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Effects of breeding success, mate fidelity and senescence on breeding dispersal of male and female blue-footed boobies

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Summary

1. Understanding the effects of individual and population factors on variation in breeding dispersal (the movement of individuals between successive breeding sites) is key to identifying the strategies behind breeders' movements. Dispersal is often influenced by multiple factors and these can be confounded with each other. We used 13 years of data on the locations, mates, breeding success and ages of individuals to tease apart the factors influencing breeding dispersal in a colonially breeding long-lived seabird, the blue-footed booby *Sula nebouxii*.
2. Breeding dispersal varied among and within years. Males dispersed further in years of higher population density, and late breeding males and females dispersed further than early breeders. This temporal variation related to changes in competition for territory was taken into account in all tests of individual factors influencing breeding dispersal.
3. Individuals that retained their mates from the previous year dispersed shorter distances than those that changed their mates.
4. The effect of previous breeding success depended on mate fidelity. Unsuccessful breeding induced greater dispersal in birds that changed their mates but not in birds that retained their mates, indicating that breeders who change mates may take their own previous breeding experience into account during habitat selection. Faithful individuals may have to stay close to their previous sites to encounter their mates.
5. Male divorcees dispersed over shorter distances than their former mates, possibly because males contribute more than females to establishing territories.
6. Dispersal of males and females declined with increasing age over the first 10–11 years of life, then increased in old age, possibly due to senescent decay in the ability to compete for mates and territories.

Key-words: ageing, decision making, habitat selection, life-history traits, personal information hypothesis.

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Introduction

Breeding dispersal, or the movement of iteroparous animals between successive breeding sites, affects the physical habitat and social environment in which reproductive attempts are made, and can also affect the structure and dynamics of populations (Clobert *et al*. 2001). Habitat quality is often correlated with energy expenditure and breeding success (Partridge 1978; Cody 1985; Reid, Monaghan & Ruxton 2000; Kim & Monaghan 2005a,b), and social environment can determine the potential for both competitive and cooperative interactions with conspecifics (Stamps 1991; Muller *et al*. 1997), including opportunities for extra-pair behaviour (Hoi & Hoi-Leitner 1996; Danchin & Wagner 1997). Breeding dispersal is influenced by multiple factors over the animal's life cycle, and these can operate at different stages in the dispersal process. Both environmental conditions (typically habitat, food quality and demographic variables) and internal conditions (typically fat reserve, body size and competitive ability) can affect

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dispersal (Ims & Hjermann 2001), as can previous breeding success (personal information hypothesis: Switzer 1997; Danchin, Boulinier & Massot 1998). Two important factors that affect breeding dispersal are particularly poorly understood: breeding success and ageing.

Animals can use their past reproductive experience at a site to predict its current quality (win–stay, lose–switch strategy: Switzer 1993, 1997), and many empirical studies have shown that breeders are more likely to disperse from a site where they failed than from a site where they succeeded (Beletsky & Orians 1991; Wiklund 1996; Danchin *et al*. 1998; Haas 1998; Forero *et al*. 1999; Serrano *et al*. 2001; Kokko, Harris & Wanless 2004). Individuals' own breeding success at a site yields information on the quality of the site and influences the decision to retain it or move away. However, failed breeders often divorce from their mates or lose them to mortality (Ens, Choudhury & Black 1996), so greater dispersal by failed breeders could be a consequence of new pair formation rather than any decision to breed away from the last site (Morse & Kress 1984; Desrochers & Magrath 1996; Ens *et al*. 1996; Pyle, Sydeman & Hester 2001). Previous empirical studies do not allow us to tease apart the effects of mate retention and previous breeding success on displacement to the next breeding site.

Age influences breeding dispersal in long-lived avian species: as they get older, individuals tend to be more site faithful and disperse less (Greenwood & Harvey 1982; Harvey *et al*. 1984; Newton 1993; Badyaev & Faust 1996; Forero *et al*. 1999; Pyle *et al*. 2001; Andreu & Barba 2006). Foraging and breeding success of birds tend to improve with age, but in some species at least, they eventually decline with senescence (Desrochers & Magrath 1993; Forslund & Pärt 1995; Daunt *et al*. 1999; Espie *et al*. 2000; Green 2001; Reid *et al*. 2003; Velando, Drummond & Torres 2006). If breeding dispersal depends on competitiveness, then distances should increase with senescence, but no studies have tackled this question. Longitudinal studies are required to detect a decline in breeding dispersal with senescence because cross-sectional studies may wrongly estimate the abilities of young breeders by including low-quality poorly performing individuals that die young or individuals that invest heavily in reproduction and survive few breeding seasons (Reid *et al*. 2003; Velando *et al*. 2006).

We examined breeding dispersal of the blue-footed booby *Sula nebouxii* (Milne-Edwards), a long-lived seabird that breeds in island colonies. Observations on numerous ringed individuals over 13 seasons were used to evaluate how dispersal is affected by breeding success, contrasting individuals that retained their previous mates and those that changed mates, and to document changes in individual dispersal between recruitment and old age. If failed breeders disperse further only to form a new pair, breeders that change mates should disperse farther than faithful birds irrespective of previous breeding success. If failed breeders disperse further to find a better site as well as a new mate, then the dispersal of mate changing birds should increase in line with the degree of failure. If more competitive birds disperse less, and competitiveness first improves with age (and experience) and then declines with senescence, dispersal should decline over the life span and show an upturn in old age. We also discuss implications of temporal variation in breeding dispersal for population density. Males and females were analysed separately because they can have different roles in territory acquisition and defence (Serrano *et al*. 2001), and because female birds tend to disperse more often or further than males (Greenwood 1980).

Methods

STUDY AREA AND SPECIES

Blue-footed boobies of our study colony nest on the ground in a dense forest of *Crataeva tapia* (Linnaeus) on Isla Isabel, Nayarit 21°52′N, 105°54′W, off the Pacific coast of Mexico. Since 1989, all nests in a 20 800 m^2 section of the forest were marked and mapped every year, and all fledglings and most breeders were marked with numbered metal rings. Marked birds seldom nest outside the study area (Drummond, Torres & Krishnan 2003) and earlier analyses indicated that boobies are faithful over at least several years to the neighbourhood where they were born (Osorio-Beristain & Drummond 1993).

Blue-footed boobies are territorial throughout the breeding season and breeders and chicks are strongly attached to their territories until fledging. Generally, males obtain territories of 7–20 m^2 early in the 7-month breeding season (Gonzalez & Osorno 1987; Stamps *et al*. 2002), then females arrive and pair with the males on their territories (Nelson 1978; Stamps *et al*. 2002). After this, male and female jointly select the location of the nest site within the territory (Stamps *et al*. 2002) and jointly care for the clutch and brood during roughly $5^1/_2$ months, until their offspring become independent at about age 4 months (Nelson 1978; Torres & Drummond 1999b). In the study area, one or two, occasionally as many as three eggs are laid, and usually one or two, exceptionally three chicks fledge. Roughly 20–30% of eggs are infertile, abandoned, predated or accidentally broken and 40% of chicks die through starvation, siblicidal expulsion (associated with underfeeding), predation or infanticidal attacks of neighbours (Torres, Rodríguez & Drummond unpublished). In males at least, decline in breeding success with senescence occurs after age 8–10 years (Velando *et al*. 2006).

FIELD PROCEDURES

Between 1993 and 2005, all nests in the study area were surveyed every few days from shortly after the start of hatching until each chick fledged (reached age 70 days), the last chicks doing so in July. Total number of nests in the study area during the season was used as an index of population density. Nests within 20 m of the study area

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were included if either of the breeders was marked. Nests (sites with a clutch or brood) were marked with numbered wooden stakes and chicks were marked with numbered plastic rings after hatching, then with steel rings at fledging. On average, 685 ± 38 pairs (mean ± SE) nested each year in the study area (range = 489 pairs in 2003; 973 pairs in 2001). Each breeder's ring number was confirmed by independent readings on up to 3 days. On average, 56% of male breeders and 57% of female breeders were identified, over the 13 breeding seasons. Dates of laying and hatching were recorded when they occurred during the survey period. Otherwise, laying dates were estimated from hatching dates and from estimates of chick ages based on length of ulna and culmen at first encounter (see also Torres & Drummond 1999a; Drummond *et al*. 2003).

BREEDING DISPERSAL MEASUREMENTS

The study area comprised 37 plots of roughly 20 × 20 m defined by permanent marker trees at their corners, which were mapped at the start of the population study. Each nest was mapped by measuring the distance (nearest 10 cm) and direction (nearest 2°) of its centre from the ground-level estimated centre of the closest marker tree's trunk (see also Osorio-Beristain & Drummond 1993). Nest locations were expressed in two linear coordinates originating at the marker tree in one corner of the study area.

SAMPLING AND STATISTICAL ANALYSES

We used data from all identified males and females in the study area that bred in at least two consecutive years (years t and $t - 1$). Birds that dispersed out of the study area could not be included, but minimal bias is expected because long-distance dispersal is uncommon: only 1·0% of males and 0·9% of females bred in the other dense and closely monitored study area that lies just 0·35 km away from the study area. If an individual attempted to breed more than once in a year, then the first event was selected for analysis. Overall 5·5% of identified individuals made second breeding attempts in the same season, and only 9·7% of second attempts fledged a chick.

Breeding dispersal was the distance moved by breeders between years t and $t - 1$. Mate fidelity was a binomial variable indicating whether each individual retained the same mate or changed to a new mate between year $t - 1$ and year t, among pairs where both males and females were identified. Laying dates were expressed as proportional rank, ranging from 0 to 1 in each year (0: the earliest breeder; 1: the latest breeder of each year), as timing of the breeding season varied across years and the distribution differed from normal. Breeding success of individuals in any season was standardized using the z-transformation (mean = 0, SD = 1) to take variation among years into account. Mean breeding success (number of chicks fledged) in the study area varied among years between 1993 and 2004 (ANOVA $F_{11,8120} = 131{\cdot}49$, $P < 0{\cdot}001$). To compare the breeding dispersal of males and females, we selected divorced males and females that bred together in year $t - 1$ then both bred with different mates in year t. To examine the effect of age on breeding dispersal, we used all 42 males and 44 females that were ringed as fledglings and continued to breed until 13–16 years old.

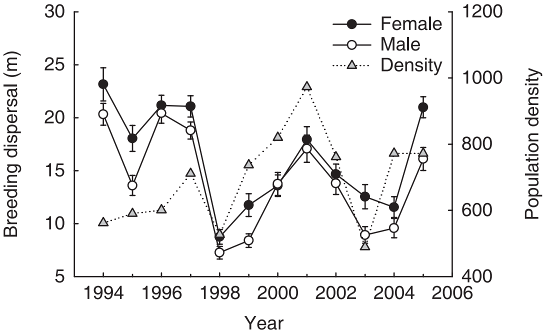

Fig. 1. Breeding dispersal of male and female blue-footed boobies (mean ± SE) in relation to calendar year and population density. Sample sizes in successive years: males: 166, 215, 254, 327, 252, 249, 387, 401, 348, 199, 191, 131; females: 164, 223, 253, 319, 253, 243, 382, 413, 347, 208, 214, 355. Samples of males and females include stable pairs of individuals that were faithful to their mate in successive years (dispersal distances identical for male and female) and individuals whose mate was unidentified or different in the second year. Number of nests in the study area in year t is an index of breeding population density.

First we tested for effects of year and laying date on dispersal. Subsequent analyses included these two variables in the model along with the independent variables of interest, to control for their (rather large) effects. Controlling for laying date may also help to control partially for effects of breeder quality as early breeding seabirds are usually good quality individuals (Perrins 1970; van Noordwijk, McCleery & Perrins 1995; Verhulst, van Balen & Tinbergen 1995). We analysed males and females separately, to avoid replication of data points from paired birds, and because females dispersed 2·3 m further than males on average (n = 12 years; see also Fig. 1). In addition, we compared the two sexes using additional analyses when needed.

We used Generalized Linear Mixed Models (GLMMs) with breeder identity included as a random effect as many individuals yielded data for more than one consecutive breeding record across the 13 years of the study. Initially all the explanatory variables and their two-way interactions were fitted in the model, then nonsignificant terms were dropped sequentially and finally the model with the lowest AIC value was selected and the significance of the remaining variables was tested using null-hypothesis tests. The significance reported for each remaining variable is the Likelihood ratio (L. ratio), and we used maximum likelihood estimation (ML) in GLMMs (Crawley 2003). Although information-theoretic methods are often recommended

Table 1. Summary of two GLMMs examining the effects of laying date and year on breeding dispersal of males and, separately, females (random effect: breeder identity)

	Males			Females		
Variable	L. ratio	d.f.	*P*	L. ratio	d.f.	*P*
Lay date	115·98	1	< 0·001	121·37	1	< 0·001
Year	211·47	11	< 0·001	192·72	11	< 0·001
Lay date × year	112·66	11	< 0·001	70·60	11	< 0·001

for observational studies (but not always, Stephens *et al.* 2005), we report null-hypothesis tests because we tested each factor of interest, or pair of factors of interest, in a separate model (together with a few crucial confounded factors) rather than inserting all factors into the same model. To ascertain whether magnitude of breeding success affects dispersal, we further compared the main model with a submodel in which nest success of one chick, two chicks and three chicks were combined (Crawley 2003). Analyses were carried out in SPSS (SPSS Inc., Version 12·0) and R (R Development Core Team, Version 1·9·1). All tests were two-tailed, and throughout the results we report mean ± SE.

Results

EFFECTS OF YEAR AND LAYING DATE

A total of 913 marked male and 991 marked female boobies nested in consecutive seasons between 1993 and 2005, performing 3120 and 3374 consecutive breeding events, respectively. Breeding dispersal ranged from 0 to 181·1 m in males and 0–174·4 m in females, and varied with year and laying date. Overall, breeding dispersal differed significantly among years, mean distances of both sexes varying two- or threefold from their lowest to highest values (Fig. 1; Table 1). Laying date influenced breeding dispersal of both sexes significantly when the effect of year was taken into account. Although there was a significant date × year interaction, with the strength of the relationship between laying date and dispersal differing among years, overall the later boobies of both sexes bred the further they dispersed, and the latest birds dispersed roughly twice as far as the earliest birds (Fig. 2a; Table 1).

Effects of population density (our index of annual size of the breeding population) on breeding dispersal were analysed separately for males and females, taking laying date into account. Dispersal was greater in years of higher density (Fig. 1), but this effect was significant only in males (males: L. ratio = 16·18, d.f. = 1, *P* < 0·001; females: L. ratio = 2·36, d.f. = 1, *P* = 0·12).

EFFECTS OF PREVIOUS BREEDING SUCCESS AND MATE FIDELITY

Previous breeding success and mate fidelity explained some of the variance in breeding dispersal of both males and females, when the effects of year (males: L. ratio = 171·72, d.f. = 11, *P* < 0·001; females: L. ratio = 148·49, d.f. = 11, *P* < 0·001) and laying date (males: L. ratio = 48·78, d.f. = 1, *P* < 0·001; females: L. ratio = 51·10, d.f. = 1, *P* < 0·001) were taken into account (Table 2). Overall, the more chicks a bird fledged, the shorter its dispersal to the following season's site (Table 2); faithful individuals dispersed shorter distances than those that changed mate (males 34·4 ± 5·5% shorter and females 49·6 ± 4·2% shorter, *n* = 12 years) (Fig. 2b; Table 2). When we compared breeding dispersal between sexes among divorcees only, overall female divorcees dispersed further than their divorced mates (females: 21·8 ± 0·9 m; males: 17·1 ± 0·7 m; paired *t*-test: t_{591} = –4·32, *P* < 0·001).

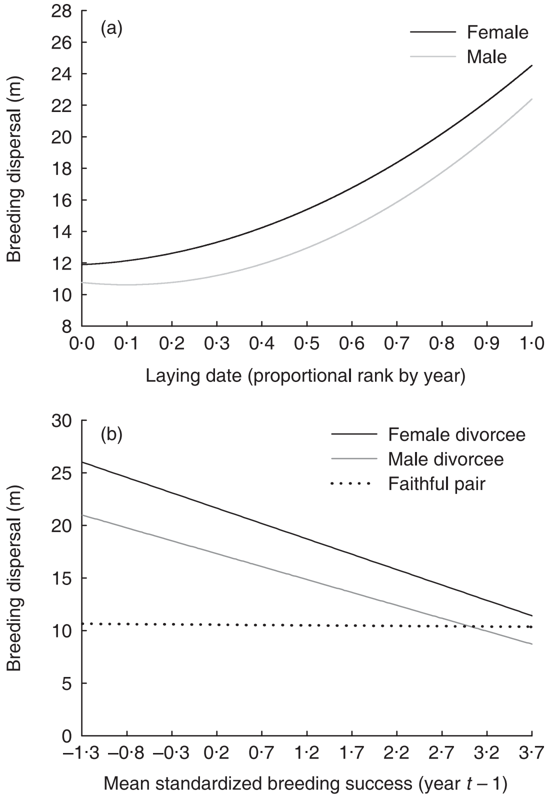

Fig. 2. Relationships between (a) laying date (proportional rank by year) and breeding dispersal of 913 male and 991 female blue-footed boobies observed over 13 years; (b) standardized previous breeding success (year *t* – 1) and breeding dispersal in pairs that retained the same mates (*n* = 1304) and males and females that changed their mates (males: *n* = 1300; females: *n* = 1530).

Table 2. Summary of two GLMMs examining the effects of standardized previous breeding success (number of fledglings in year $t - 1$) and mate fidelity on breeding dispersal of males and females, separately, taking year and laying date into account (random effect: breeder identity)

	Males			Females		
Variable	L. ratio	d.f.	P	L. ratio	d.f.	P
Breeding success	30·41	1	< 0·001	31·95	1	< 0·001
Mate fidelity	63·06	1	< 0·001	143·59	1	< 0·001
Breeding success × mate fidelity	13·66	1	< 0·001	20·11	1	< 0·001

However, the effect of breeding success on dispersal depended on whether birds remained faithful or changed mates between years (significant interactions in Table 2), so we tested birds that retained mates and changed mates separately, while taking annual and seasonal effects into account. These analyses showed that breeding success had no influence on the breeding dispersal of faithful birds (Fig. 2b; L. ratio = 0·46, d.f. = 1, $P = 0{\cdot}50$) but affected dispersal distances of both males and females that changed mates (Fig. 2b; males: L. ratio = 26·89, d.f. = 1, $P < 0{\cdot}001$; females: L. ratio = 33·67, d.f. = 1, $P < 0{\cdot}001$). In the untransformed data for birds that changed mates, dispersal was largely unaffected by whether a male or female produced 1, 2 or 3 fledglings the year before, but dispersal was 4·9 m and 5·1 m further for males and females, respectively, that produced 0 fledglings.

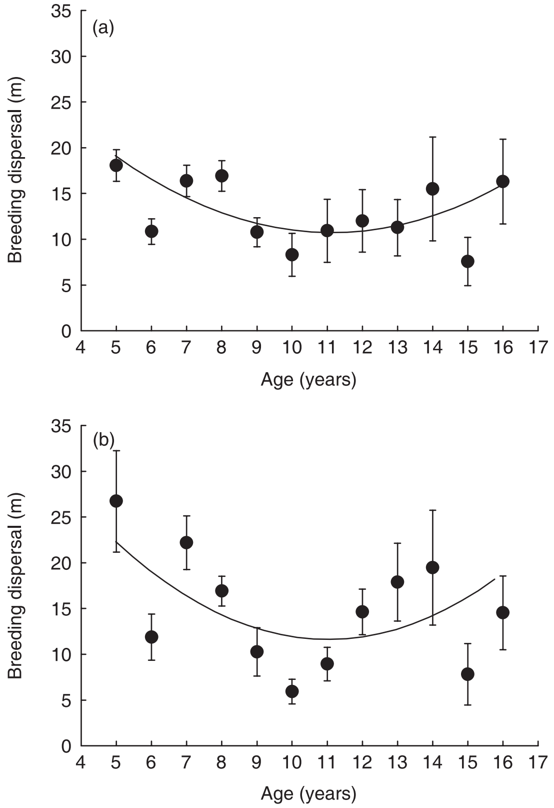

Fig. 3. Effect of age on breeding dispersal. Mean ± SE distances of (a) 42 males (F-test for quadratic regression: $F_{2,317} = 4{\cdot}12$, $P < 0{\cdot}05$) and (b) 44 females (F-test for quadratic regression: $F_{2,332} = 5{\cdot}58$, $P < 0{\cdot}01$) that survived at least 13–16 years.

EFFECT OF AGE

Age explained some of the variance in the breeding dispersal of both sexes when year and laying date were controlled for (Fig. 3). Taking year (males: L. ratio = 26·59, d.f. = 11, $P < 0{\cdot}01$; females: L. ratio = 28·17, d.f. = 11, $P < 0{\cdot}01$) and laying date (males: L. ratio = 7·47, d.f. = 1, $P < 0{\cdot}01$; females: L. ratio = 2·57, d.f. = 1, $P = 0{\cdot}10$) into account, breeding dispersal varied significantly with age in both sexes (males: L. ratio = 23·92, d.f. = 13, $P < 0{\cdot}05$; females: L. ratio = 23·34, d.f. = 12, $P < 0{\cdot}05$). In both males and females, dispersal declined progressively to roughly half the initial distance over the first 10–11 years of life; afterwards, dispersal distances tended to increase up to at least age 16 years, as shown by the significant quadratic regressions (Fig. 3). Furthermore, when all recruits that bred in consecutive years were included regardless of their longevity (551 males, 613 females), the quadratic relationship between age and breeding dispersal was highly significant for both sexes (F-test for quadratic regression: males: $F_{2,1797} = 17{\cdot}95$, $P < 0{\cdot}001$; females: $F_{2,1870} = 14{\cdot}48$, $P < 0{\cdot}001$).

Discussion

Our main results indicate the environmental and internal conditions that probably influence breeding dispersal of the blue-footed booby: (1) males, but not necessarily females, increased their dispersal when nesting was denser; (2) individuals that changed their mates dispersed further than those that retained their mates, and female divorcees dispersed further than male divorcees; (3) birds that retained their mates were unaffected by previous breeding success, but birds that changed mates dispersed less distances if they had been more successful in breeding; and (4) breeding dispersal of males and females declined over the first 10–11 years of life, then increased in old age.

The blue-footed booby is highly site faithful throughout its lifetime. Breeders select a territory and nest site close to their previous territory and site or possibly the natal territory/site (unpublished data; Osorio-Beristain & Drummond 1993), probably benefiting from familiarity with the local habitat and neighbours (Beletsky & Orians 1991; Forero *et al.* 1999) and reducing the temporal and energetic costs of obtaining a new territory/site and mate (Danchin & Cam 2002). However, mate fidelity, previous breeding success and age all seem to affect the magnitude of displacement from that site, as does annual and seasonal variation in nest density.

TEMPORAL VARIATION IN BREEDING DISPERSAL AND DENSITY EFFECT

Effects of breeding dispersal on the structure and dynamics of animal populations are well documented (Greenwood & Harvey 1982; Johnson & Gaines 1990; Paradis *et al.* 1998; Dieckmann, O'Hara & Weisser 1999; Sutherland, Gill & Norris 2002), but effects of population dynamics on dispersal are poorly understood (but see Paradis *et al.* 1998; Travis, Murrell & Dytham 1999). In colonial breeders, habitat choice is influenced not only by the availability of appropriate habitat, but also by competition with other members of the colony for territories and mates (Milinski & Parker 1991; Krause & Ruxton 2002). In territorial species, less competitive breeders are forced by others to move into suboptimal habitats, particularly when breeder density is high and competition is more intense (Sutherland 1997). The positive relationship between annual density of breeding boobies and annual dispersal distances of males, and possibly females, suggests that competition for nest sites obliges boobies to disperse further.

Increase in dispersal distances as each season progressed is additional evidence for a positive effect of nest density, mediated by competition. In colonial breeding birds with long reproductive seasons, availability of nest sites decreases as the season progresses and late breeders disperse further, to less favoured sites (Sutherland 1997). Distribution models predict that due to territorial or dominance behaviour, the suitability of available patches declines as settling progresses (Fretwell & Lucas 1970; Sutherland 1997). Alternatively, late breeders may disperse further because they are uncompetitive birds. Late breeding blue-footed boobies are often inexperienced or senescent individuals (Peña-Alvarez unpublished), and these have low breeding success (Velando *et al.* 2006) and are likely to be poor competitors. However, this alternative explanation could not account for the interannual association between dispersal and breeding density and probably accounts for only part of the increase in dispersion over each season.

INTERACTING EFFECTS OF MATE FIDELITY AND PREVIOUS BREEDING SUCCESS

Blue-footed boobies that retained their mates dispersed shorter distances than those that divorced or whose mate died, similar to other long-lived birds (Pyle *et al.* 2001; Serrano *et al.* 2001; Catlin, Rosenberg & Haley 2005; Andreu & Barba 2006). Mate-retaining pairs may jointly defend their territories better or from an earlier date than those establishing new pair bonds, and consequently disperse shorter distances. Alternatively, mate-retaining breeders may return to the same site to find last year's mate, whereas mate-changing breeders may seek new mates away from the previous site. Breeders that voluntarily change mate (and indeed their abandoned partners) may need to move in order to secure an attractive partner or site. Breeders who find that their former mate is occupying their site of the previous season (not necessarily the abandoning partner) may be obliged to move on. Faithfulness to mate and site are such highly correlated traits that direct behavioural observation is needed to tease apart the relationships between them and factors such as breeding experience and internal condition.

While dispersal after a poor breeding performance is frequently found in birds (Beletsky & Orians 1991; Forero *et al.* 1999; Pyle *et al.* 2001; Serrano *et al.* 2001), early studies have not distinguished whether increased dispersal results from changes of mates rather than effects of breeding failure and subsequent decisions on changing sites. Our results suggest that the effect of previous breeding success on dispersal depends on mate fidelity. When they retain the same mate, boobies stay close to their previous nest site, whatever their previous breeding success, but when they change their mates a poor breeding outcome induces them to disperse further. Boobies that are faithful to their mates may have to stay close to their previous nest sites to encounter the mates, after which the possible benefits of moving to a new site may not exceed the costs of dispersing and losing the mates, even for boobies that failed in the previous season. Boobies that fail in their breeding attempt and change mate, may disperse the furthest because they seek both a better site and a new mate. Quality of candidate sites is difficult to assess (Valone & Templeton 2002; Dall *et al.* 2005) and assessment can be direct or based on previous experience at the site (Switzer 1993, 1997). While other cues, such as physical condition (Kim & Monaghan 2005a,b) and the presence of conspecifics (Stamps 1991), may also provide information on the suitability of a site, breeding success may be the most accurate and direct information to use (Boulinier & Danchin 1997; Switzer 1997).

Effects of breeding success on dispersal could be confounded with effects of breeder quality. High-quality breeders that succeed in their previous reproduction are likely to be superior competitors who can secure a territory close to where they seek one. However, to some extent the effect of breeder quality was controlled for by incorporating laying date in the model, and even so, previous breeding failure led to increased dispersal of mate-changers. Therefore, we conclude that acquired information from a booby's own breeding success substantially influences the decisions involved in its breeding dispersal.

SEXUAL DIFFERENCE

Among divorcees, females dispersed further than their male mates. A number of studies of birds have reported greater dispersal by females than males (Shields 1984; Jackson 1994; Schjørring, Gregersen & Bregnballe 2000; Serrano *et al*. 2001). Greater dispersal by females is consistent with sex-specific roles during the pre-laying period, when male birds are more responsible for territory establishment and females for mate selection (Greenwood 1980; Pyle *et al*. 2001). The cost of dispersal is likely to be greater in males as males contribute more to establishing and defending breeding territories (Schjørring *et al*. 2000).

AGE EFFECT

Our results support the suggestion that the widespread finding of decreased dispersal with increasing age in birds and other species is due to improvement in territorial establishment and defence with age or experience (Forslund & Pärt 1995; Sutherland 1997). Our longitudinal and cross-sectional analyses both documented increasing site fidelity in the early years, followed by increasing dispersal of both sexes after roughly age 11 years. Even when their late nesting was taken into account, old birds dispersed further. Declines in breeding performance, such as clutch size, the probability of breeding successfully and fledging success, have been reported in both longitudinal and cross-sectional studies of many species, suggesting reproductive senescence (Clutton-Brock 1988; Reid *et al*. 2003). In ageing boobies, progressive increase in breeding dispersal, along with diminishing nest success (Velando *et al*. 2006) and progressively later nesting in the season (Peña-Alvarez unpublished), is probably due to senescent decline in competitive abilities (cf. Clutton-Brock 1988; Stearns 1992; Jones, Balmford & Quinell 2000). Evidence that animals decline in their ability to compete for sites or mates in old age is scarce (but see McDonald, Fitzpatrick & Woolfenden 1996; Cam & Monnat 2000).

Our observational data reveal novel effects of ageing and interacting effects of breeding success and mate change on breeding dispersal. The data document senescence of the ability to compete for breeding sites, but additional longitudinal data on long-lived individuals are needed to document this in more detail. Furthermore, manipulative field experiments are needed to confirm and explore the effects of breeding success and mate change on breeding dispersal.

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