fine-tuning of breeding behaviour

between mates (Nelson 1972, Rowley 1983, Black 1996, Ens et al. 1996). Prior residence at a territory has been associated to advantages in competition for feeding and breeding resources possibly because of familiarity with physical characteristics of the territory and its social neighbourhood (Greenwood and Harvey 1982, Koivula et al. 1993, Haley 1994, Ens et al. 1995, Schjørring et al. 2000, Forstmeier 2002, Hardwood et al. 2003). Mate and nest site selection are entangled, and a positive relationship between the degree of mate and site fidelity has been reported in several species (Cézilly et al. 2000). As reunited individuals have lower dispersal probability than divorced ones (Coulson and Thomas 1983, Gratto et al. 1985), pair duration and prior residence (i.e. the number of breeding attempts at the same nest site) are likely to be positively correlated (Ens et al. 1996). Mate and site fidelity may prevail if benefits of mate and site familiarity outweigh costs of divorce and dispersal. Hence, we might expect divorce and dispersal probability to decrease with pair duration and prior residence respectively.

Arrival asynchrony

Divorce may occur when costs of mate fidelity are too high. If previous mates arrive asynchronously at breeding grounds, the first-arrived bird has to decide whether re-mating or waiting for the previous mate. In many species, an association between early start of breeding and high performance suggests pressures favouring early breeding (Moreno 1998, Bried et al. 1999, Wendeln et al. 2000). If the previous mate is late, favouring an early start means divorcing. In several species, divorce probability increases with the magnitude of arrival asynchrony (Coulson and Thomas 1980, 1983, Davis and Speirs 1990, Dhondt et al. 1996, Bried et al. 1999, González-Solís et al. 1999, Handel and Gill 2000). Arrival asynchrony may explain why some pairs divorce when previous breeding success would suggest fidelity to be favoured.

Habitat quality

Theories of habitat selection preview that individuals should disperse if site fidelity is associated to lower fitness prospects (Fretwell and Lucas 1970, Holt and Barfield 2001). In predictable environments, it is sound to hypothesize that past breeding performance provides information on future fitness prospects (Switzer 1993, Boulinier and Danchin 1997, Danchin et al. 1998, Schjørring 2000, Suryan and Irons 2001). However, in species breeding in discrete habitat patches (e.g. colonies, sub-colonies, Cadiou 1999), site selection may depend not only on individual breeding success (Newton and Marquiss 1982, Schieck and Hannon 1989, Desrochers

and Magrath 1993b, Switzer 1997, Reed et al. 1999), but also on the performance of neighbours (Burger 1982, Boulinier 1996, Boulinier and Danchin 1997, Danchin et al. 1998, Schjørring et al. 2000, Suryan and Irons 2001, Doligez et al. 2003). Depending on the relative weight of different sources of information on habitat quality (Clark and Mangel 2000, Danchin et al. 2001), site selection may not be consistent with decisions expected under the assumption that individual breeding performance is the only information taken into account. In agreement with previous studies (Danchin et al. 1998), we might expect dispersal probability in failed individuals to be lower in highly productive patches than in unsuccessful ones. Moreover, we also investigated whether local productivity may indirectly influence pair reunion probability. Failed birds may reunite because both male and female decided to re-nest at a site within a productive area. In addition, divorce may be a by-product of dispersal. Indeed, the great majority of dispersers are also divorcees despite the fact that pairs are able to reunite on a new territory (Ollason and Dunnet 1978, Ainley et al. 1990, Aebischer et al. 1995, Fairweather and Coulson 1995, Bried and Jouventin 1999, Handel and Gill 2000, Jouventin and Bried 2001). We might expect lower divorce probability in highly productive patches than in others.

Cumulative information on individual performance

Several theoretical models of habitat choice consider that information on patch quality is updated on multiple occasions (Clark and Mangel 2000). A way to increase reliability of basis for a dispersal decision may be to integrate information on multiple breeding attempts rather than to solely rely on the outcome of the most recent one. If individuals gather information over a few years, certain dispersal decisions may appear atypical when one considers only performance in the most recent breeding attempt. Here we assessed whether dispersal probability depends on individual breeding performance in consecutive years. We might expect reinforcement of a negative influence of breeding failure on dispersal probability as failures accumulate over time.

Methods

We used data from an ongoing monitoring program carried out in Brittany (France), which started in 1979. This program documented the breeding history of individuals identified by a numbered metal band and a combination of coloured plastic bands (Danchin and Monnat 1992, Cam et al. 2003). Kittiwakes are cliff-nesting birds; nestlings and adults were captured using a hook-pole by researchers rappelling cliffs. Between the

first arrivals at the colony (January) and the period of nest construction (mid-April), colonies were visited at least once a week. In May and June colonies were visited about twice a week, and in July and August visits were daily. Observations from individuals were summarized to determine yearly breeding status, breeding performance, and mate and nest site fidelity.

Definitions

Pairs were considered as breeders if they completely built a nest (i.e. a flat platform of mud and grass with a deep cup; Paludan 1955, Cullen 1957, Maunder and Threlfall 1972). Breeding performance was defined as "success" (at least one chick raised to independence) or "failure". Timing of failure was considered as "early" (no laying or clutch loss) or "late" (failure after hatching). We distinguished "first-time breeders" (first breeding attempts) and "experienced breeders" (birds that bred at least once before). Numerous studies have shown much higher breeding performance in experienced breeders compared to first-time ones (Newton 1986, Sæther 1990, Bradley and Wooller 1991, Desrochers and Magrath 1993a, Cam and Monnat 2000a, Barbraud and Weimerskirch 2005). We chose this way of quantifying experience because we dealt with a high degree of data stratification, which implies sample size constraints. Our main objective was not to address the influence of experience per se on mate and site choice, but to control for this well-known source of variation in breeding performance.

For analyses of pair reunion and divorce probability, we selected pair-years where both male and female were banded, survived between years t and $t+1$, and whose breeding performance in year t was known. Sex was identified through behaviour. We considered a male and a female to be paired if they were repeatedly resighted together during a breeding season and performed behavioural displays of pair formation and coordination (Moynihan 1955, Tinbergen 1959, Brown 1967). Pair bond status was "reunited" (birds that formed a pair in two consecutive years) or "divorced" (both individuals of a pair in year t are known to be alive in year $t+1$ but did not resume their pair bond). Widowed birds (i.e. those that survived from year t to $t+1$, but not their previous mate) were excluded from analyses of divorce probability.

Some non-breeders may establish a certain degree of territoriality as well as a partially or fully developed pair bonding (Jones and Montgomerie 1991, Cam and Monnat 2000b). Sample sizes concerning non-breeders were relatively small because non-breeders are less numerous than breeders in the study population (Cam et al. 1998) and it is not always possible to ascertain their territorial and pairing status. In addition, there is

evidence that divorce and dispersal are more common in non-breeders than in breeders (Minton 1968, Jones and Montgomerie 1991, Rees et al. 1996). For these reasons, we excluded non-breeders from all analyses.

Arrival asynchrony (year t) was the number of days elapsed between the first record at breeding grounds of birds that formed a pair in the previous year. Pair duration quantified the number of successive years (inclusive of year t) a male and a female bred together regardless of whether the bond continued or not afterwards. Prior residence was the number of successive years an individual used the same nest site. When quantifying pair duration and prior residence, pair reunion and site fidelity status were taken into account for non-breeders that formed a pair and/or settled at a specific site.

Habitat patches were defined as cliff sections of tens or hundreds of meters in length delimited by topographical discontinuities. Only patches hosting at least ten nest sites were included in analyses. Patch size varied between 10 and 256 nest sites (39.41 ± 34.00 SD, $n = 545$ patch-years). To address the influence of habitat quality on individual decisions concerning mate and nest site fidelity, we used the proportion of successful nests within a patch as a measure of productivity. The performance of the focal individual was excluded from the calculation of "local productivity" in order to grant independence between individual breeding success and local productivity. This approach was similar to that used by Danchin et al. (1998) and by Cam and Monnat (2000a, 2000b).

A bird was considered a disperser if breeding in year $t+1$ took place at a nest site different from the one used in year t . Each definition of dispersal has limitations because of the difficulty in identifying the meaningful scale of movement (Clobert et al. 2001). For instance, 67% of the dispersal events in the largest sample used in this study (8512 breeder-years) occurred within habitat patches (i.e. a "cliff"). In our study system, "cliffs" are easily delimited based on topographical discontinuities of the coastline. However, the spatial scale of factors likely to affect breeding performance does not necessarily conform to cliff boundaries. Our decision to assess dispersal at the scale of the nest site (i.e. not accounting for dispersal distance) derives from the fact that we knew no objective criterion to identify meaningful spatial units along the coastline. It is sound to assume that any change of nest site implied changes in the immediate social context as well as in specific site attributes (size and inclination of the ledge, accessibility to predators, presence of parasites) whatever the distance of dispersal. However, a change of nest site did not necessarily involve a change in local productivity. Our questions concerned whether an individual stayed at a given nest site despite its own breeding failure or despite low local productivity. Whether individuals leave low productivity patches

towards high productivity ones was beyond the scope of this study and has been addressed elsewhere (Danchin and Monnat 1992, Danchin et al. 1998).

Statistical approach and modelling

As re-sighting probability in the studied system is very close to one from the first breeding attempt onwards (Cam et al. 1998), we used modelling tools not incorporating the probability of recapture of marked individuals (Williams et al. 2002). Divorce and dispersal probability were modelled as linear combinations of explanatory variables using a logit link function (Agresti 1990). Sets of models included a general model with the appropriate covariates and their interactions, simplifications of the general model, and a model with no covariates (intercept only). Covariates were represented by capital letters (A: arrival asynchrony, D: pair duration, E: breeding experience, L: local productivity, R: prior residence, S: breeding performance, T: timing of failure) and pairwise interactions by \times (e.g. $A \times S$). Analyses were performed using the software SAS (SAS® 1999). Arrival asynchrony, pair duration, and prior residence were continuous variables. To avoid too small sample sizes, extreme high values were pooled (arrival asynchrony ≥ 65 days, pair duration ≥ 5 years, prior residence ≥ 5 years for divorce probability, prior residence ≥ 8 years for dispersal probability). Local productivity in habitat patches (i.e. the proportion of successful nests) was transformed (arcsine of the square root).

To address probability of divorce and pair reunion, we randomly chose one bird per pair-year because pair bond status is the same for both mates. Samples used to assess site fidelity probability included pairs where both mates were banded as well as banded birds mated with non-banded individuals. In case of divorce, dispersal status is necessarily different for each of the previous mates, so both of them were included in analyses. After procedures of random selection, records of a same individual were not necessarily consecutive in the sample used. Consequently, we used a covariance structure "compound symmetry" (Littell et al. 1996). To account for a possible bias related to non-independence among records of a same individual or pair we used the "repeated" statement of "proc genmod" (Littell et al. 1996).

Model selection was based on the information-theoretic approach, which allows considering non-exclusive candidate models (Burnham and Anderson 1998). We used Akaike's information criterion (AIC) to assess model parsimony and AIC weights (AICw) to account for model selection uncertainty. Adjustments for quasi-likelihood or small sample bias were not needed (results not presented here). Probabilities were estimated

by model averaging so every model within a set was taken into account at the measure of its AICw. We present models that build up at least 95% of the sum of AICw within each set (Burnham and Anderson 1998, Anderson and Burnham 2002). We present all models in the set addressing the influence of either pair duration or prior residence on the probability of pair reunion in failed birds because of the particular approach used in these analyses (below).

Reunion in failed pairs

The covariates considered in this set of models were “timing of failure”, “local productivity”, and either “pair duration” or “prior residence”. As pair duration and prior residence are likely to be correlated, they were not simultaneously included in a same model. We assessed how models including pair duration or prior residence fit the data (i.e. this set comprises two non-nested general models).

Site fidelity in failed individuals

Here we considered “local productivity”, “prior residence”, and “timing of failure” as covariates. In the kittiwake, males predominate in territorial activities, and in general they have lower dispersal probability than females (Coulson and Thomas 1980, Greenwood 1980). For this reason, we also took sex into account in all analyses of dispersal probability. Our main question here was whether individuals choose to stay at a nest site because of potential benefits of site familiarity (i.e. long prior residence) despite the fact that such a site is in an unsuccessful patch.

Divorce in successful pairs

The main covariates in this analysis were “local productivity” and “arrival asynchrony”. Several studies have shown that divorce probability is higher after the first breeding attempt than in more experienced birds (Richdale 1957, Mills 1973, Coulson and Thomas 1983, Harris et al. 1987, Emslie et al. 1992, Hannon and Martin 1996). For this reason, we controlled for an effect of experience.

Cumulative information on individual performance

These analyses included both successful and failed birds. We used memory models to assess the influence of consecutive breeding outcomes and habitat productivity on the probability of site fidelity. We selected data from individuals that used the same nest site for at least three consecutive years. We first addressed the influence of breeding performance in years t-2, t-1, and t on dispersal probability in year t+1. As models including performance in year t-2 had little support, this covariate was not included in a second set of models addressing the influence of multiple previous performance (years t-1

Table 2. Pair reunion and site fidelity according to previous breeding performance.

	Breeding performance in the previous year	
	Failure	Success
Pair reunion probability (n = 1004 pair-years)	0.53 (0.59–0.48)	0.87 (0.90–0.84)
Site fidelity probability (n = 1223 pair-years)		
Females	0.40 (0.46–0.34)	0.81 (0.85–0.76)
Males	0.50 (0.56–0.44)	0.91 (0.93–0.87)

and t), local productivity (year t), and sex on the probability of site fidelity.

Results

Reunion in failed pairs

Overall probability of reunion in failed pairs was 0.53 (Table 2). Accounting for the effect of timing of failure, pair duration or prior residence, and local productivity on the probability of reunion in failed pairs, models including pair duration had little support (only 14% of the sum of AICw, Table 3). Consequently, we estimated

Table 3. Influence of timing of failure, local productivity, and prior residence on the probability of pair reunion in failed birds.

Description of the model	NP	AIC	Δ_i	AICw
Pair duration or prior residence? (n = 259 pair-years)				
T R T × R	5	344.57	0.00	0.42
T R L T × R	6	346.41	1.84	0.17
T R	4	347.12	2.55	0.12
T D T × D	5	348.10	3.53	0.07
T R L T × R T × L	7	348.12	3.55	0.07
T R L	5	349.01	4.44	0.05
T D L T × D	6	349.65	5.09	0.03
T D L T × D T × L	7	350.85	6.29	0.02
T R L T × L	6	350.92	6.36	0.02
R	3	351.85	7.28	0.01
T D	4	352.57	8.00	0.01
R L	4	353.37	8.80	0.01
T D L	5	354.46	9.90	0.00
T D L T × L	6	356.08	11.51	0.00
T	3	357.32	12.75	0.00
D	3	357.62	13.05	0.00
D L	4	359.17	14.60	0.00
T L	4	359.32	14.75	0.00
T L T × L	5	361.18	16.61	0.00
Intercept only	2	362.18	17.61	0.00
L	3	364.07	19.50	0.00
Prior residence (n = 259 pair-years)				
T R T × R	5	344.57	0.00	0.49
T R L T × R	6	346.41	1.84	0.20
T R	4	347.12	2.55	0.14
T R L T × R T × L	7	348.12	3.55	0.08
T R L	5	349.01	4.44	0.05

T: timing of failure (early failure, late failure). R: prior residence. D: pair duration. L: local productivity. NP: number of estimated parameters. AIC: Akaike's information criterion. Δ_i = AIC_i - AIC_{min}, AICw: AIC weight

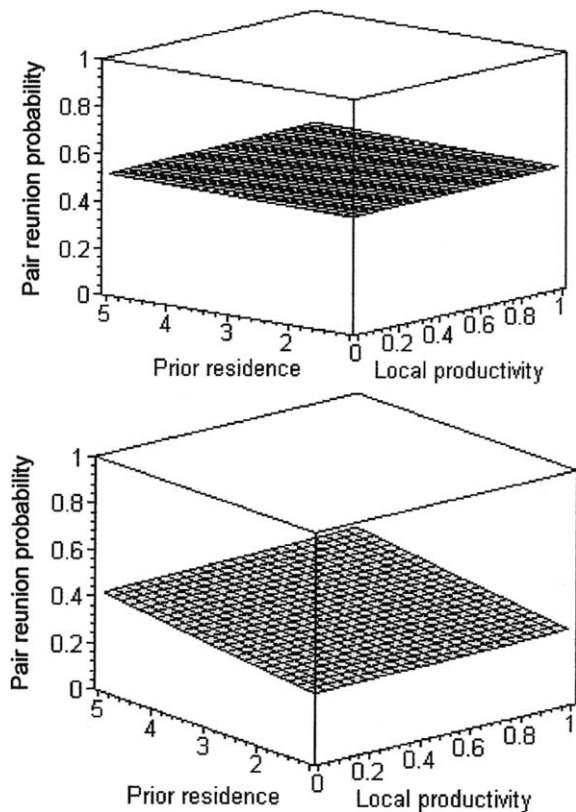


Fig. 1. Probability of reunion in late failed (top) and early failed pairs (bottom). Prior residence: number of successive years at the same nest site. Local productivity: proportion of successful nests in the habitat patch.

pair reunion probabilities considering a complete set of models including prior residence (Table 3). Late failed pairs had higher probability of reunion than early failed

ones (Fig. 1). Local productivity did not affect pair reunion probability. Prior residence had a clear positive effect on the probability of reunion in early failed pairs (the interaction between prior residence and timing of failure was present in models with large AIC weight, Table 3), but such an effect was weak in late failed pairs (Fig. 1).

Site fidelity in failed individuals

Overall, site fidelity probability was 10% lower in females than in males regardless of previous breeding performance (Table 2). Failed males had equal probability of being site faithful or of dispersing while site fidelity probability was 91% in successful males (Table 2). The relationship between site fidelity and both prior residence and local productivity did not differ between sexes (we present only results for males, Table 4, Fig. 2). Early failed birds had lower probability of site fidelity than late failed ones. In both early and late failed birds, site fidelity probability increased with prior residence. Site fidelity probability was positively related to local productivity in early failed birds, but this relationship was quite weak in late failed ones (Fig. 2).

Divorce in successful pairs

Divorce probability in successful pairs was 0.13 (Table 2). Considering arrival asynchrony, breeding experience, and local productivity (Table 5), divorce probability was higher in first-time breeders than in experienced ones (Fig. 3). In both categories of individuals, divorce probability increased with arrival asynchrony, but it was not affected by local productivity (Fig. 3).

Table 4. Influence of timing of failure, prior residence, and local productivity on the probability of re-nesting on the same site in failed birds ($n = 1574$ breeder-years).

Description of the model	NP	AIC	Δ_i	AICw
L R T S L \times T	7	2029.74	0.00	0.22
L R T S L \times T T \times S	8	2031.21	1.47	0.10
L R T S L \times T R \times S	8	2031.49	1.75	0.09
L R T S L \times T L \times S	8	2031.74	2.00	0.08
L R T S L \times T R \times T T \times S	9	2032.24	2.50	0.06
L R T S	6	2032.66	2.92	0.05
L R T S L \times T L \times S R \times T	9	2032.72	2.98	0.05
L R T S L \times T R \times S T \times S	9	2032.96	3.22	0.04
L R T S L \times T L \times S T \times S	9	2033.21	3.47	0.04
L R T S L \times T L \times S R \times S	9	2033.48	3.74	0.03
L R T S L \times T R \times T R \times S T \times S	10	2033.99	4.25	0.03
L R T S T \times S	7	2034.00	4.26	0.03
L R T S R \times T	7	2034.21	4.47	0.02
L R T S L \times T L \times S R \times T T \times S	10	2034.23	4.49	0.02
L R T S R \times S	7	2034.28	4.54	0.02
L R T S L \times T L \times S R \times T R \times S	10	2034.49	4.75	0.02
L R T S L \times S	7	2034.65	4.91	0.02
L R T S L \times T L \times S R \times S T \times S	10	2034.95	5.21	0.02
L R T S R \times T T \times S	8	2035.57	5.83	0.01

L: local productivity. R: prior residence. T: timing of failure (early failure, late failure). S: sex. NP: number of estimated parameters. AIC: Akaike's information criterion. $\Delta_i = AIC_i - AIC_{min}$, AICw: AIC weight

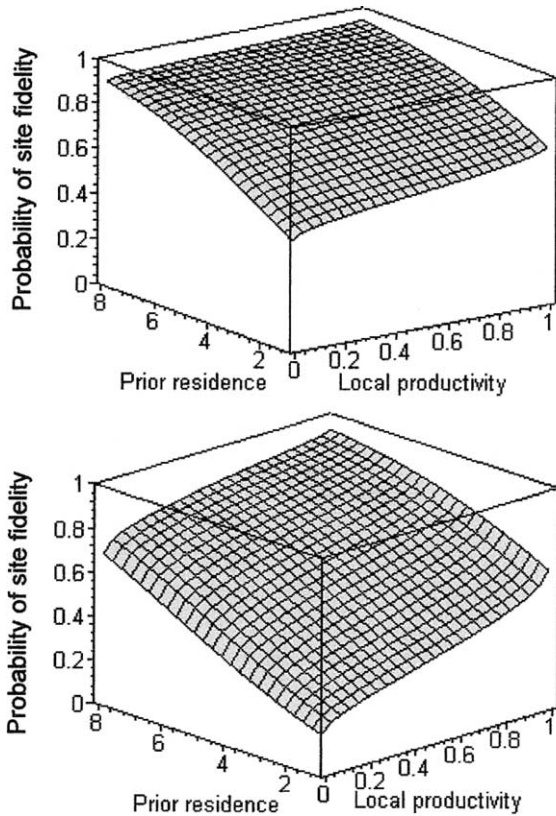


Fig. 2. Probability of nest site fidelity in males that experienced late (top) and early (bottom) breeding failure. Prior residence: number of successive years at the same nest site. Local productivity: proportion of successful nests in the habitat patch. Females had lower probability of site fidelity, but the relationship between site fidelity probability and both prior residence and local productivity did not differ between sexes.

Cumulative information on individual performance

Considering the influence of the outcome of the three most recent breeding attempts on site fidelity probability (year $t+1$), models including breeding performance in year $t-2$ had weaker support (sum of $AIC_w = 0.45$) than models including years $t-1$ and t (sum of $AIC_w = 1.0$ in both cases, Table 6). Consequently, we assessed site fidelity probability as a function of local productivity

Table 5. Influence of breeding experience, arrival asynchrony, and local productivity on the probability of divorcing in successful birds ($n = 534$ pair-years).

Description of the model	NP	AIC	Δ_i	AIC_w
E A	4	368.07	0.00	0.38
E A E \times A	5	369.35	1.27	0.20
E A L	5	369.53	1.46	0.18
E A L E \times L	6	370.83	2.76	0.10
E A L E \times A	6	370.89	2.82	0.09

E: breeding experience (first-time breeder, experienced breeder)
 A: arrival asynchrony, L: local productivity. NP: number of estimated parameters. AIC: Akaike's information criterion
 $\Delta_i = AIC_i - AIC_{min}$, AIC_w : AIC weight

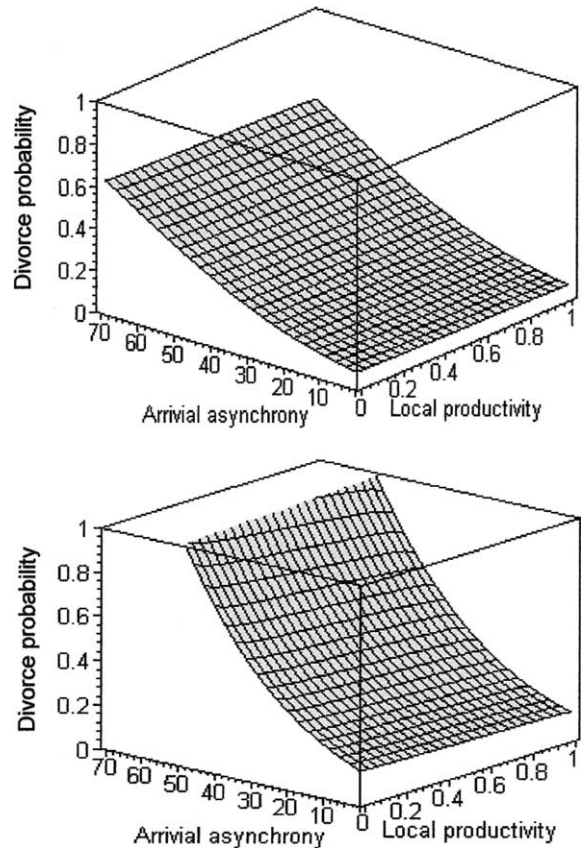


Fig. 3. Divorce probability in successful pairs of experienced breeders (top) and in pairs including first-time breeder(s) (bottom). Arrival asynchrony: number of days between arrival of previous mates at breeding colony. Local productivity: proportion of successful nests in the habitat patch.

and breeding performance in years $t-1$ and t (Table 7). Regardless of breeding performance, females always had lower site fidelity probability than males (Fig. 4). We identified hierarchical levels of response according to the recent history of individual breeding performance. For birds that successfully bred in year t , local productivity had little if any effect on site fidelity probability, which was very high. For birds that failed one or both of the two most recent breeding attempts, site fidelity probability increased with local productivity. Site fidelity probability was lower in birds that failed in year t than in birds that failed in $t-1$. The lowest site fidelity probability occurred in individuals that cumulated successive breeding failures (Fig. 4).

Discussion

Our results confirmed that breeding performance is a major component of the decision-making process regarding nest site and mate choice, as has been found elsewhere (Mills 1973, Coulson and Thomas 1983,

Table 6. Influence of breeding performance in years $t-2$, $t-1$, and t on nest site fidelity ($t+1$) ($n=1000$ breeder-years).

Description of the model	NP	AIC	Δ_i	AICw
$S_{t-1} S_t$	4	763.86	0.00	0.40
$S_{t-2} S_{t-1} S_t$	5	765.62	1.76	0.17
$S_{t-1} S_t S_{t-1} \times S_t$	5	765.86	2.00	0.15
$S_{t-2} S_{t-1} S_t S_{t-2} \times S_t$	6	767.45	3.59	0.07
$S_{t-2} S_{t-1} S_t S_{t-2} \times S_{t-1}$	6	767.46	3.60	0.07
$S_{t-2} S_{t-1} S_t S_{t-1} \times S_t$	6	767.62	3.77	0.06
$S_{t-2} S_{t-1} S_t S_{t-2} \times S_{t-1} S_{t-2} \times S_t$	7	769.29	5.44	0.03
$S_{t-2} S_{t-1} S_t S_{t-2} \times S_t S_{t-1} \times S_t$	7	769.44	5.58	0.03

S_{t-2} : breeding performance in year $t-2$. S_{t-1} : breeding performance in year $t-1$. S_t : breeding performance in year t . NP: number of estimated parameters. AIC: Akaike's information criterion. $\Delta_i = AIC_i - AIC_{min}$, AICw: AIC weight

Johnston and Ryder 1987, Bradley et al. 1990, Dubois and Cézilly 2002). However, deviations from the general pattern success-stay/failure-leave were common in several strata of the study population. Factors other than individual breeding performance may substantially influence divorce and dispersal decisions within specific strata.

We found evidence that timing of failure played an important role in nest site and mate choice in the next season. Pair reunion probability was close to 0.5 in failed birds, but late failed birds consistently had higher probability of pair reunion and site fidelity than early failed ones. We hypothesised that timing of failure provides information on habitat and mate quality, which in turn provide insight into future fitness prospects associated to fidelity. In other systems, habitat and mate characteristics may not be predictable, and such factors may cause failure at different stages of breeding cycle. Whenever habitat quality is correlated over time and breeding performance is used to assess future fitness prospects, one might expect an influence of "state" (timing of failure) on dispersal probability.

Prior residence better explained variability in the probability of reunion in failed pairs than pair duration. The positive influence of prior residence on the probability of reunion was perceptible only in early failed pairs. A possible explanation is that costs of divorce may not increase with pair duration. Pairs may accumulate consecutive breeding failures if a substantial proportion

of failed pairs do not divorce, as found in this study. If so, long pair duration may not be associated with increased probability of breeding successfully.

We found no evidence of influence of patch productivity on mate choice either in failed or in successful pairs. This did not support the hypotheses that reunion in failed pairs results from site fidelity, or that divorce in successful pairs is a direct consequence of dispersal. However, we acknowledge that we did not fully meet the conditions required to address the latter hypothesis because the majority of dispersal events in successful individuals corresponded to changes of nest site within habitat patches. Direct measures of nest site quality will be needed to address divorce and dispersal in successful birds. If site quality varies over space, successful birds may disperse if there are available sites of better quality (i.e. relative quality, Nichols and Kendall 1995, Cam et al. 2004). Addressing this hypothesis requires comparison of quality between the sites of origin and of destination. In species where territories hold feeding resources, territory quality may be directly assessed by the quantity or quality of its resources (Newton and Wyllie 1996, Forstmeier 2002). Some studies have used indirect measures of site quality such as the number of years it has been occupied or breeding performance of the owners (Newton and Marquiss 1982). However, it is unclear how to assess site quality independently from breeding performance in species like the kittiwake where the territory is limited to the nest site.

Table 7. Influence of local productivity, individual breeding performance in years $t-1$ and t , and sex on nest site choice in year $t+1$ (failed and successful birds, $n=1575$ breeder-years).

Description of the model	NP	AIC	Δ_i	AICw
$L S_{t-1} C L \times S_{t-1}$	8	1360.93	0.00	0.27
$L S_{t-1} C L \times S_{t-1} S_{t-1} \times C$	11	1361.01	0.08	0.26
$L S_{t-1} C S_{t-1} \times C$	10	1362.27	1.34	0.14
$L S_{t-1} C L \times S_{t-1} L \times C$	11	1362.99	2.05	0.14
$L S_{t-1} C L \times S_{t-1} L \times C S_{t-1} \times C$	14	1362.99	2.06	0.10
$L S_{t-1} C$	7	1363.12	2.19	0.09
$L S_{t-1} C L \times C S_{t-1} \times C$	13	1364.79	3.85	0.04

L: local productivity. S_{t-1} : breeding performance in year $t-1$ (success, failure). C: categorical combination of breeding performance in year t (success, failure) and sex. NP: number of estimated parameters. AIC: Akaike's information criterion. $\Delta_i = AIC_i - AIC_{min}$, AICw: AIC weight

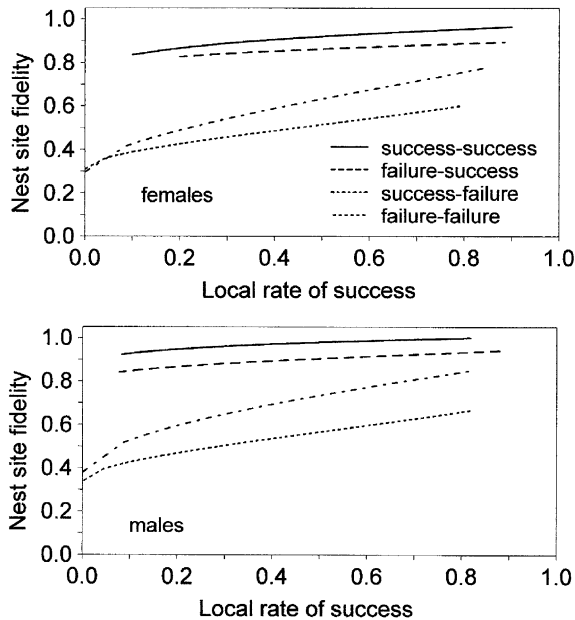


Fig. 4. Probability of nest site fidelity in females (top) and males (bottom) according to individual breeding performance in years $t-1$ and t . Local productivity: proportion of successful nests in the habitat patch.

We found evidence that arrival asynchrony positively influenced divorce probability in previously successful pairs. In an optimality framework, mate and site fidelity might be favoured when leading to higher fitness prospects than divorce and dispersal. Waiting for the previous mate may result in reduced probability of breeding or of breeding successfully (i.e. increased costs of mate fidelity). Postponing breeding while waiting for the previous mate may be costly if breeding conditions deteriorate during the season (decreasing feeding resources, increasing predation pressure, unfavourable climate conditions; “timing hypothesis” Arnold et al. 2004). Moreover, several studies have documented earlier arrival date in older, more experienced individuals suggesting that these are of higher quality than others (Coulson and White 1961, Porter and Coulson 1987, Hatchwell 1991, Brinkhoff et al. 1997, Dittmann and Becker 2003, Arnold et al. 2004). Intra-sexual competition for high-quality mates (or sites) may favour early pairing and lead to divorce if one mate is late regardless of previous breeding performance (“parental quality hypothesis”; Penney 1968, Ens et al. 1996, Cezilly et al. 1997, Moreno 1998). We found that divorce probability in successful pairs was higher in first-time than in experienced breeders. Other than experience per se, this may also be explained by factors correlated to experience such as arrival date (Arnold et al. 2004). Age-related changes in the proportion of higher-quality individuals may also underlie the influence of experience

on divorce probability (“mortality selection” sensu Manton and Stallard 1981, Endler 1986).

Our results supported the hypothesis that dispersal decisions may not be consistent with those expected under the assumption that individual breeding performance is the only source of information taken into account to assess future fitness prospects. Local productivity positively influenced site fidelity probability in early failed birds, but not in late failed ones. This agrees with results by Danchin et al. (1998), who reported a negative influence of patch productivity on dispersal probability in failed birds, but not in successful ones. In our study, individuals that failed in successful patches had site fidelity probability higher than 0.5 (i.e. they were majority). If breeding patches are homogenous in quality, the relative value of patch productivity and of individual performance as sources of information can be explained as follows: breeding success of one nest site is a Bernoulli trial with probability p , the number of successful sites (X) can be modelled using a binomial random variable, and the proportion P of successful sites is $\frac{X}{N}$ (J. Nichols, pers. comm.). The larger the sample size, the smaller the variance of P . Hence, integrating information from neighbouring nest sites leads to smaller uncertainty about patch success compared to information from a single nest site. Doligez et al. (2003) have shown that an individual strategy of habitat selection integrating information on performance of conspecifics should result in higher fitness than alternative strategies.

We further showed that site selection is not based solely on the performance of neighbours and on individual performance in the most recent breeding attempt. Using memory models, we provided evidence that dispersal decisions integrate information on individual breeding performance in a temporal scale longer than one year. This complements the concept that dispersal decisions integrate different sources of information. Informed dispersal decisions may avoid unnecessary costs of dispersal.

Across species, deviations from the success-stay/failure-leave pattern seem to depend on the overall degree of mate fidelity. The occurrence of divorce in successful pairs seems to increase with divorce rate, whereas the occurrence of pair reunion after failure decreases with divorce rate (Table 1). This is not observed in species where there is no evidence of an influence of previous breeding performance on mate choice (Penney 1968, Tickell 1968, Harris 1979, Reilly and Cullen 1981, Southern and Southern 1982, Cuthbert 1985, Gratto et al. 1985, Wiens and Cuthbert 1988, Murphy 1996, Murray and McKinney 1996, Russell and Rowley 1996). This is only a very general picture since divorce rates may vary among populations of a same species. Within species or populations, beyond the probability of pair reunion or site fidelity corresponding to specific cate-

gories of individuals (e.g. late failure, long prior residence, high local productivity), whether a behaviour is the rule depends on how individuals are distributed among the categories (i.e. proportions). Studies of deviations from general trends are needed to understand the diversity of responses observed in populations.

Understanding the evolution of general behavioural rules requires the specification of a range of character states (the strategy set, Seger and Stubblefield 1996) and evaluation of the relative fitness of each state. It has been emphasized that the correct specification of the “state space” is critical to the success of the study (McNamara and Houston 1992, 1996). Using optimisation approaches, optimal decisions can be identified if the state-space does not include irrelevant mixtures of states that obscure the hierarchy in the fitness gains associated to the different strategies (Mangel and Clark 1988, McNamara and Houston 1992, Morris 1998, Pettifor et al. 1998, Clark and Mangel 2000). The specification of the strategy set is also important when using other approaches, such as game theory (Maynard Smith 1982, Clark and Mangel 2000). Regardless of the theoretical framework chosen, the identification of constraints is one of the main difficulties in specifying the set of options open to individuals (Seger and Stubblefield 1996). For example, unbalanced sex ratios may lead to shortage in potential mates making re-mating difficult. As we determined sex through behaviour, our sample of known-sex birds included only those that survived long enough to have their sex assigned. Such a sample does not necessarily represent the population. Information on actual population sex ratio is needed to assess this hypothesis.

Incorporation of heterogeneity in diverse areas of biological sciences raises several difficulties. Here we used a fine stratification of data to account for heterogeneity in mate and nest site choice. However, stratification requires large sample sizes. Recent progress in modelling tools provides different solutions to account for sources of heterogeneity among individuals (McNamara and Houston 1992, Clark and Mangel 2000, Cooch et al. 2002). Such advances open perspectives since finely stratified data cannot be considered as collections of unique events that do not inform us on their likelihood in other individuals, places, or time. Biologists must be able to provide interpretations with value in terms of generalization (Nichols 2002). Only a state-based approach may allow assessment of variability in divorce rate between and within populations (Boekelheide and Ainley 1989, Dhondt et al. 1996, Pampus et al. 2005) because there may be non-alternative coexisting strategies of mate and habitat selection. As we focused on atypical cases, the questions we addressed might be considered unimportant. However, several studies have provided evidence that a small fraction of individuals in populations produces offspring and contributes to future

generations (Clutton-Brock 1988, Newton 1989). From this perspective, only the set of behavioural strategies open to such individuals may be subjected to natural selection. Regardless of whether the optimisation approach is relevant, natural selection may operate on slight fitness differences that cannot be detected without high levels of stratification according to the appropriate individual and habitat attributes. This study contributed to the identification of relevant states to be considered when addressing mate and nest site choice. Other studies will highlight relevant states specific to other biological systems.

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