

Lifetime philopatry in the blue-footed booby: a longitudinal study

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Philopatry over the lifetime and its relationship with reproductive success were examined using longitudinal records of nest location and reproduction of individual blue-footed boobies. Males showed shorter natal dispersal than females, and natal dispersal distance of both sexes were unrelated to either first reproductive success or lifetime reproductive success. Throughout the early lifetime, males and females nested closer to their first breeding sites than to their natal sites, and comparison with a simulation of successive breeding dispersals in random directions showed that male and female blue-footed boobies are philopatric to the first breeding site. Therefore, throughout the early lifetime, the first breeding site seems to function as a point of reference for breeding site use together with the previous season's site. Males and females with shorter natal dispersal distances showed stronger lifetime philopatry to their first breeding sites, suggesting stable individual variation in competitive ability or dispersal phenotype. However, early lifetime philopatry to first breeding sites was unrelated to annual breeding success. Compared with simple fidelity to previous breeding sites, lifetime philopatry to first breeding sites should result in increased kin interactions and greater selection for kin recognition, altruism and inbreeding avoidance, as well as long-term familiarity with neighbors. *Key words:* fitness, longitudinal study, natal dispersal, philopatry, *Sula nebouxii*. [*Behav Ecol* 18:1132–1138 (2007)]

Dispersal and philopatry influence the spatial and temporal patterns of distribution of individuals within and between populations (Greenwood and Harvey 1982), with important consequences for the dynamics and genetics of populations (Jones et al. 1988; Lambin 1994) and the evolution of social behavior. Whenever familiarity with a breeding area benefits breeders philopatry is likely to be selected for (Forero et al. 2002), although individuals can sometimes increase their fitness by dispersing away from their natal or previous breeding sites after experiencing unfavorable conditions there (Danchin et al. 1998; Ims and Hjernmann 2003; Kim et al. 2007). Familiarity with habitat or neighbors may facilitate retention of a territory in the next season or reduce the costs of residence in it (Greenwood 1980).

Numerous theoretical and empirical studies have analyzed the patterns, mechanisms, and adaptive consequences of natal philopatry, the return of individuals to their natal sites for first breeding attempts, and breeding philopatry, the return of individuals to their previous breeding sites (e.g., Greenwood 1980; Greenwood and Harvey 1982; Jones et al. 1988; Nilsson 1989; McGuire et al. 1993; Lambin 1994; Forero et al. 1999, 2002; Kim et al. 2007). However, longitudinal patterns of philopatry over the lifetime have been ignored, doubtless due to the difficulty of maintaining longitudinal records of spatial location and reproduction of identified individuals (Hansson et al. 2004). The typical observations of individuals breeding near their last recorded sites do not tell us whether the natal site, the first breeding site, or last year's site is the reference point for the next reproductive event. Lifelong philopatry to the natal or first breeding site would tend to bind a long-lived animal to its original habitat and possibly to its relatives and neighbors (cf., Waser and Jones 1983), whereas serial philopatry to the last breeding site would allow it to progressively

distance itself from natal site, relatives, and neighbors or progressively approach attractive habitat or social environments. The study of black brants (*Branta bernicla*) of Lindberg et al. (1998) appeared to show that natal philopatry of females increased with age, but their cross-sectional data actually documented greater natal philopatry and breeding probability of females that survived until old ages. Longitudinal studies are required to discern patterns of philopatry over the lifetime and effects of those patterns on lifetime reproductive success.

The 2 sexes may differ in the pattern of lifetime philopatry, particularly when the cost of territory settlement is greater for one sex. Males may incur greater costs than females early in reproduction because generally they compete more than females for territories (Michener and Lockler 1990). Greater philopatry by males has been observed in many studies and explained as adaptive behavior that reduces settlement costs to males (Greenwood 1980; Pyle et al. 2001; Kim et al. 2007).

Studies relating natal dispersal and reproductive success of birds in the first breeding attempt or over the lifetime have documented 2 apparently contradictory patterns: individual lifetime reproductive success can either increase or decrease with natal dispersal (Nilsson 1989; Forero et al. 2002; Hansson et al. 2004; Steiner and Gaston 2005). The negative relationship could be due to high-quality individuals being superior at both competing for space and reproduction, or it could reveal the costs of settling and breeding in less familiar habitat (Forero et al. 2002; Hansson et al. 2004). The positive relationship has been attributed to high quality or adventurous birds obtaining better quality sites or mates by dispersing farther (Nilsson 1989; Steiner and Gaston 2005). Reproductive consequences of breeding dispersal have been tested in birds (Forero et al. 1999; Pyle et al. 2001), but clear patterns have not emerged, possibly due to the difficulty of teasing apart the effects of individual competitive ability and the availability of sites and mates. Patterns and reproductive consequences of long-term philopatry to natal or first breeding sites have not been analyzed.

We characterized the lifetime philopatry of the blue-footed booby (*Sula nebouxii*) and analyzed its reproductive

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consequences using longitudinal records on the nest location and reproductive performance of hundreds of identified individuals of the highly philopatric population on Isla Isabel, off the Pacific coast of Mexico (21°52'N, 105°54'W). Although most studies on movements of birds have focused on long-distance movements during relatively short periods (Serrano et al. 2005), it is potentially illuminating to track movements of individuals within the colony over their lifetimes in species with overall high philopatry to their original colonies. Specifically, we examined 1) the relationships between natal dispersal and both first breeding success and early lifetime reproductive success; 2) whether individuals disperse nonrandomly in relation to their natal sites or first breeding sites in subsequent breeding seasons; 3) the pattern of longitudinal philopatry across the early lifetime (up to 8 years of age); 4) the relationship between natal dispersal distance and longitudinal philopatry; and 5) the relationship between philopatry to first breeding site and annual reproductive success.

All sampling was on Isla Isabel so our study does not embrace dispersal to distant islands/populations. Over 19 years, 10 839 fledglings and roughly 3160 adults in the study population were marked with permanent steel rings, and roughly 40% of fledglings recruit into the same population, mostly at 3–5 years of age (Drummond et al. 2003). We have not encountered these rings during occasional study of booby populations in the Islas Marietas or on Isla San Pedro Mártir (130 and 903 km distant, respectively). Seven males and six females ringed on Isla Isabel as fledglings nested 476 km away on El Rancho island (25°08'N, 108°14'W) during 2003–2006, at least 4 of them doing so repeatedly. Hence, long-distance dispersal from Isla Isabel may be uncommon and carried out by first breeders rather than experienced breeders.

METHODS

Field procedures

We studied the Isla Isabel blue-footed boobies from 1993 to 2005. These boobies are socially monogamous and their ground-level nest scrapes are widely distributed in the forests and adjacent grasslands of the 82-hectare island. The majority of nests are concentrated every year in loose seasonal synchrony in a band roughly 660 m long and up to 100 m wide, close to the island's east shore. Breeding environments within the study colony show patchiness in both abiotic and biotic factors such as exposure to predators, proximity of terrain for taking off and landing (Montes-Medina AC, Kim S-Y, Drummond H, in preparation), and breeding density (Kim S-Y, Boulinier T, Torres R, Drummond H, unpublished data). Generally, males obtain nesting territories (of an average 7.6 m²) and then pair with females (Nelson 1978; Gonzalez and Osorno 1987; Stamps et al. 2002). After this, male and female jointly select the location of the breeding site (nest) within the territory (Stamps et al. 2002). Although most breeding sites are recognizable until the next year, philopatric birds may move their breeding sites within their previous territories (Kim et al. 2007).

Distributions of all breeding sites (nest scrapes with a clutch or brood) in a 20 800 m² study area that includes both dense and sparse nesting were marked and mapped every year from 1993 to 2005, starting in February. 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 long-term population study. Sites were marked with numbered wooden stakes, and all fledglings and most breeders were marked with numbered metal rings (Drummond et al. 2003). Each already marked breeder's ring number at most breeding sites was confirmed by independent readings on up

to 3 days to minimize reading errors. Marked birds seldom nest outside the study area, and earlier analyses indicated that boobies are generally faithful to the neighborhood where they were hatched or nested in the previous season (Kim et al. 2007; Osorio-Beristain and Drummond 1993). Each breeding site in the study area was mapped by measuring the distance (nearest 10 cm) and direction (nearest 2°) of its center from the ground-level estimated center of the closest marker tree's trunk (Kim et al. 2007). For analysis, breeding site locations were expressed in 2 linear coordinates originating at the marker tree in one corner of the study area.

Every year, breeding sites were surveyed every few days from shortly after the start of hatching of early chicks until each chick died or fledged (reached 70 days of age), the last chicks fledging in late July. Therefore, some early breeders that failed during incubation could have escaped sampling. Sex of fledglings was not known, but sex of breeders was reliably known from their voices (males whistle and females grunt), so sex of fledglings was identified when they eventually recruited. Hatching date of each chick at each site was recorded during the surveys or estimated from length of ulna and culmen at first encounter (Drummond et al. 2003).

Sampling, definitions, and statistical analyses

We analyzed breeding records up to 8 years of age for each of five cohorts of fledglings ringed between 1993 and 1997. Fledglings that bred only once in the 8 years were excluded from all analyses because transients generally perform differently from repeat breeders (Oro D, Drummond H, in preparation). Of a total of 3186 fledglings, 243 males and 373 females returned and bred repeatedly, starting from 1 to 6 years old (median: males, 4 years; females, 3 years). Among these repeat breeders, 240 males and 311 females survived and bred until at least 8 years-old. Longitudinal data from repeated breeding by those birds (males: $n = 792$ events; females: $n = 980$ events) were used to analyze philopatry to the natal site and the first breeding site (examples in Figure 1). Whenever an individual attempted to breed more than once in a year, the first event was selected for analysis (see also Kim et al. 2007). To test for the relationship between natal dispersal distance and early lifetime reproductive success, we used total number of chicks fledged during the first 11 years of life of the 1993 and 1994 cohorts, including all 180 males and 123 females that recruited, no matter how many times they bred.

We mostly use the terminology of Greenwood (1980) and Greenwood and Harvey (1982; but see Lindberg et al. 1998; Rockwell and Barrowclough 1987). Natal dispersal is the distance between a bird's natal site and its first breeding site; breeding dispersal is the distance between 2 successive breeding sites (years t and $t - 1$). Distances between an individual's breeding sites in its first 8 years and either its natal site or its first breeding site were calculated to compare early lifetime philopatry with these 2 sites.

Boobies could be attracted to their first breeding sites throughout the lifetime, or they might tend to remain near them as a fortuitous consequence of making short successive breeding dispersals each one related only to the previous site. To resolve this, we used a simulation to test whether successive breeding dispersals in random direction over the observed distances would carry boobies further from their first breeding sites than they actually traveled. For each individual, we simulated the second breeding location predicted by dispersal in random direction (in a range of 0–360°) over the observed dispersal distance between the first and second breeding events, then simulated dispersal from this site to the third breeding site in the same way, and so on. Breeding success of individuals (number of chicks fledged) in any season was

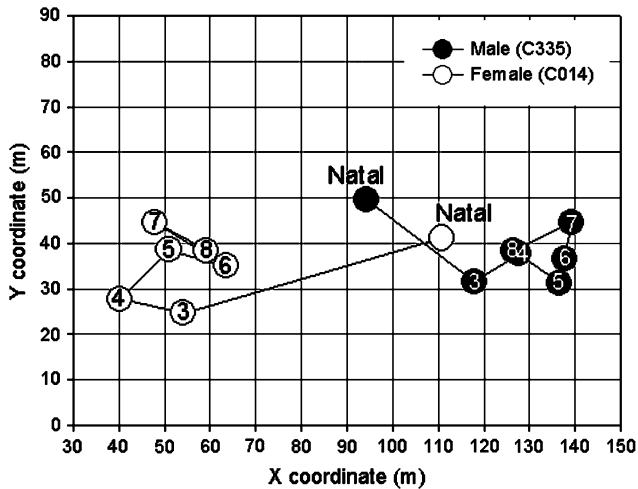


Figure 1
Examples of early lifetime movements from natal sites to successive breeding sites from first reproduction at 3 years until 8 years of age in an identified male (ring number: C335) and female (ring number: C014). Numbers on sites represent the bird's age.

standardized with a z -transformation to take variation among years into account (Zar 1999).

We first compared natal dispersal distances of males and females and examined the relationship between natal dispersal distance and standardized first breeding success using generalized linear models (GLMs) with a normal error distribution and an identity link. The relationship between natal dispersal distance and lifetime reproductive success was analyzed in a GLM with a Poisson error distribution and a log link. To examine the relationship between lifetime philopatry to the first breeding site and both age and natal dispersal distance and the relationship between lifetime philopatry and annual breeding success, we used general linear mixed models (GLMMs) with maximum likelihood estimation. Breeder identity was included as a random effect in GLMMs because many individuals yielded more than one breeding record. We analyzed males and females separately to avoid replication of data points from paired birds and because female boobies disperse further from their previous breeding sites than males (Kim et al. 2007). For all models, initially all explanatory variables and their 2-way interactions were fitted in the maximal model and then nonsignificant interactions, quadratic terms, and main terms were dropped sequentially to simplify the model. We used deletion tests to assess the significance of the increase in deviance (in GLMs with a Poisson error distribution), F ratio (in GLMs with a normal error distribution), or Likelihood ratio (L. ratio; in GLMMs) that resulted when a given term was removed from the minimal adequate model (Crawley 2003, 2005). Analyses were carried out with R v2.3.1 (R Development Core Team 2006), and we report means \pm standard errors throughout.

RESULTS

Natal dispersal and reproductive success

Natal dispersal distance differed significantly between the sexes when effect of year was taken into account (GLM: sex: $F_{1,614} = 7.48$, $P < 0.01$; year: $F_{10,605} = 2.11$, $P < 0.05$): females nested an average of 6.1 m further from their natal sites than males (females: 36.6 ± 1.4 m, $n = 373$; males: 30.5 ± 1.7 m, $n = 243$; see also Figure 2a). The interaction between sex and

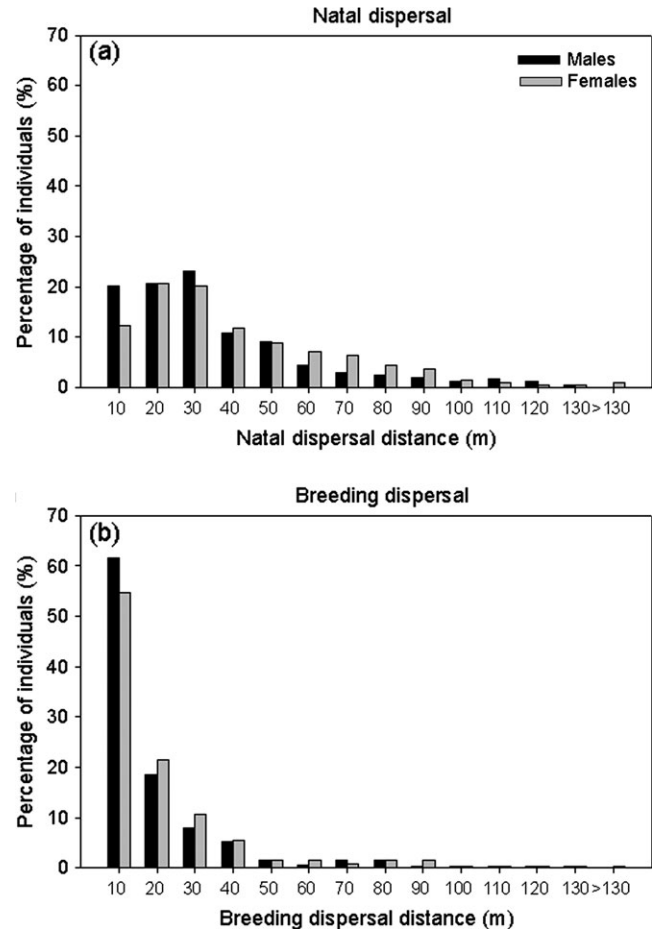


Figure 2
Distributions of (a) natal dispersal distances (males: median = 23.8 m, $n = 243$ individuals; females: median = 28.6 m, $n = 373$ individuals) and (b) breeding dispersal distances (males: median = 6.8 m, $n = 488$ dispersals; females: median = 8.4 m, $n = 565$ dispersals).

year was not significant ($F_{6,609} = 1.17$, $P = 0.32$). When we tested for the effects of natal dispersal distance and sex on standardized reproductive success at the first attempt, none of the terms was significant (GLM: natal dispersal distance: $F_{1,614} = 2.15$, $P = 0.14$; sex: $F_{1,614} = 0.01$, $P = 0.91$; natal dispersal distance \times sex: $F_{1,614} = 0.82$, $P = 0.37$). Early lifetime reproductive success in birds of the 1993 and 1994 cohorts was greater in females than in males (males: 3.5 ± 0.2 chicks; females: 4.1 ± 0.3 chicks; GLM: deviance $_{1,301} = 7.15$, $P = 0.01$) but did not vary with natal dispersal distance or with its interaction with sex (GLM: natal dispersal distance: deviance $_{1,301} = 0.001$, $P = 0.97$; natal dispersal distance \times sex: deviance $_{1,301} = 0.86$, $P = 0.35$).

Distance from natal site, first breeding site, and previous breeding site

When males and females were on their second to maximum sixth breeding attempts, on average, they nested closer to their first breeding sites than to their natal sites, and this difference was significant for all age classes between 4 and 8 years (Table 1a; Figure 3). We compared breeding dispersal distance and distance between current and first breeding sites when the 2 sexes were on their third to sixth breeding attempts; the second breeding attempt was not included because there the 2 distances were the same. The distance

Table 1

Wilcoxon signed ranks tests for comparisons between distance between first breeding site and current breeding site (year t) and (a) distances between natal site and current breeding site (year t); (b) breeding dispersal distance (year $t \sim$ year $t-1$); and (c) distance between first breeding site and predicted current breeding site under simulated dispersal in random direction

Age	(a)			(b)			(c)		
	Z	n	P	Z	n	P	Z	n	P
Male									
4 years	4.17	64	<0.001						
5 years	6.44	147	<0.001	3.66	52	<0.001	1.11	147	0.27
6 years	7.06	182	<0.001	5.19	118	<0.001	2.28	182	<0.05
7 years	7.72	194	<0.001	6.08	149	<0.001	3.97	194	<0.001
8 years	5.96	204	<0.001	6.74	169	<0.001	4.05	204	<0.001
Female									
4 years	6.52	163	<0.001				0.06	163	0.96
5 years	6.87	220	<0.001	4.71	119	<0.001	2.81	220	<0.01
6 years	6.42	198	<0.001	4.97	153	<0.001	4.09	198	<0.001
7 years	5.87	200	<0.001	6.64	143	<0.001	4.14	200	<0.001
8 years	5.30	175	<0.001	6.13	135	<0.001	4.95	175	<0.001

between current breeding site and first breeding site was longer than breeding dispersal distance between current (year t) and previous (year $t - 1$) sites at all ages (Table 1b; breeding dispersal distance: males, 13.16 ± 0.81 m; females, 15.60 ± 0.89 m; see also Kim et al. 2007). Distributions of breeding dispersal distances of males and females are shown in Figure 2b. Hence, successive short breeding dispersals tended to maintain males and females at an average of 19.0–28.9 and 22.5–30.5 m, respectively, from their first breeding sites and 34.9–39.4 and 36.4–42.2 m, respectively, from their natal sites (Figure 3). Therefore, we analyzed early lifetime philopatry to the first breeding site rather than to the natal site in subsequent analyses.

Lifetime philopatry to the first breeding site

Simulated successive dispersals in random directions over the observed distances carried individuals progressively further from their first breeding sites (Figure 3). Distance between the first breeding site and current breeding site was significantly longer in simulated random dispersal than in observed dispersal at 6–8 years of age in males and 5–8 years of age in females, but not significantly longer at earlier ages (Table 1c).

Relationships between lifetime philopatry, age, and natal dispersal distance

Among male repeat breeders, distance from the first breeding site varied with age, age², and natal dispersal distance (GLMM with breeder identity as a random effect: age, L. ratio = 5.53, degrees of freedom [df] = 1, $P < 0.05$; age², L. ratio = 8.47, df = 1, $P < 0.01$; natal dispersal, L. ratio = 6.65, df = 1, $P < 0.01$), and among 2-way interactions, only age \times natal dispersal was significant (L. ratio = 6.97, df = 1, $P < 0.01$). In female repeat breeders, distance from the first breeding site varied with age and natal dispersal distance (GLMM: age, L. ratio = 42.26, df = 1, $P < 0.001$; natal dispersal, L. ratio = 11.85, df = 1, $P < 0.001$) and no 2-way interaction was significant. Males nested closer to the first breeding site with increasing age up to 6 years old, and thereafter up to 8 years old they nested further away, whereas in females, distance from the first breeding site increased progressively until 8 years old (Figure 3). Overall, the shorter their natal dispersal, the more philopatric were both sexes to their first

breeding sites up to at least 8 years of age (Figure 4). When we analyzed males separately at each age in view of the significant interaction reported above, the effect of natal dispersal on distance from the first breeding site was significant at 6 and 8 years of age (Figure 4a; GLM: 6 years, $F_{1,180} = 4.94$, $P < 0.05$; 8 years, $F_{1,202} = 6.47$, $P < 0.05$).

Relationship between philopatry to first breeding site and annual breeding success

In repeat breeders of both sexes (243 males and 373 females from 5 cohorts), neither distance from first breeding site (GLMMs: males, L. ratio = 0.02, df = 1, $P = 0.89$; females, L. ratio = 0.06, df = 1, $P = 0.81$) nor age (GLMMs: males, L. ratio = 0.12, df = 1, $P = 0.73$; females, L. ratio = 1.41, df = 1, $P = 0.24$) explained variation in standardized annual breeding success over 3–8 years of age.

DISCUSSION

We showed longitudinal philopatry to the first breeding site during the early lifetime of blue-footed boobies. Distance between the first breeding site and current breeding site was significantly longer in simulated random dispersal than in observed dispersal at 6–8 years of age in males and 5–8 years of age in females. Our results suggest that 1) males show shorter natal dispersal than females; 2) natal dispersal distance is not associated with reproductive success of either sex at first breeding or over the first 11 years of life; 3) in the early lifetime, male and female repeat breeders nest closer to their first breeding sites than to their natal sites at all ages between 4 and 8 years because they disperse every year in relation to their previous site and their first site; 4) philopatry to first sites increases up to 6 years of age, then declines up to at least 8 years of age in males, and declines monotonically with age in females; 5) in both sexes, birds with shorter natal dispersal distances show stronger philopatry to first breeding sites during the early lifetime; and 6) however, early lifetime philopatry to first breeding sites was unrelated to annual breeding success.

Male blue-footed boobies dispersed a shorter distance from their natal sites than females in the first breeding attempt, confirming a nonsignificant trend in the smaller sample of Osorio-Beristain and Drummond (1993). Although male and female

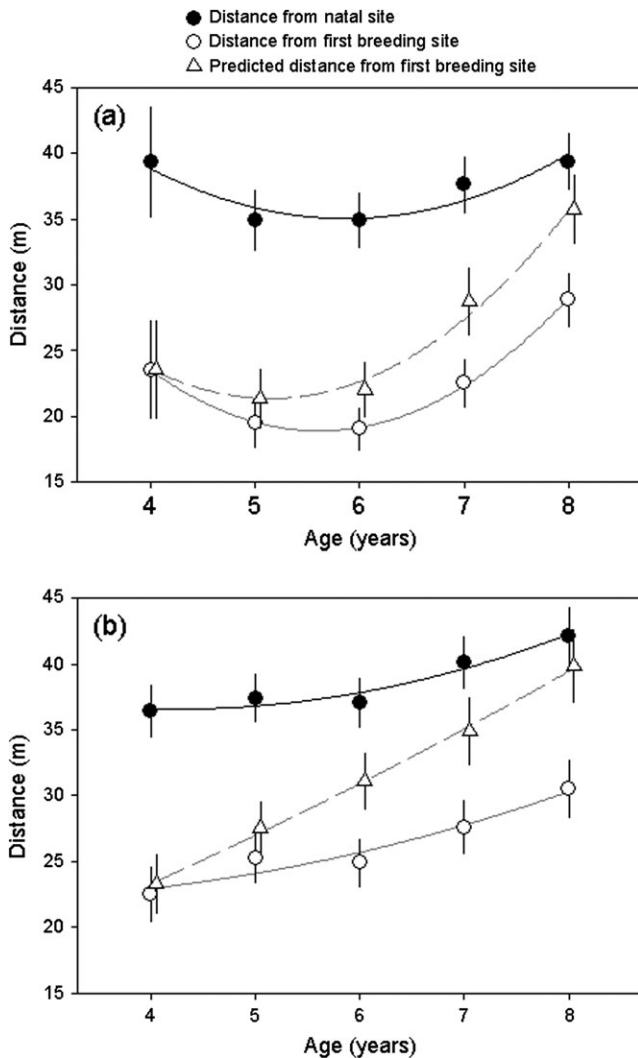


Figure 3 Distances between current breeding site and natal site; current breeding site and first breeding site; and predicted current breeding site after simulated dispersal in random direction and first breeding site in (a) males and (b) females. Ages of 2–3 years are not shown because sample sizes were small. The fitted lines are quadratic regressions.

boobies jointly guard their territories throughout the prelaying, incubation, and chick rearing periods (Nelson 1978; Stamps et al. 2002), males generally arrive first and obtain territories before pairing (Gonzalez and Osorno 1987). Therefore, males may be more philopatric than females because it is usually males that select the territory (cf., Greenwood 1980). Sex biased natal dispersal may reduce the probability of inbreeding with relatives through spatial segregation (Greenwood and Harvey 1982; Wheelwright and Mauck 1998; Forero et al. 2002; Perrin and Goudet 2003). Although dispersal of boobies in the study colony is over short distances, the rate of inbreeding, at least with parents and broodmates, seems minimal (Drummond H, Torres R, Kim S-Y, in preparation).

After showing initial philopatry to their natal sites, repeat breeders nest closer to their first breeding sites than to their natal sites throughout their early lifetime and possibly thereafter. Therefore, it may be more appropriate to focus on philopatry to the first breeding site when analyzing lifetime philopatry in this species and some other birds. Boobies show long-term, possibly lifelong, attachment to the sites where

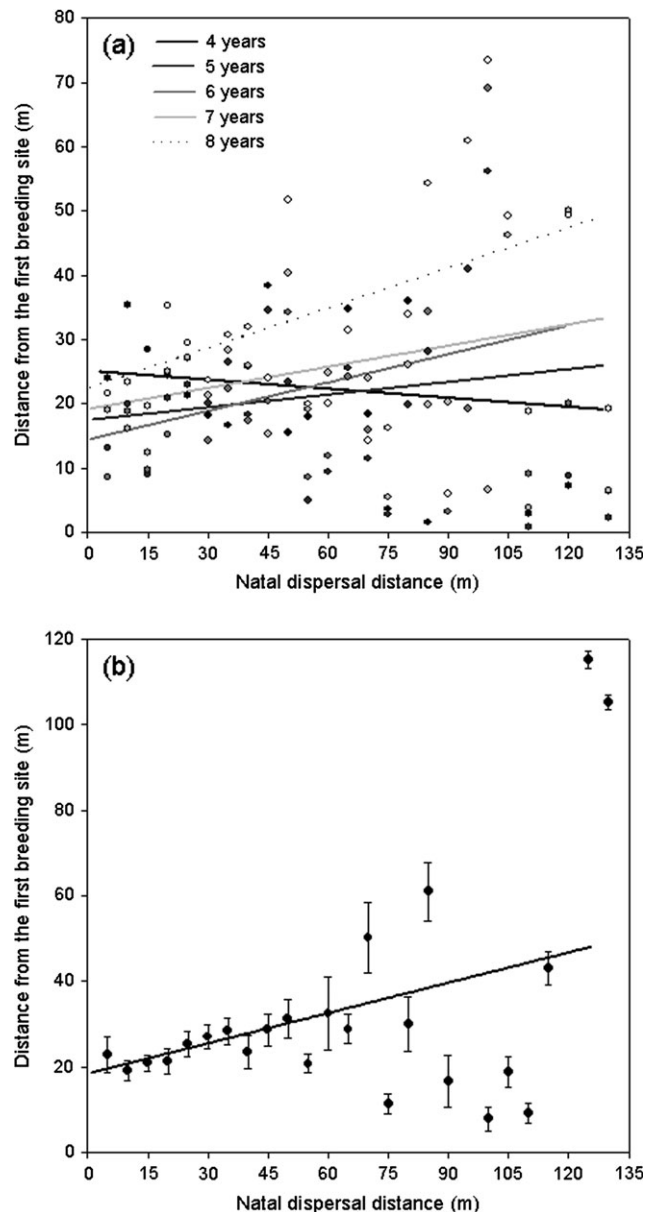


Figure 4 Relationship between natal dispersal and distance from the first breeding site at different ages of (a) males (ages separated; 4 years: $n = 64$, 5 years: $n = 147$, 6 years: $n = 182$, 7 years: $n = 194$, 8 years: $n = 204$) and (b) females (ages pooled; $n = 980$). Linear regressions were fitted using observed data and means (\pm standard errors) are presented for each 5 m of natal dispersal.

they obtain their first authentic experience of territorial defense and breeding (as opposed to tryouts during the nestling and juvenile periods). This attachment is evidently stronger than any attachment to the natal site but ensures long-term proximity to the natal site simply because the natal site is usually close to the first site. Young boobies seem to look for suitable sites for their first reproduction and nest close to those sites ever after.

Although birds of all age classes nested closer to their previous sites than to their first sites, our simulation showed that the first site probably functions throughout the early lifetime as an additional point of reference. Consequently, any male's or female's successive sites and the successive sites of their

mature offspring from the same and different seasons must sometimes be close, thereby creating opportunities for boobies to interact socially with offspring, grand offspring, siblings, half siblings, and cousins.

Age-related change in competitiveness due to maturity, experience, and habitat familiarity could account for some patterns. Natal dispersal distances could be considerably greater than subsequent breeding dispersal distances because first breeders are less competitive than experienced breeders (Greenwood and Harvey 1982). Males may nest progressively closer to their first breeding sites during the first 6 years of life because their competitiveness improves over this span (Pärt 2001); 2-year studies of other birds have documented age-related decreases in breeding dispersal (Newton 1993; Badyaev and Faust 1996; Forero et al. 1999; Pyle et al. 2001). However, increasing distance from the first site over the next 2 years is unlikely to be due to decline in competitiveness because senescence does not set in until about 10–11 years of age (Velando et al. 2006; Kim et al. 2007). The optimal trade-off between philopatry and dispersal should vary with age if the costs of dispersal vary with age/experience (Greenwood and Harvey 1982), and 6- to 8-year-old males may be better able to take advantage of dispersal opportunities than younger males. The tendency of males and females with shorter natal dispersal to show greater philopatry to the first breeding sites throughout their early lifetime could be due to stable individual variation in competitive ability or dispersal phenotype.

Our results for males and females revealed no relationship between natal dispersal distance and breeding success either at the first attempt or over the first 11 years of life or between philopatry to the first breeding site and breeding success in the next year. This result is puzzling and contrasts with the positive fitness consequences of natal dispersal reported for the marsh tit (*Parus palustris*; Nilsson 1989) and thick-billed murre (*Uria lomvia*; Steiner and Gaston 2005) and the negative consequences in the black kite (*Milvus migrans*; Forero et al. 2002) and great reed warbler (*Acrocephalus arundinaceus*; Hansson et al. 2004). It is possible that limited natal dispersal and lifelong philopatry both confer such substantial benefits that natural selection has eliminated variation in these traits from the population. The population's remaining variation in dispersal and lifelong philopatry within the colony (we did not analyze dispersal to other populations) may be of minor importance.

Alternatively, the observed variation could produce positive effects in some boobies and negative effects in others, and these effects could cancel each other out at the population level. Previously, we showed that breeders disperse further from natal sites or previous breeding sites when local nest density there is currently suboptimal (too high or too low; Kim S-Y, Boulinier T, Torres R, Drummond H, unpublished data) and after experiencing reproductive failure there (Kim et al. 2007). Therefore, it is plausible that effects of philopatry on reproductive success could sometimes be obscured by the boobies' flexible responses to circumstances. In the blue-footed booby, breeding dispersal distance varies among years, with individuals dispersing a greater distance in years when the population density is high (Kim et al. 2007). It is also possible that the benefits of philopatry are expressed late in the lifetime or that our sampling of consequences was sometimes biased by failure to include birds that failed during incubation. Future studies need to separate birds that previously experienced optimal and suboptimal environments to examine the reproductive consequences of adaptable strategies to stay or move away.

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