



Pair duration, breeding success and divorce in a long-lived seabird: benefits of mate familiarity?

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Previous studies have reported that pair duration is positively related to breeding performance and negatively related to divorce probability. According to the concept of 'mate familiarity', a long-term improvement in pair coordination with pair duration results in increased breeding performance. We assessed whether breeding experience, costs of mate change, individual quality and prior residence explained relationships involving pair duration in the kittiwake, *Rissa tridactyla*. We used specific samples (groups of individuals) where confounding factors were not relevant. In the complete data set (a heterogeneous group of individuals), breeding success probability increased with pair duration. Such variation in fitness may reflect changes at the individual level, or in the proportion of individuals of different quality. Breeding experience accounted for a sharp increase in success probability between the first and second years of pair duration. This trend was not observed in new pairs composed of only experienced breeders. Success probability did not increase with pair duration within groups of pairs with the same total duration, or in high-quality birds (using longevity as an index of quality). Finally, mate fidelity and site fidelity may be confounding factors. Prior residence (length of residence at the nest site) better explained variation in success and divorce probabilities than did pair duration. Overall, we found no evidence of a continuous increase in success probability with pair history that could be attributed to mate familiarity. This study highlights the need to consider within-population heterogeneity when assessing the evolution of life history traits.

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Avian mating systems are predominantly monogamous (Lack 1968). Pairs may form only during the breeding season (part-time partnership), or the male and female may remain together all year (continuous partnership) (Black 1996a). Repeated breeding with the same mate (mate fidelity) and repeated use of the same territory (site fidelity) are widespread among birds (Bried & Jouventin 2002). Previous breeding performance influences the occurrence of pair reunion or divorce (pair disruption when both mates are known to be alive; Ens et al. 1996; Bried & Jouventin 2002; Dubois & Cézilly 2002). Successful breeding is

generally associated with higher probability of pair reunion while failure is followed by increased divorce probability. This pattern gave origin to the hypothesis that divorce is a strategy for avoiding repetition of poor performance with a low-quality mate. Other hypotheses have been put forward to explain divorce in circumstances where breeding performance has no influence on mate selection (Rowley 1983; Johnston & Ryder 1987; Owen et al. 1988; Dhondt & Adriaensen 1994; Choudhury 1995; Ens et al. 1996; Taborsky & Taborsky 1999). From an evolutionary perspective, understanding mate selection requires assessment of fitness prospects associated with either fidelity or divorce, as well as of relationships between mate and site selection.

A positive relationship between pair duration and breeding performance has been reported in several avian species (Mills 1973; Brooke 1978; Coulson & Thomas 1983; Ollason & Dunnet 1988; Bradley et al. 1990; Black 2001). A 'mate familiarity' effect may explain this relationship.

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This hypothesis proposes that repeated breeding with the same mate allows fine tuning of behaviour between the male and female, which in turn translates into improved breeding performance (Nelson 1972; Rowley 1983; Black 1996b; Ens et al. 1996). Mate familiarity refers to a long-term adjustment of within-pair behaviour, as opposed to an initial process of coordination during pair formation (Moynihan 1955; Tinbergen 1959; Brown 1967). Many species have a complex set of breeding behavioural displays (Tinbergen 1963; Nelson 1978; Chardine 1983), and poor coordination between mates is thought to cause breeding failure (Coulson 1972). Furthermore, a negative relationship between pair duration and divorce probability was observed in the kittiwake, *Rissa tridactyla* (Coulson & Thomas 1980) and in the oystercatcher, *Haematopus ostralegus* (Harris et al. 1987). The ultimate nature of relationships involving pair duration remains the focus of active research (Black 1996a, 2001; Pärt & Forslund 1996). Pair duration may be confounded with other variables whose influence on breeding performance is difficult to disentangle. Mainly in species with part-time partnerships, age-related factors (experience, social rank, individual quality) may explain relationships involving pair duration (Davis 1976; Brooke 1978; Coulson & Thomas 1980; Bradley et al. 1990; Orell et al. 1994; Black 1996a; Desrochers & Magrath 1996; Naves 2005; Naves et al. 2006).

We assessed relationships involving pair duration using data from a long-term study of a colonial seabird with a part-time pair bond, the kittiwake. Absence of gaps in individual histories is a distinctive feature of this data set, making it appropriate for the study of sequences of events in the history of individuals and pairs (Danchin et al. 1998; Cam et al. 2002). We first assessed the overall relationship between pair duration and breeding success probability. Our results were consistent with those of previous studies. We then assessed three hypotheses to explain the positive influence of pair duration on success probability unrelated to the benefits of increased familiarity with the mate. As a corollary, such hypotheses may also explain a negative relationship between pair duration and divorce probability. In the first two hypotheses, we assessed whether an overall increase in breeding success probability with pair duration results from a combination of patterns associated with groups of individuals with different characteristics (experience, costs of mate change, individual quality). Unlike previous studies, our approach did not aim to control for confounding factors by including them as covariates in models of breeding success and divorce probability. Instead, we selected specific samples where confounding factors were not relevant. The third hypothesis concerns the relative importance of mate familiarity and nest site familiarity on breeding performance and mate selection.

Biological Hypotheses and Predictions

Hypothesis 1: the syndrome of the first-year bond

Several studies of birds have found that breeding performance of newly formed pairs is lower than that of reunited pairs (Mills 1973; Coulson & Thomas 1985; Perrins & McCleery 1985; Ollason & Dunnet 1988; Emslie

et al. 1992). We hypothesized that both lack of experience and costs of mate change may result in poorer breeding performance in newly formed pairs than in older pairs. Based on this hypothesis, we predicted that breeding performance would increase sharply between the first and second years of a pair bond, but not afterwards. Conversely, if mate familiarity influences breeding performance beyond the year of pair formation, we predicted that the increase in success probability with pair duration might extend beyond 2 years.

Individual experience positively influences breeding performance and negatively influences divorce and dispersal probabilities (Richdale 1957; Mills 1973; Coulson & Thomas 1983; Harris et al. 1987; Bradley et al. 1990; Emslie et al. 1992; Hannon & Martin 1996). Several studies have also reported contrasting performance between first-time breeders (individuals that have not previously bred) and individuals that have bred at least once before (Newton 1986; Saether 1990; Bradley & Wooller 1991; Desrochers & Magrath 1993; Cam & Monnat 2000a). Long pair duration can be observed only in experienced individuals, and pair duration is always equal to 1 year in first-time breeders. When researchers compare breeding performance in the first year between pairs including at least one first-time breeder and pairs including only experienced breeders, any differences may reflect an underlying influence of individual experience on breeding success probability (Davis 1976; Brooke 1978; Perrins & McCleery 1985; Desrochers & Magrath 1996).

In some studies that accounted for experience, new pairs also performed more poorly than did reunited pairs (Davis 1976; Perrins & McCleery 1985; Catry et al. 1997). Costs of pair formation may explain this pattern (Perrins & McCleery 1985; Bradley et al. 1990; Emslie et al. 1992; Fowler 1995). Indeed, mate and territory acquisition require energy and time-consuming behaviours (Penney 1968; Nelson 1978; Danchin 1987; Sullivan 1994). Mate fidelity may be advantageous by preventing costs of forming a new pair ('pair-bond investment hypothesis'; Fowler 1995). Costs of pair formation concern first-time breeders as well as experienced individuals that are divorced or widowed. Divorced breeders may also incur costs associated with conflict with the previous mate, including territorial competition (Coulson & Thomas 1983). We refer here to costs of disruption of the previous bond and costs of formation of a new bond altogether as 'costs of mate change'.

If an increase in breeding performance is observed solely between the first and second years of pair duration, this result may reflect lack of experience and costs of mate change rather than a mate familiarity effect. Our reasoning relies on the premise that mate familiarity corresponds to a long-term adjustment of within-pair behaviour as opposed to an initial process of pair formation.

Hypothesis 2: Individual quality underlying pair duration

The distribution of pair duration is related to the age structure of the population, because long-term pair bonds

concern long-lived individuals. Studies of biological processes involving changes in fitness components throughout life face the challenge of unravelling genuine effects of a given factor in a population composed of individuals with different life spans. The development of the concept of 'individual quality' (Curio 1983) drew attention to the likelihood that populations are heterogeneous. The 'selection hypothesis' proposes a progressive concentration of high-quality individuals with high survival probability in older age classes (Vaupel & Yashin 1985; Endler 1986; Cam & Monnat 2000a; Cam et al. 2002; Mauck et al. 2004). Positive relationships between components of fitness suggest that higher-quality individuals have not only higher breeding performance but also higher survival probability than lower-quality individuals (the 'good gene hypothesis'; Reilly & Cullen 1981; Ollason & Dunnet 1988; Thomas & Coulson 1988; Bradley et al. 1989; Cam et al. 1998, 2002; Cam & Monnat 2000a). Populations may be mixtures of groups of individuals in different states defining constant differences in fitness components between individuals.

We hypothesized that changes over time in the proportions of individuals of different quality may account for a positive effect of pair duration on breeding performance in studies that have not accounted for heterogeneity in longevity (Ens et al. 1996). Previous studies have shown that individual survival, breeding probability and breeding success probability are positively correlated in our study population (Link et al. 2002; Cam et al. 2002). Based on our second hypothesis, we predicted no influence of pair duration on the probabilities of breeding success (year t) and of divorce (year $t + 1$) in a group of individuals more homogeneous in quality (i.e. long life span) than the greater population. This prediction relies on the assumption that age-related changes in mean breeding performance observed in our study system (Cam & Monnat 2000a) result from selective mortality. High-quality individuals may account for a large proportion of long-lasting pairs because of high individual survival. High-quality individuals may also have higher breeding performance than other individuals because of better feeding, territorial and parental skills (Bradley et al. 1990).

Hypothesis 3: Prior residence underlying pair duration

Mate fidelity may be a by-product of site fidelity if pair reunion results from attachment of both the male and the female to a nesting site (Burger 1974; Morse & Kress 1984; Cuthbert 1985; Pietz & Parmelee 1994; Ens et al. 1996). If so, the evolution of mate fidelity may not be related to fitness benefits of long-term pair bonds. In species where territories hold feeding resources, evidence suggests that habitat selection may be more important than mate selection (Alatalo et al. 1986; Desrochers & Magrath 1996; Newton & Wyllie 1996). The nature of the relationship between mate fidelity and site fidelity remains unclear, especially in species where the territory is limited to the nesting site, as in cliff- and burrow-nesting birds (Ollason & Dunnet 1978; Ainley et al. 1990; Aebischer et al. 1995;

Fairweather & Coulson 1995; Handel & Gill 2000; Jouventin & Bried 2001; Pyle et al. 2001; Catlin et al. 2005; Setiawan et al. 2005).

A positive relationship between mate fidelity and site fidelity has been reported in a diversity of species (Cézilly et al. 2000). Reunited pairs have lower dispersal probability than divorced individuals (Coulson & Thomas 1983), so pair duration (number of successive breeding attempts with the same mate) is likely to be correlated with prior residence (number of successive breeding attempts on the same nest site). We hypothesized that prior residence also explains, or better explains, variation in the probabilities of both breeding success and of divorce than does pair duration. Evidence suggests that familiarity with the physical and social environment enhances the ability to acquire and keep territorial, feeding and breeding resources (Koivula et al. 1993; Haley 1994; Schjørring et al. 2000; Forstmeier 2002; Hardwood et al. 2003). In monogamous species, competitive benefits derived from prior residence may explain fidelity of both mates to the same nest site.

METHODS

Data Collection and Selection

Data were collected in Brittany, France, at five breeding colonies of kittiwakes monitored since 1979, which in total comprised about 1000 pairs (Danchin & Monnat 1992). The colonies were a few kilometres apart, and situated on a set of cliffs delimited by indentations of the coastline. Individual nest sites were identified in cliff maps. Nestlings and adults of unknown age were marked with a combination of coloured plastic bands and a numbered metal band. Each nest site was monitored at least once a week between January (upon arrival) and mid-April (nest construction). Each nest was monitored about twice a week in May and June (laying and incubation), and daily in July and August (chick rearing). Observations from each bird were summarized to determine yearly breeding status, reproductive performance, mate fidelity and nest site fidelity.

We selected information collected between 1982 and 2004 from 1506 pair-years where both the male and the female were banded. Sex of individuals was assigned through behavioural criteria. Birds were considered as breeders when they had completed the construction of a nest as a flat platform of mud and grass with an inner cup (Paludan 1955; Cullen 1957; Maunder & Threlfall 1972). Individual breeding experience was defined either as 'first-time breeder' (inexperienced birds in their first breeding attempt) or 'experienced breeder' (subsequent attempts). Analyses based on first-time breeders included pairs with at least one first-time breeder. Analyses based on experienced breeders included only pairs composed of two experienced individuals. The pair bond status of 'reunited' or 'divorced' was based on 2 consecutive years (t and $t + 1$). Divorced birds were those that formed a pair in year t but not in year $t + 1$, if both

individuals were known to be alive. Widowed birds (i.e. those whose previous mate did not survive to year $t + 1$) were excluded from analyses of divorce probability. Breeding performance was defined as 'success' (production of at least one fledgling) or 'failure' (no laying, no hatching, or fledgling). Such a binary definition, rather than the actual number of chicks reared per nest, is supported by differences in nest attendance and prospective behaviour between failed and successful birds (Cadiou & Monnat 1996; Cadiou 1999), which may influence divorce probability (Naves 2005). Furthermore, a binary definition of breeding performance was needed to simplify the modelling design. Experienced breeders that skipped a breeding attempt in year t (i.e. nonbreeders) were excluded from all analyses. 'Prior residence' (year t) represented the number of successive years that an individual settled on the same nest site, inclusive of that year.

'Pair duration' (year t) corresponded to the number of years that a male and a female formed a pair, regardless of whether the bond continued afterwards. We considered a male and a female to be paired when they were resighted together on multiple occasions during a breeding season. Paired birds perform behavioural displays of pair formation and pair coordination (Moynihan 1955; Tinbergen 1959; Brown 1967), which were also used to determine pair bond status. Nonbreeders may form a pair or establish a territory (Jones & Montgomerie 1991; Cam & Monnat 2000b). Such cases were considered as pair reunion and site fidelity, respectively, when quantifying pair duration and prior residence.

We pooled data from the five colonies. We were unable to identify factors attributable to the colonies themselves that could cause variability in the extent of a mate familiarity effect or in the occurrence of divorce. Previous studies in the same region have shown that mean breeding success may vary among colonies and among cliffs within a colony (Danchin et al. 1998; Cam & Monnat 2000b) because of localized predation pressure and ectoparasite infestation (Boulinier & Danchin 1996; Cam et al. 2004). In addition, the proportion of individuals at different breeding experience or age classes may vary according to colony history (Kharitonov & Siegel-Causey 1988). We were unable to further increase the stratification level in our analyses to simultaneously account for effects of year and cliff. However, we specifically addressed the influence of experience and age (i.e. longevity) on breeding success probability. In analyses of divorce probability, we accounted for an effect of breeding performance. Moreover, the colonies were close together and the birds do disperse among them (Danchin & Monnat 1992; Danchin et al. 1998; Cam et al. 2004), which is likely to preclude evolution of distinct strategies of mate selection within the study area.

Statistical Approach and Modelling

In our study system, resighting probability of marked individuals is very close to one from the first breeding attempt onwards ($\hat{p} \pm SE = 0.998 \pm 0.89 \times 10^{-2}$; Cam et al.

1998). This evidence allowed us to use modelling tools not incorporating this parameter (Williams et al. 2002). Whether mortality observed in the study area partially reflects emigration is unknown (Link et al. 2002). Breeding success probability and divorce probability were modelled as combinations of explanatory variables using a logit-link function (Agresti 1990), and the software SAS (SAS Institute 1999). Sets of models included a general model with up to three covariates, simplifications of it, and a model including only the intercept (no covariates). Main effects are represented by capital letters (U : pair duration as continuous variable, U^B : pair duration as binary variable, R : prior residence as continuous variable, R^B : prior residence as binary variable, S : breeding performance in year t) and pairwise interactions by an asterisk (e.g. U^*S).

To assess the increase in breeding success probability only between the first and second years of pair duration, we considered pair duration as a binary variable (=1 year, >1 year). To address whether the influence of pair duration on breeding success and divorce probability extends over a few or several years, we considered pair duration as a continuous variable (because of small sample sizes, we pooled values ≥ 7 years). Similarly, we considered prior residence as a binary variable (=1 year, >1 year) and as a continuous variable (values ≥ 7 years were pooled). We contrasted models including a binary variable (U^B or R^B) with models including a continuous one. When evaluating a continuous variable, we included quadratic terms (U^2 , R^2) to account for the possibility that their influence on breeding success or divorce probability is not linear on the logit scale.

When assessing divorce probability, we included previous breeding performance as a control covariate because of its influence on mate fidelity (Ens et al. 1996; Dubois & Cézilly 2002), and because individual performance may be correlated in successive years (Cam & Monnat 2000a).

We randomly chose one bird from each pair-year because breeding outcome and pair bond status is always the same for both mates. To avoid a bias related to nonindependence among records of a same pair or individual, we used the 'repeated' statement of Proc Genmod in SAS (Littell et al. 1996). Records of a same individual or pair were not necessarily consecutive because of the procedure of random selection, so we used a covariance structure, 'compound symmetry' (Littell et al. 1996).

Model selection was based on the information-theoretic approach, which permits consideration of a set of nonexclusive biological hypotheses (Burnham & Anderson 1998). Our hypotheses involved only a few covariates simultaneously, so some of our sets of models could be assessed using classical hypothesis testing based on t tests or F tests. However, the information contained in the data does not always allow for identification of a single model. Contrary to hypotheses testing, the information-theoretical approach accounts for uncertainty in the process of model selection (Burnham & Anderson 1998). Moreover, we used two non-nested general models when addressing the influence of pair duration and prior residence on success probability (hypothesis 3). This design precludes hypothesis testing, whereas an information-theoretical approach is well suited.

Akaike's information criterion (AIC) allows identification of models within a given set that satisfactorily describe the data (i.e. small bias) without including too many parameters, which leads to poor precision in estimates (i.e. large variance) (Burnham & Anderson 1998). The AIC allows the evaluation of the relative performance of models within a set without using arbitrary type I error risks whose theoretical basis is unclear (Burnham & Anderson 1998). A modified version of AIC (AICc) accounts for bias when the sample size is small relative to the number of parameters (NP) of the general model (number of records/NP < 40; Burnham & Anderson 1998). Adjustments for small sample bias were not necessary here. A third version of AIC (QAIC) accounts for 'overdispersion' (i.e. when the sampling variance exceeds the theoretical variance predicted by the binomial model). Lack of independence among records in the data set is one of the causes of overdispersion (Burnham & Anderson 1998). An overdispersion factor indicates whether AIC needs to be corrected for (i.e. its value should not be larger than 4; Littell et al. 1996; Burnham & Anderson 1998). Quasilikelihood adjustments (QAIC) were not needed here, because overdispersion factors of general models were always close to one (results not presented).

We used AIC weights (AIC_w) to account for model selection uncertainty. AIC weights quantify the relative support for models given the data and the complete set of models specified. Furthermore, we used model averaging to estimate probabilities. This means that every model within a set was taken into account at the measure of its AIC_w . The metric quantifying the relative support for each model within a set was used to weigh estimated probabilities, so there was no need to pinpoint a single model (the one with the lowest AIC_w). We present the models that made up at least 95% of the sum of AIC_w within each set (Burnham & Anderson 1998; Anderson & Burnham 2002). When addressing the effect of either pair duration or prior residence on breeding success and divorce probabilities, we present the complete set of models because of the particular approach that we used in these analyses (see above).

The syndrome of the first-year bond

First, to address an underlying influence of experience on the relationship between pair duration and breeding success probability, we excluded all records from pairs composed of two experienced breeders with a pair duration of 1 year (i.e. the year of pair formation). In this analysis, all records where pair duration equalled 1 year concern pairs that included at least one first-time breeder. Using this approach, we also addressed an underlying influence of experience on the relationship between pair duration and divorce probability.

Second, we addressed costs of mate change. Although it is not possible to disentangle effects of experience and of costs of pair formation on breeding performance in first-time breeders, costs of mate change may be detectable in experienced breeders. Therefore, for this analysis, we excluded all records from pairs that

included at least one first-time breeder to assess an underlying influence of mate change costs on the relationship between pair duration and breeding success probability. This procedure aimed to minimize the effect of experience on performance when addressing the hypothesis that costs of mate change at least partly account for the influence of pair duration on breeding success probability.

Individual quality

We first investigated the relationship between pair duration and pair quality. For this analysis, we estimated breeding success probability through the history of pairs grouped according to their total length of pair duration (i.e. number of successive years that a male and a female formed a pair until the bond was disrupted by divorce or widowhood).

Second, we compared the influence of pair duration on breeding success probability in 'high-quality' individuals and in the 'complete data set' (i.e. a heterogeneous group of individuals). High-quality individuals may have higher breeding performance than mean-quality individuals regardless of individual experience and length of pair bond. We used longevity as an index of individual quality. There is a trade-off between sample size and the age threshold used to select data for a group of individuals with high survival prospect (i.e. more homogeneous in quality than the overall population). We assumed that high-quality (long-lived) birds were those that had survived for at least 8 years (10.8% of the number of birds in the complete data set). The identification of high-quality individuals can be difficult (Moreno 2003), and observable covariates based on arbitrary criteria may not adequately account for within-population heterogeneity (Hougaard 1991; Cooch et al. 2002). Despite these limitations, longevity can be used as a surrogate for individual quality (Cooch et al. 2002).

Prior residence

Prior residence and pair duration are likely to be correlated, so these variables were not simultaneously included in the same model. Using AIC weights, we assessed how non-nested models of breeding success and of divorce probability that included each of these variables fit the data.

RESULTS

Using the complete data set, we found evidence of influence of pair duration on breeding success probability (Table 1, 'Complete data set'). Breeding success probability initially increased with pair duration, and decreased with longer pair duration (Fig. 1, Complete data set). Divorce probability was influenced by both pair duration and previous breeding performance (Table 2, 'Complete data set'). Divorce probability slightly decreased with pair duration, and was higher in pairs that had previously failed than in pairs that had been previously successful (Fig. 2). This

Table 1. Influence of pair duration on breeding success probability (year *t*)

Model description	NP	AIC	Δ_i	AIC _w
Sample: Complete data set (<i>N</i> =1344 pair-years)				
$U U^2$	4	1791.17	0.00	0.51
U^B	3	1791.30	0.13	0.48
Sample: Experience (all records where pair duration equals 1 year concern pairs with at least one first-time breeder; <i>N</i> =871 pair-years)				
U^B	3	1108.70	0.00	0.99
Sample: Costs of mate change (all records where pair duration equals 1 year concern pairs with experienced breeders only; <i>N</i> =851 pair-years)				
$U U^2$	4	1100.85	0.00	0.30
U^B	3	1100.94	0.09	0.29
Intercept only	2	1101.11	0.26	0.26
U	3	1102.30	1.45	0.15
Sample: Individual quality (high-quality, long-lived birds only; <i>N</i> =478 pair-years)				
Intercept only	2	633.04	0.00	0.53
U^B	3	635.01	1.97	0.20
U	3	635.04	2.00	0.20
$U U^2$	4	636.93	3.89	0.08
Sample: Complete data set (<i>N</i> =948 pair-years)				
$R^2 R$	4	1227.29	0.00	0.81
R^B	3	1230.22	2.93	0.19
R	3	1259.04	31.76	0.00
$U^2 U$	4	1270.27	42.98	0.00
U^B	3	1271.16	43.87	0.00
U	3	1272.67	45.39	0.00
Intercept only	2	1294.37	67.09	0.00

U: pair duration (continuous variable); U^B : pair duration (binary variable: 1 year, >1 year); *R*: prior residence (continuous variable); R^B : prior residence (binary variable: 1 year, >1 year); NP: number of estimated parameters; AIC: Akaike's information criterion; $\Delta_i = AIC_i - AIC_{min}$, where AIC_i is the value for model *i* and AIC_{min} is the lowest AIC value within the set of models; AIC_w: AIC weight.

trend was observed in the three samples considered (i.e. Complete data set, Experience, Individual quality), and differences between these categories of individuals were slight.

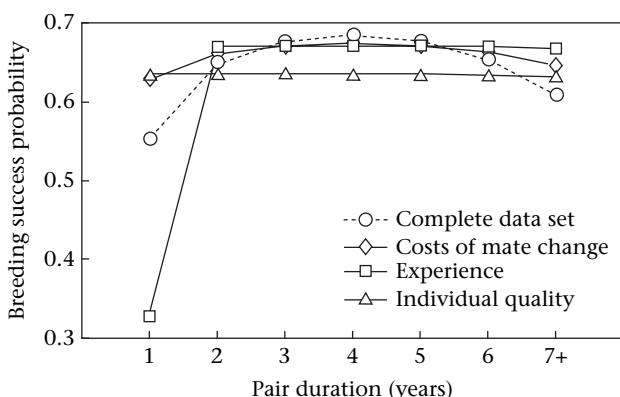


Figure 1. Influence of pair duration on breeding success probability (year *t*). Complete data set: a heterogeneous group of individuals; 'Experience': all records where pair duration equalled 1 year concern pairs with at least one first-time breeder; 'Costs of mate change': all records where pair duration equalled 1 year concern pairs with experienced breeders only; 'Individual quality': high-quality, long-lived individuals only. See Appendix, Table A1 for confidence intervals.

The Syndrome of the First-year Bond

When evaluating the influence of experience in the relationship between pair duration and breeding success probability (i.e. when excluding pairs of two experienced breeders in their first year of bond), we found a sharp increase in breeding success probability between the first and second years of pair duration, but no increase afterwards (Table 1, Fig. 1, 'Experience'). Lack of experience in pairs that included at least one first-time breeder (Fig. 2, 'Experience') accounted for higher divorce probability in this sample than in the 'complete data set' (Fig. 2).

Table 2. Influence of pair duration on divorce probability (year *t* + 1)

Model description	NP	AIC	Δ_i	AIC _w
Sample: Complete data set (<i>N</i> =957 pairs-year)				
$U S U^* S$	5	926.54	0.00	0.32
$U S$	4	926.85	0.31	0.27
$U U^2 S U^* S$	6	928.38	1.84	0.13
$U U^2 S U^2 S$	6	928.66	2.12	0.11
$U U^2 S$	5	928.85	2.31	0.10
$U U^2 S U^* S U^2 S$	7	930.38	3.84	0.05
Sample: Experience (all records where pair duration equals 1 year concern pairs with at least one first-time breeder; <i>N</i> =626 pairs-year)				
$U S$	4	595.39	0.00	0.30
$U S U^* S$	5	595.54	0.15	0.28
$U U^2 S$	5	597.06	1.67	0.13
$U U^2 S U S$	6	597.37	1.98	0.11
$U U^2 S U^2 S$	6	597.64	2.25	0.10
$U U^2 S U^* S U^2 S$	7	599.34	3.95	0.04
Sample: Individual quality (high-quality, long-lived birds only; <i>N</i> =366 pairs-year)				
$U S$	4	304.92	0.00	0.32
$U^B S$	4	306.07	1.14	0.18
$U S U^* S$	5	306.74	1.81	0.13
$U U^2 S$	5	306.80	1.87	0.13
$U^B S U^B S$	5	308.06	3.14	0.07
S	3	308.25	3.33	0.06
$U U^2 S U^2 S$	6	308.55	3.63	0.05
$U U^2 S U^* S$	6	308.63	3.71	0.05
Sample: Complete data set (<i>N</i> =671 pairs-year)				
$R S$	4	669.63	0.00	0.57
$R^2 R S$	5	671.50	1.87	0.22
$R^2 R S R^2 S$	6	673.45	3.82	0.08
$R^2 R S R^* S$	6	673.49	3.86	0.08
$R^2 R S R^2 S R^* S$	7	675.28	5.65	0.03
$R^B S$	4	678.80	9.17	0.01
$R^B S R^B S$	5	680.79	11.16	0.00
$U S$	4	686.55	16.91	0.00
$U^2 U S$	5	688.45	18.81	0.00
$U^B S$	4	688.57	18.94	0.00
$U^B S U^B S$	5	689.03	19.40	0.00
$U^2 U S U^* S$	6	689.03	19.40	0.00
$U^2 U S U^2 S$	6	689.29	19.66	0.00
$U^2 U S U^2 S U^* S$	7	691.00	21.36	0.00
S	3	696.91	27.27	0.00
R	3	749.98	80.35	0.00
$R^2 R$	4	750.94	81.31	0.00
R^B	3	756.02	86.38	0.00
U	3	778.33	108.70	0.00
$U^2 U$	4	779.63	110.00	0.00
U^B	3	780.88	111.25	0.00
Intercept only	2	801.85	132.22	0.00

S: breeding performance in year *t* (failure, success). All other variables and parameters as defined in Table 1.

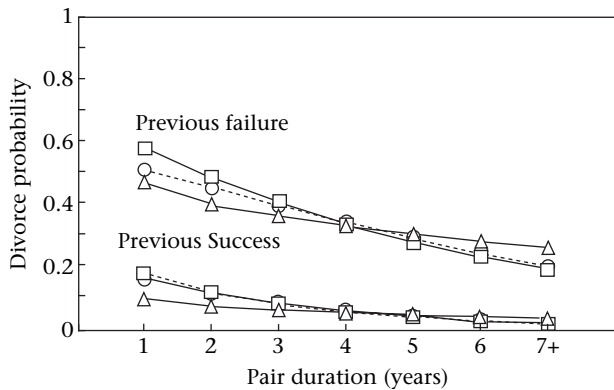


Figure 2. Influence of pair duration on divorce probability (year $t + 1$). Symbol designations as given in Fig. 1. See Appendix, Table A2 for confidence intervals.

Concerning the influence of costs of mate change on breeding success probability (i.e. when excluding pairs with at least one first-time breeder), model averaging supported the hypothesis of a slight increase in breeding success probability between the first and second years of pair duration (Table 1, Fig. 1, ‘Costs of mate change’).

Individual Quality

Breeding success probability did not increase with pair duration in pair bonds with the same total duration (Table 3, Fig. 3). The overall level of breeding success probability increased with total duration across groups of pairs. Pairs that lasted only 1 year had much lower breeding success probability than did pairs that lasted 4 or more years (Fig. 3).

In high-quality individuals, we found no evidence of an influence of pair duration on breeding success probability (Table 1, Fig. 1, ‘Individual quality’). We found a negative effect of pair duration on divorce probability, which was clear in failed birds but almost imperceptible in successful birds (Table 2, Fig. 2, ‘Individual quality’).

Table 3. Breeding success probability through the history of pairs grouped according to total pair duration

Model description	NP	AIC	Δi	AIC _w
Sample: Total pair duration 1 (N=386 pair-years)				
U	3	532.96	—	—
Sample: Total pair duration 2 (N=376 pair-years)				
Intercept only	2	509.78	0.00	0.52
U	3	509.96	0.18	0.48
Sample: Total pair duration 3 (N=211 pair-years)				
U ^B	3	251.62	0.00	0.38
U	3	251.76	0.14	0.35
U U ²	4	253.33	1.71	0.16
Intercept only	2	254.08	2.45	0.11
Sample: Total pair duration 4+ (N=350 pair-years)				
U	3	404.49	0.00	0.50
U U ²	4	405.39	0.91	0.32
Intercept only	2	407.22	2.73	0.13

U: pair duration (continuous variable); U^B: pair duration (binary variable: 1 year, >1 year). All parameters of analysis as defined in Table 1.

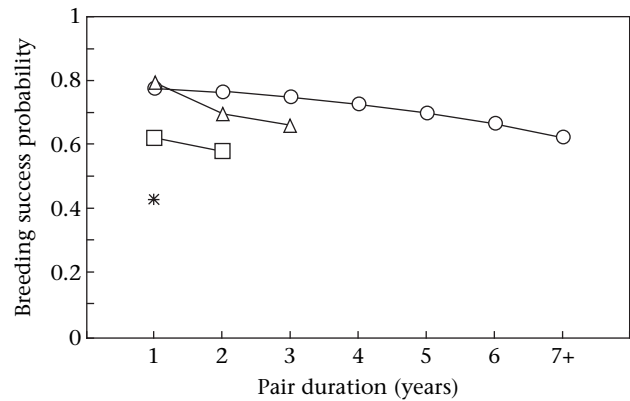


Figure 3. Breeding success probability (year t) through the history of pairs grouped according to the total pair duration. *: pairs that lasted only 1 year. □: pairs that lasted 2 years. Δ: pairs that lasted 3 years. ○: pairs that lasted 4 or more years. See Appendix, Table A3 for confidence intervals.

Prior Residence and Pair Duration

Pair duration was positively correlated with prior residence ($R^2 = 0.53, P < 0.000$). Prior residence better explained variability in both breeding success and divorce probabilities than did pair duration (Tables 1, 2). Models including prior residence accumulated 100% of the AIC_w for both the probability of breeding success and divorce. Models including pair duration had high Δi values ($\Delta i \geq 42.98$ for breeding success probability, $\Delta i \geq 16.91$ for divorce probability). This result means that such models had very little support because of their poor fit to the data. The relationships between prior residence and the probabilities of breeding success and of divorce (results not presented here) followed the same trend as those concerning pair duration (Figs 1, 2).

DISCUSSION

The Syndrome of the First-year Bond

Individual experience accounted for a sharp increase in breeding performance between the first and second years of pair duration, but not afterwards. A previous study of the same population found that breeding success probability of first-time breeders was lower than that of experienced breeders (Cam & Monnat 2000a). The influence of breeding experience on the relationship between pair duration and performance has been evaluated in other bird species. In blackbirds, *Turdus merula*, Desrochers & Magrath (1996) found no evidence of a relationship between pair duration and breeding performance when yearling females were excluded from analysis. Brooke (1978) found that new pairs of Manx shearwaters, *Puffinus puffinus*, formed by two experienced breeders performed as well as did reunited pairs. Similar results have been found in new pairs of Arctic skua, *Stercorarius parasiticus* (Davis 1976): higher performance in reunited pairs was related to higher performance in experienced breeders.

Fitness costs associated with pair formation may also contribute to higher performance in reunited pairs. Consistent with this hypothesis, our results provide evidence that breeding success probability slightly increases between the first and second years of the pair duration in experienced breeders. This relationship, however, was no longer observed after the second year of the pair bond. Behavioural observations might provide insight into the nature of mate change costs. In the prelaying period, newly formed kittiwakes pairs spend more time in within-pair interactions than do reunited pairs, which may result in less time devoted to other activities such as feeding (Chardine 1987). In addition, in Chardine's study, peak sexual behaviour was better timed in relation to egg fertilization in reunited pairs. Nelson (1972) reported higher frequencies of aggressive behaviour in new pairs than in reunited pairs of gannets, *Morus bassanus*. According to McGraw & Hill (2004), reunited pairs of the house finch, *Carpodacus mexicanus*, interact more frequently than do new ones. In the Arctic skua, mating often occurs with minor courtship display in reunited pairs (O'Donald 1983). In addition, pair formation and dispersal are commonly simultaneous processes. Territory acquisition involves agonistic displays, including direct confrontation (Penney 1968; Nelson 1978; Danchin 1987). This finding suggests that settling a new pair bond and a new territory are likely to be energetically costly, at least in the prelaying period (Thomas & Coulson 1988; Bradley et al. 1990; Catry et al. 1997).

Both lack of experience and costs of mate change may contribute to poor breeding performance in the first year of pair formation, independently of an increase in mate familiarity (i.e. a fine tuning of breeding behaviour). Concurrent with Sydeman et al. (1996), we found evidence that an increase in breeding performance occurs only between the first and second years of pair duration. Similarly, O'Donald (1983) observed late onset of breeding in new pairs of Arctic skuas, but not in pairs with 2 or more years of duration. We used different samples to address the hypothesis of the first-year bond syndrome, so we were unable to draw inferences about the relative weight of experience and of costs of mate change by comparing models using AIC. Nevertheless, our results suggest that experience accounts for much greater variability in breeding success probability than do costs of mate change. We know of no other studies that have assessed the relative weight of such factors. Besides, several studies have shown that, although breeding success probability does not differ between reunited and new pairs, nonbreeding probability is much higher after pair disruption (Penney 1968; Ens et al. 1993; Hannon & Martin 1996; Catry et al. 1997; González-Solís et al. 1999; Jouvantin et al. 1999; Setiawan et al. 2005). This evidence suggests that overall costs of mate change are not limited to a possible reduction in success probability in a new pair bond. This issue was beyond the scope of this study, because the mate familiarity effect does not logically concern nonbreeding probability after pair disruption.

Individual Quality and Pair Duration

In the complete data set, breeding success probability increased during the few years that followed pair formation and decreased afterwards. In contrast, there was no initial increase in breeding success probability when pairs were grouped by total pair duration. In general, breeding success probability decreased with longer pair duration. This result may reflect a negative influence of age on breeding performance in very old birds (Thomas & Coulson 1988; Pugsek & Diem 1990; Wooller et al. 1990).

Breeding success probability increased with the total number of years that a pair bred together. Bradley et al. (1990) also observed that breeding success of long-lasting pairs of short-tailed shearwaters, *Puffinus tenuirostris* is higher than that of short-duration pairs, and that this difference is evident early in the history of the bond. Progressive disappearance of pairs with short total duration and low performance may explain the initial increase in breeding success probability with pair duration in our complete data set. The positive correlation between pair duration and breeding performance reported in earlier studies may result from the fact that a majority of studies have used samples that included pairs with different total pair bond durations (Black 1996b). This condition does not allow assessment of variation in breeding performance within a pair over time. However, some researchers have found a positive correlation between total pair duration and breeding performance (Ollason & Dunnet 1978; Bradley et al. 1990; Emslie et al. 1992). It is difficult to assess whether such results reflect a true mate familiarity effect, because studies largely differ in which factors have been controlled for (e.g. experience, age) and in the procedures used to avoid pseudoreplication of records of individuals or pairs (Ens et al. 1996).

We did not find evidence of a relationship between pair duration and breeding success probability in the sample of high-quality (long-lived) individuals. Assuming that individual quality and pair quality are not independent, these results may reflect a higher proportion of pairs of higher quality, higher performance and longer duration in the sample of long-lived individuals than in the complete data set. Our results support the idea that a within-generation mortality selection process (Endler 1986) contributes to a positive relationship between pair duration and breeding performance in a heterogeneous group of individuals. This hypothesis highlights the need to consider demographic processes when addressing behavioural hypotheses on the evolution of life history traits.

In the barnacle goose, *Branta leucopsis*, a species with continuous partnership, Black (2001) observed a positive relationship between pair duration and lifetime reproductive success while controlling for longevity. This result may be explained by the fact that year-round intrapair cooperation is important to ensure social rank and access to feeding and breeding territories previously used by the pair (Black 2001). This is one mechanism that may explain the consistency in the

relationship between pair duration and breeding performance in species with continuous partnership (Ens et al. 1996).

Mate Familiarity or Site Familiarity?

We found a negative relationship between pair duration and divorce probability regardless of the sample used (with or without first-time breeders, etc.). One possible explanation is a genuine effect of mate familiarity (i.e. the longer the pair bond, the stronger the advantage in reuniting). However, our results concerning the relationship between pair duration and breeding success probability did not support a mate familiarity effect in our study system. Another possible explanation for the consistency in the relationship between divorce probability and pair duration is an influence of prior residence on divorce probability. Indeed, prior residence and pair duration were positively correlated, and prior residence better explained variability in divorce and breeding success probability than did pair duration.

Increased competitive ability associated with prior residence is well documented in a diversity of animal groups (Koivula et al. 1993; Haley 1994; Forstmeier 2002; Hardwood et al. 2003). Ens et al. (1995) concluded that site-specific dominance plays an important role in recruitment strategies in the oystercatcher. These authors integrated prior residence in the context of the 'queuing hypothesis' and argued that individuals gain site-specific experience by limiting territorial activities to a few sites (see also Heg et al. 2000). Also in kittiwakes, territory acquisition is preceded by the concentration of prospective activities to a limited area, or to a specific nesting site, which, in this species, is equivalent to a territory (Cadiou et al. 1993, 1994). Zack & Stutchbury (1992) reported that the probability of occupying a vacant territory decreases with the number of territories visited. Familiarity with the local topography, knowledge of local resources and establishment of social relationships are all important in territory acquisition (Ens et al. 1995).

Our results support the idea that the positive influence of pair duration on breeding performance can be at least partially explained by 'the syndrome of the first-year bond' (i.e. a simultaneous effect of experience and of costs of mate change when pair duration is equal to 1 year), as well as by an age-related change in the proportion of individuals of different quality. Moreover, prior residence (site familiarity) seemed to better explain variability in breeding success and divorce probability than did pair duration. The different mechanisms that we considered to explain relationships involving pair duration are not mutually exclusive. In addition, one must expect differences between species in life history features, including the extent of effects of experience, costs of mate change, individual quality and site familiarity on breeding performance. These differences in life history features allow mate familiarity to affect mate selection, although our results suggest that it may not be the case in our study system. Evidence supporting differences in behaviour

between new pairs and reunited pairs remains limited to the prelaying period, when pair formation takes place (Nelson 1972; O'Donald 1983; Chardine 1987; McGraw & Hill 2004). Future studies focusing on differences between new pairs and reunited pairs in the postlaying period might provide insight on the nature of relationships involving pair duration.

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Table A1. Influence of pair duration on breeding success probability: estimated probabilities (as in Fig. 1) and 95% confidence intervals

Pair duration (years)	Complete data set	Experience	Costs of mate change	Individual quality
1	0.55 (0.52–0.59)	0.33 (0.27–0.38)	0.63 (0.58–0.68)	0.64 (0.58–0.69)
2	0.65 (0.61–0.69)	0.67 (0.63–0.71)	0.66 (0.62–0.70)	0.64 (0.59–0.68)
3	0.68 (0.63–0.72)	0.67 (0.63–0.71)	0.67 (0.63–0.71)	0.64 (0.58–0.69)
4	0.69 (0.64–0.73)	0.67 (0.63–0.71)	0.67 (0.63–0.72)	0.64 (0.58–0.69)
5	0.68 (0.62–0.73)	0.67 (0.63–0.71)	0.67 (0.62–0.72)	0.64 (0.58–0.69)
6	0.65 (0.58–0.72)	0.67 (0.63–0.71)	0.66 (0.60–0.72)	0.63 (0.57–0.69)
7+	0.61 (0.51–0.71)	0.67 (0.63–0.71)	0.65 (0.56–0.73)	0.63 (0.56–0.7)

Table A2. Influence of pair duration on divorce probability: estimated probabilities (as in Fig. 2) and 95% confidence intervals

Pair duration (years)	Complete data set	Experience	Individual quality
Previously successful			
1	0.15 (0.12–0.19)	0.18 (0.12–0.26)	0.09 (0.05–0.15)
2	0.11 (0.09–0.14)	0.11 (0.08–0.15)	0.07 (0.04–0.11)
3	0.08 (0.05–0.12)	0.08 (0.05–0.12)	0.06 (0.03–0.10)
4	0.06 (0.03–0.10)	0.05 (0.03–0.09)	0.05 (0.03–0.10)
5	0.04 (0.02–0.08)	0.04 (0.02–0.08)	0.04 (0.02–0.10)
6	0.03 (0.01–0.08)	0.03 (0.01–0.08)	0.04 (0.02–0.11)
7+	0.02 (0.01–0.08)	0.02 (0.01–0.08)	0.04 (0.01–0.12)
Previously failed			
1	0.51 (0.45–0.56)	0.57 (0.50–0.65)	0.47 (0.37–0.57)
2	0.45 (0.39–0.51)	0.48 (0.42–0.55)	0.40 (0.31–0.49)
3	0.40 (0.32–0.48)	0.40 (0.32–0.50)	0.36 (0.27–0.47)
4	0.34 (0.25–0.45)	0.34 (0.24–0.45)	0.33 (0.23–0.45)
5	0.29 (0.18–0.43)	0.28 (0.17–0.42)	0.30 (0.19–0.45)
6	0.24 (0.13–0.42)	0.23 (0.12–0.41)	0.28 (0.16–0.46)
7+	0.20 (0.08–0.43)	0.20 (0.08–0.43)	0.27 (0.13–0.49)

Table A3. Influence of pair duration on breeding success probability in pairs with the same total duration: estimated probabilities (as in Fig. 3) and 95% confidence intervals

Pair duration (years)	Pairs that lasted only 1 year	Pairs that lasted 2 years	Pairs that lasted 3 years	Pairs that lasted 4+ years
1	0.43 (0.38–0.48)	0.62 (0.56–0.68)	0.79 (0.70–0.86)	0.78 (0.70–0.84)
2	—	0.58 (0.52–0.64)	0.70 (0.62–0.77)	0.77 (0.71–0.81)
3	—	—	0.66 (0.56–0.75)	0.75 (0.70–0.80)
4	—	—	—	0.73 (0.67–0.78)
5	—	—	—	0.70 (0.63–0.77)
6	—	—	—	0.67 (0.58–0.75)
7+	—	—	—	0.63 (0.51–0.74)