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Simultaneous positive and negative density-dependent dispersal in a colonial bird species

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Abstract. Contradictory patterns of density-dependent animal dispersal can potentially be reconciled by integrating the conspecific attraction hypothesis with the traditional competition hypothesis. We propose a hypothesis that predicts a U-shaped relationship between density and both natal and breeding dispersal distance. Using 10 years of observations on a breeding colony of the Blue-footed Booby (*Sula nebouxii*), the hypothesis was confirmed by documenting simultaneous positive and negative density-dependent dispersal distances in natal and breeding dispersal of males and breeding dispersal of females within the colony. Point-pattern analyses demonstrated that the breeding sites of Blue-footed Boobies were highly aggregated in all years within a large study area, and aggregation presumably resulted in heterogeneity in patch density throughout the colony. As predicted, at moderate to high densities, dispersal distances showed positive density dependence, with individuals moving to lower density patches. In contrast, at low to moderate densities, dispersal distances showed negative density dependence, with individuals moving to higher density patches. In both sexes of the 1994 cohort, the higher the mean density in patches used by an individual over the long term (up to age 11 years), the fewer fledglings it produced. A positive effect of density on long-term reproductive success was not detected, possibly because birds that failed during pair formation or incubation were not sampled. Density of conspecifics may be an important influence on habitat selection of breeders, and dispersal may tend to carry individuals to patches where pair formation opportunities are better and negative effects of competition on reproductive success are reduced.

Key words: Allee effect; Blue-footed Booby; competition; conspecific attraction; density dependence; dispersal; Isla Isabel, Nayarít; patchiness; Ripley's K; Sula nebouxii.

Introduction

It has long been accepted that individual fitness of territorial animals is inversely related to population density (Stamps 1994), and most habitat-selection models have assumed that individual fitness declines monotonically as the density of conspecifics increases, due to increased competition for resources (Fretwell and Lucas 1970, Fretwell 1972). Accordingly, most empirical and theoretical studies have focused on negative effects of density through competition, predation, and abiotic stress (Bruno et al. 2003). However, some authors have recognized that conspecifics can also have positive effects on individual fitness (Stamps 1994) and that habitat selection of animals may respond to both negative and positive effects of conspecifics on fitness (Stephens and Sutherland 1999, Greene and Stamps 2001, Serrano et al. 2003, 2005). Theoretical benefits of conspecific presence include habitat conditioning, improved predator detection and defense, better assessment of habitat quality, and increased opportunity for mate choice, pair formation, and extra-pair mating (Wagner 1993, Stamps 1994, Danchin and Wagner 1997, Doligez et al. 2003).

Both positive and negative effects of conspecific presence can be present in the same population and even act on the same individuals. Recent models and experiments have explored how positive and negative effects of density can interact to influence settlement patterns, based on Allee's (1951) insights (Greene and Stamps 2001, Leslie 2005, Donahue 2006). Positive and negative effects of density should influence the evolution of settlement behavior, molding migration, dispersal, and habitat selection. In a patchy environment where patch quality differs spatially or temporally within a population, dispersal behavior is selected to increase individual fitness by carrying animals to suitable patches (Travis and Dytham 1998). Dispersal includes natal dispersal, the movement between birth site and first breeding site, and breeding dispersal, the movement between two successive breeding sites (Greenwood 1980).

High conspecific density is traditionally expected to favor increased dispersal (Greenwood 1980), but positive and negative effects of density at the natal or previous breeding patch seem likely; individuals may move away from both low and high density areas.

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TABLE 1. Results from empirical studies of birds and mammals showing relationships between population densities that varied in temporal or spatial scale and natal or breeding dispersal (distance or probability).

Study	Species	Scale of density variation	Dispersal parameter	Effect of density on dispersal
Natal dispersal				
Nilsson (1989)	Marsh Tit (*Parus palustris*)	temporal	distance	positive
Negro et al. (1997)	Lesser Kestrel (*Falco naumanni*)	temporal	probability	positive
Jones et al. (1988)	kangaroo rat (*Dipodomys spectabilis*)	temporal	distance	negative
McGuire et al. (1993)	prairie vole (*Microtus ochrogaster*)	temporal	probability	negative
Forero et al. (2002)	Black Kite (*Milvus migrans*)	spatial	distance	negative
Serrano et al. (2003)	Lesser Kestrel (*Falco naumanni*)	spatial	probability	negative
Støen et al. (2006)	brown bear (*Ursus arctos*)	temporal	distance and probability	negative
Breeding dispersal				
Paradis et al. (1998)	various migratory birds	overall	distance	positive
Aars and Ims (2000)	root vole (*Microtus oeconomus*)	spatial	probability	positive
Kim et al. (2007)	Blue-footed Booby (*Sula nebouxii*)	temporal	distance	positive
Oro and Pradel (2000)	Audouin's Gull (*Larus audouinii*)	temporal	probability	negative
Serrano et al. (2001, 2005)	Lesser Kestrel (*Falco naumanni*)	spatial	probability	negative
Cam et al. (2004)	Audouin's Gull (*Larus audouinii*)	spatial	probability	negative

Dispersal should depend most basically on whether the natal or previous patch contains any conspecifics (Smith and Peacock 1990, Stamps 1991, Muller et al. 1997, Serrano and Tella 2003, Serrano et al. 2003, 2005) and secondly on the density of conspecifics there. Empirical studies of birds and mammals reveal a positive relationship between density and dispersal in some populations and a negative relationship in other populations (Table 1). These studies related natal or breeding dispersal (either distance or probability) to seasonal, annual, or spatial variation in density.

We propose a hypothesis of simultaneous positive and negative density effects that predicts a U-shaped relationship between density and dispersal and test it by analyzing the relationships between density, natal and breeding dispersal distances, and reproductive success over the long term (up to age 11 years) in a colonial marine bird, the Blue-footed Booby (*Sula nebouxii*). Colonial breeders are especially likely to show such effects because for them the presence of conspecifics is particularly important (Oro and Pradel 2000, Serrano et al. 2001, 2005). We analyzed dispersal distances within a single-island colony rather than probability of dispersal to other islands/colonies.

A U-shaped relationship between density at the natal or previous site and dispersal distance will result in movement from high or low density patches to moderate density patches. Specifically, (1) for individuals dispersing from sites with relatively moderate to high local density, dispersal distance will be positively related to density at the natal or previous site and the new site will have a lower density than the individual's natal or previous breeding site; and (2) for individuals dispersing from natal or previous breeding sites with low to moderate local density, dispersal distance will be negatively related to density at the natal or previous site and the disperser's new site will have a higher density than its natal or previous breeding site.

METHODS

Study area and species

We studied the colony of Blue-footed Boobies on Isla Isabel, Nayarít (21°52′ N, 105°54′ W), off the Pacific coast of Mexico (see Plate 1). Blue-footed Boobies are territorial throughout the breeding season, and breeders and chicks are strongly attached to their territories until fledging (Nelson 1978). Territories can include or be bounded by trees, rocks, and patches of vegetation, and they contain no food. On Isla Isabel, males generally obtain territories of 7–20 m^2 early in the seven-month breeding season (Stamps et al. 2002). During several days or weeks, they spend a few hours each day wandering in the nesting area, displaying to other males, and eventually settling on a territory; then females arrive and pair with the males on their territories (Stamps et al. 2002). After this, the male and female both guard the territory and jointly select a site for the nest (Stamps et al. 2002), then jointly tend the clutch and brood during roughly five and one-half months (Nelson 1978). Blue-footed Boobies are socially monogamous, and roughly half of the pairs in the study population retain the same mates in the following breeding season (Kim et al. 2007).

Over 19 years, 10 839 fledglings and roughly 3160 adults in the study population were banded, and ~40% of fledglings recruited into the same population, females generally nesting for the first time at age 2–6 years and males at age 3–6 years (Osorio-Beristain and Drummond 1993, Drummond et al. 2003). We have not encountered boobies banded on Isla Isabel during occasional study of booby populations on the Islas Marietas or on Isla San Pedro Mártir (130 km and 903 km distant, respectively). Seven males and six females marked on Isla Isabel as fledglings nested 476 km away on El Rancho island (25°08′ N, 108°14′ W) during 2003–2006, at least four of them doing so repeatedly (E.

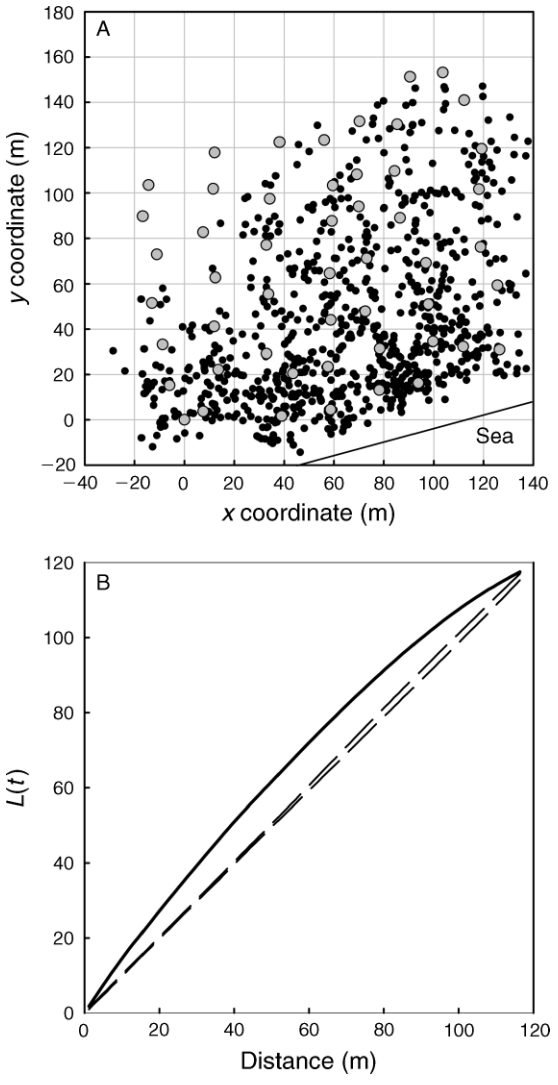


FIG. 1. (A) Distribution of Blue-footed Booby (*Sula nebouxii*) breeding sites (black circles) in 2005 and marker trees (gray circles) for plots in the study area, expressed in x, y coordinates with a distance scale in meters. (B) The corresponding plot of $L(t) = \sqrt{K(t)/\pi}$ against distance t. Similar results were obtained every year during 1996–2004 (figures not presented). In panel B, the solid bold line represents the L value (linearized form of the Ripley's K function) for the observations ($n = 770$ booby nests); dashed lines correspond to the upper and lower limits obtained by simulation on the assumption that the distribution was random.

Mellinck, *unpublished data*). Hence, long-distance dispersal from Isla Isabel may be rare and carried out by first breeders rather than experienced breeders.

Field procedures

Since 1989, all breeding sites (nests) in a 20 800-m^2 study area in the forest were marked and mapped every year. Physical conditions such as vegetation, slope, and substrate are roughly homogeneous throughout the study area. 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 (Fig. 1A). The plots occupied the complete study area. All breeding sites in the study area with a clutch or brood were marked with numbered wooden stakes and all fledglings and most breeders were marked with numbered metal bands. The study area is in the island's largest subcolony, and this contains about half of all nests on the island.

In parts of the study area, patch density is negatively correlated with distance from the shoreline (Fig. 1A), boobies apparently preferring to nest close to the shore, where they can readily take off and land without having to walk overland (A. C. Montes-Medina, H. Drummond, and S.-Y. Kim, *unpublished data*). Dispersal distances from nests near the center of the study area, where density is moderate, could be underestimated, compared to dispersal from nests at the edges because sampling ended at the edges and central nests are relatively close to all edges (Fig. 1A). However, little bias is expected because few study birds dispersed more than 80 m (male natal dispersers, 7.1%; female natal dispersers, 6.9%; male breeding dispersers, 1.5%; female breeding dispersers, 2.1%), which is the maximum distance that a bird in the center can move within the study area. Banded birds seldom nest outside the study area (Drummond et al. 2003).

Each breeding site 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. Breeding site locations were expressed in two linear coordinates originating at the marker tree in one corner of the study area. We used data from 1996 to 2005, during which 716 ± 45 pairs (mean ± SE) nested each year (range = 489–973 pairs, in 2003 and 2001) and 98.8 ± 0.3% of nests in the study area were mapped.

Every year, to record chick survival all breeding sites in the study area were surveyed every few days over a period of 20 weeks from shortly after the start of hatching until each chick fledged (reached age 70 d), the last chicks doing so in July. Each breeder's band number was confirmed by independent readings on up to three days. Overall, 86% of male and female breeders were identified over the 10 breeding seasons. Date of laying of the first egg in each nest was recorded when it occurred during the survey period or estimated from observed hatching date or chick-age estimates based on length of ulna and culmen at first encounter (Drummond et al. 2003). Our samples did not include birds that attempted to breed and failed to mate or birds that abandoned their clutches before we could read their bands. In low density areas, unpaired males were more frequently observed and breeders tended to abandon their clutches more often, in comparison with high density areas (S.-Y. Kim, *personal observation*).

Sampling and measurements of density and dispersal distance

For natal dispersal, we used data from all 635 identified males and 578 identified females that bred for the first time between 1996 and 2005 when 1–6 years old (median ages 4 and 3 years for males and females, respectively). Natal dispersal distance was the distance between their natal sites and their first breeding sites. For breeding dispersal, we used data from all identified males and females that bred in two consecutive years (years $t - 1$ and t). If an individual attempted to breed more than once in a year, then the first event was selected for analysis. A total of 977 marked males and 949 marked females nested in consecutive seasons over the 10 years, performing 2851 and 2910 consecutive breeding events, respectively. Breeding dispersal distance was the distance between each focal individual's breeding sites in years $t - 1$ and t.

Local density was the number of breeding sites (excluding the focal one) within 10 m of each natal or previous breeding site (year $t - 1$) in the current season (year t), and within 10 m of each current breeding site (year t) during the current breeding season (year t), calculated using ArcView GIS v. 3.2 (ESRI, Redlands, California, USA). We assumed that nests within 10 m constituted the neighborhood because social interactions with neighboring breeders are observed within this distance (A. C. Montes-Medina, H. Drummond, and S.-Y. Kim, *unpublished data*). We excluded focal individuals that bred near the edge of the study area because failure to map nearby breeding sites outside the study area would result in underestimation of local density. To test for long-term consequences of local density, we calculated the mean density at each male or female's successive breeding sites and its reproductive success (total number of chicks fledged) up to age 11 years. We used the 127 male and 88 female recruits from the 1994 cohort of fledglings, the earliest cohort for which we could track successive breeding sites and performances starting with the first breeding attempt using data from the study period (1996–2005).

Current density at the natal site (CDNS, the local density at the natal site during the first breeding season) and current density at the previous breeding site (CDPS, the local density at the previous breeding site during the current season) were related to natal and breeding dispersal distances and to density at the current breeding site. By using CDNS and CDPS instead of density there in the year of birth or previous breeding, we sidestepped complications arising from interannual variation in population density (Kim et al. 2007). In principle, dispersal distance could be influenced by either local density at the earlier site in the current year or local density there in the natal or previous year. It would be difficult to tease apart these two influences because the overall pattern of spatial variation in density in the colony is relatively stable across years.

Data analyses

Before undertaking statistical analyses, we examined the breeder distribution in the booby colony for patchiness, using point-pattern analysis and Ripley's K function. This function tests for point-process departure from randomness toward aggregation or regularity (Ripley 1977). Where λ is the mean number of points per unit area (the intensity of the pattern) and $\lambda K(r)$ is the expected number of neighbors within a radius r of any point of the process, the expected value of $K(r)$ under randomness is πr^2 (complete spatial randomness [CSR]). When clustering (patchiness) occurs, $K(r) > \pi r^2$ and the curve lies above the CSR curve and when the point pattern is regular, $K(r) < \pi r^2$ and the curve lies under the CSR curve. We used the L function, a linearized form of the K function, to test for clustering of nests in the study area in each of the 10 seasons. A plot of $L(t) = \sqrt{K(t)/\pi}$ against distance (t) was constructed for each year using Kfn function in R v2.3.1 (R Development Core Team 2006).

We analyzed males and females separately to avoid replication of data points from paired birds, and because female boobies disperse farther than males (Kim et al. 2007). Prior to analyses, natal and breeding dispersal distances were log transformed to obtain a normal distribution, and laying dates were transformed to proportional rank by year to take into account annual variation in timing of the breeding season. We used generalized linear models (GLMs) with a normal error distribution to test for individual variability in natal dispersal distances and local density at the first breeding site (full models: Natal dispersal distance model, CDNS + CDNS^2 + Year + Laying date + all two-way interactions; Density at the first breeding site model, CDNS + Natal dispersal distance + Year + all two-way interactions) and GLMs with a Poisson error distribution to test for effects of mean local density at breeding sites on total number of chicks fledged during all breeding attempts up to 11 years old (full model: Number of chicks model, Mean density). To analyze individual variability in breeding dispersal distances and density at the current breeding site, we used linear mixed effect models (LMEs) with maximum likelihood estimation (ML), including breeder identity as a random effect because many individuals yielded data for more than one consecutive breeding record over the 10-year study (full models: Breeding dispersal distance model, CDPS + CDPS^2 + Year + Laying date + all two-way interactions; Density at the current breeding site model, CDPS + Breeding dispersal distance + Year + all two-way interactions). Laying date and year were included as independent variables in the models when necessary, to control for their rather strong influence on both natal and breeding dispersal (Kim et al. 2007). Where relationships were nonlinear, squared terms were included in models. To test the appropriateness of a quadratic function for modeling density-dependent dispersal distance, we ran generalized additive models

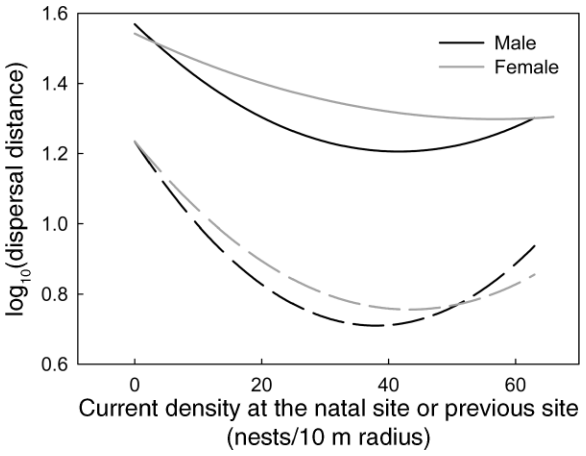


FIG. 2. Solid lines show the relationship between natal dispersal ($\log_{10}$-transformed distance between natal site and the first breeding site) and current density at the natal site (CDNS: number of breeding sites within 10 m of the natal site during the current breeding season; males 22.29 ± 0.54 nests/10 m radius [mean ± SE], $n = 635$; females, 21.49 ± 0.52 nests/10 m radius, $n = 578$). Dashed lines show the relationship between breeding dispersal ($\log_{10}$-transformed distance between nest sites in year t and $t - 1$) and current density at the previous breeding site (CDPS; number of breeding sites within 10 m of the previous breeding site during current breeding season; males, 20.76 ± 0.23 nests/10 m radius [means ± SE], $n = 2851$; females, 20.42 ± 0.23 nests/10 m radius, $n = 2910$).

(GAMs) for natal and breeding dispersal distances, including a smoothing function for CDNS and CDPS (Crawley 2007). As the smoothed model showed a humped relationship between the response variable and CDNS or CDPS in all GAMs, we fitted the quadratic term in the GLM or LME.

Initially, all explanatory variables and their two-way interactions were fitted in the model, then nonsignificant terms were dropped sequentially. We used deletion tests to assess the significance of the increase in deviance (GLMs with Poisson error distribution), the F ratio (GLMs with normal error distribution), or the Likelihood ratio (L. ratio; LMEs) that resulted when a given term was removed from the model. Analyses were carried out with R v2.3.1 (R Development Core Team 2006).

RESULTS

Point pattern analysis

Breeding sites were highly aggregated even at the smallest scales measured. Under the null hypothesis of a random distribution, the $L(t)$ observations exceeded the null expectation at scales from 0 to 120 m in years 1996–2005 (Fig. 1B). In all years, L values met with the null simulation of the random distribution approximately at 120 m. Therefore, Ripley's K function differs significantly from the random distribution at the 0–120 m scale.

Local density at the natal site and natal dispersal distance

The U-shaped relationship between CDNS (current density at the natal site) and natal dispersal distance was found in males, but not in females. In males, natal dispersal distance varied with CDNS and CDNS^2 (GLM: CDNS, $F_{1,633} = 17.19$, $P < 0.001$; CDNS^2, $F_{1,633} = 7.92$, $P < 0.01$). At local densities <40 nests/10 m radius, natal dispersal distance of males decreased as current density at the natal site increased, but above this value the relationship was inverted (Fig. 2). The effects of year and laying date were not significant (year, $F_{9,625} = 1.02$, $P = 0.43$; laying date, $F_{1,633} = 0.67$, $P = 0.42$), and none of the two-way interactions was significant. In females, when the effect of laying date ($F_{1,576} = 12.25$, $P < 0.001$) was controlled, CDNS explained some of the variability in natal dispersal distance ($F_{1,576} = 11.65$, $P < 0.001$), but neither year nor CDNS^2 was significant (year, $F_{9,568} = 1.57$, $P = 0.12$; CDNS^2, $F_{1,576} = 0.35$, $P = 0.56$). Natal dispersal distance decreased as current density at the natal site increased (Fig. 2). There was no significant two-way interaction.

Local density at the previous site and breeding dispersal distance

The U-shaped relationship between CDPS (current density at the previous site) and breeding dispersal distance was found in both males and females. In males, while taking the effects of year and laying date into account (linear mixed-effect models [LME] with male identity as a random effect: for year, L. ratio [Likelihood ratio] = 472.30, df = 9, $P < 0.001$; for laying date, L. ratio = 100.07, df = 1, $P < 0.001$), breeding dispersal distance varied with CDPS and CDPS^2 (CDPS, L. ratio = 54.66, df = 1, $P < 0.001$; CDPS^2, L. ratio = 14.02, df = 1, $P < 0.001$). Up to a local density of 38 nests/10 m radius, dispersal decreased as the current density at the previous site increased, but above this density the relationship was inverted (Fig. 2). All the two-way interactions involving the year term were significant (year × CDPS, L. ratio = 23.07, df = 9, $P < 0.01$; year × CDPS^2, L. ratio = 27.84, df = 9, $P < 0.01$). When each year's data were analyzed separately, the effect of CDPS^2 on breeding dispersal distance was significant in six of 10 years, with those six years showing similar patterns to the 10 pooled years (GLM: 1997, $F_{1,312} = 14.17$, $P < 0.001$; 1998, $F_{1,239} = 9.71$, $P < 0.01$; 1999, $F_{1,247} = 22.92$, $P < 0.001$; 2001, $F_{1,393} = 7.88$, $P < 0.01$; 2003, $F_{1,190} = 5.30$, $P < 0.05$; 2004, $F_{1,184} = 10.22$, $P < 0.01$).

In females, taking the effects of year and laying date into account (LME with female identity as a random effect: year, L. ratio = 394.71, df = 9, $P < 0.001$; laying date, L. ratio = 130.39, df = 1, $P < 0.001$), breeding dispersal distance varied with both CDPS and CDPS^2 (CDPS, L. ratio = 30.44, df = 1, $P < 0.001$; CDPS^2, L. ratio = 4.48, df = 1, $P < 0.05$). Up to a density of 43 nests/10 m radius, dispersal distance of the sample of females decreased as the current density at the previous

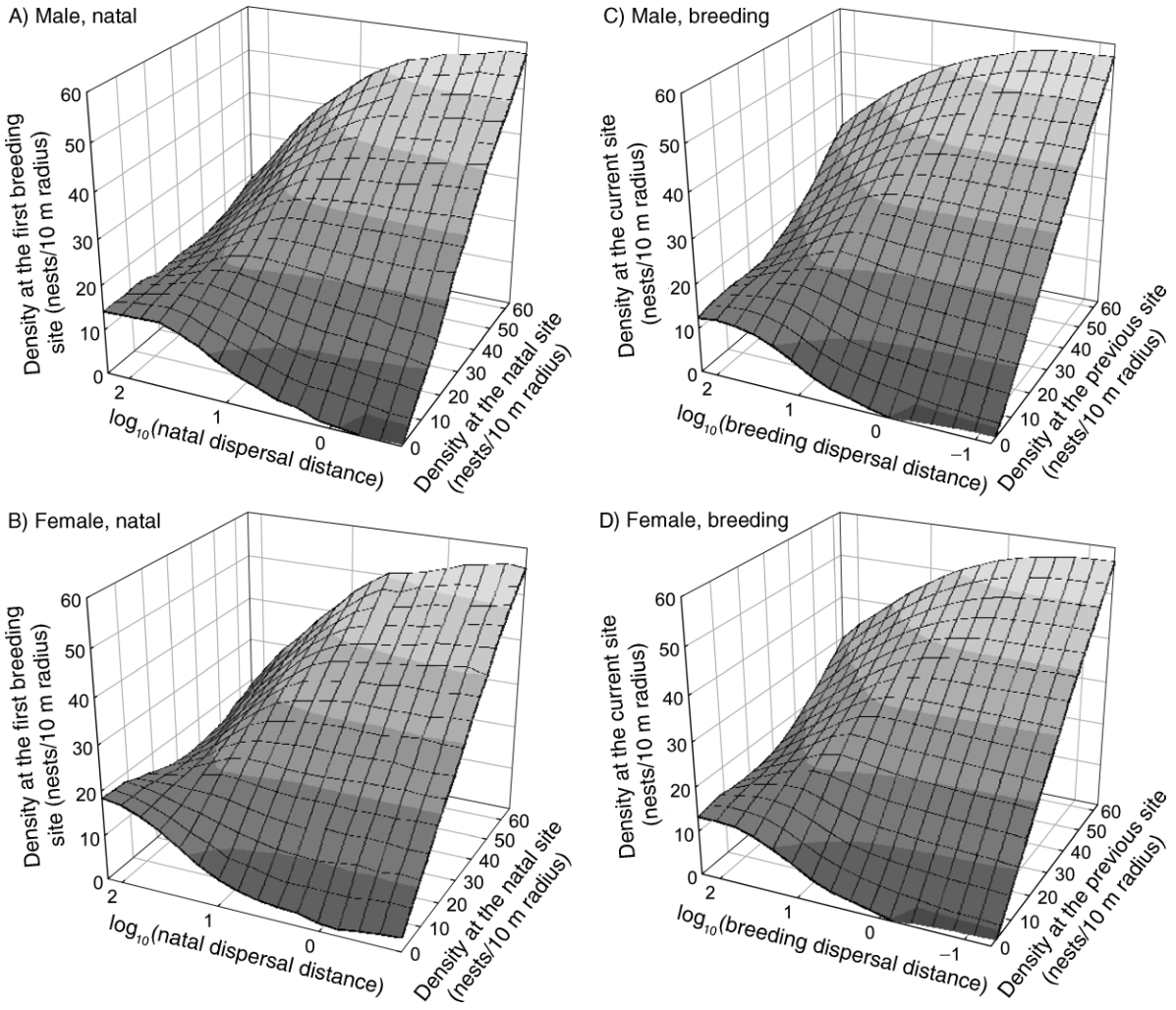


FIG. 3. Relationships between current density at the natal site or previous breeding site, dispersal distance, and density at the first breeding site or current breeding site for (A) male and (B) female natal dispersal; and (C) male and (D) female breeding dispersal. Local densities at the first breeding site and current breeding site are smoothed.

breeding site increased; above this value, dispersal distance increased, similar to males although the relationship seems weaker in females (Fig. 2). All the two-way interactions involving the year term were significant also in females (year × CDPS, L. ratio = 30.76, df = 9, $P < 0.001$; year × CDPS^2, L. ratio = 36.06, df = 9, $P < 0.001$). When analyzed separately for each year, the effect of CDPS^2 on breeding dispersal distance was significant in five of 10 years, showing similar patterns to pooled data (GLM: 1998, $F_{1,240} = 8.70$, $P < 0.01$; 1999, $F_{1,241} = 17.40$, $P < 0.001$; 2002, $F_{1,344} = 8.47$, $P < 0.01$; 2003, $F_{1,198} = 5.69$, $P < 0.05$; 2004, $F_{1,206} = 10.27$, $P < 0.01$).

Density at the first breeding site

First-breeding males and females dispersed to higher density sites when the CDNS was low but dispersed to lower density sites when the CDNS was high (Fig. 3A, B). The difference between CDNS and local density at the first breeding site was greatest when the two sexes dispersed a longer distance and negligible in short distance dispersers (Fig. 3A, B). In both males and females, local density at the first breeding site varied with CDNS (GLMs: males, $F_{1,633} = 92.11$, $P < 0.001$; females, $F_{1,576} = 77.67$, $P < 0.001$) and natal dispersal distance (males, $F_{1,633} = 24.67$, $P < 0.001$; females, $F_{1,576} = 17.66$, $P < 0.001$), while taking effects of year into account (males, $F_{9,625} = 8.25$, $P < 0.001$; females, $F_{9,568} = 5.65$, $P < 0.001$). The two-way interaction between CDNS and natal dispersal distance was also significant in both males and females (males, $F_{1,633} = 56.95$, $P < 0.001$; females, $F_{1,576} = 60.27$, $P < 0.001$).

Density at the current breeding site

Similar to what was observed for natal dispersal, breeders dispersed to higher density sites when the CDPS was low but dispersed to lower density sites when the CDPS was high, and this effect was strongest in

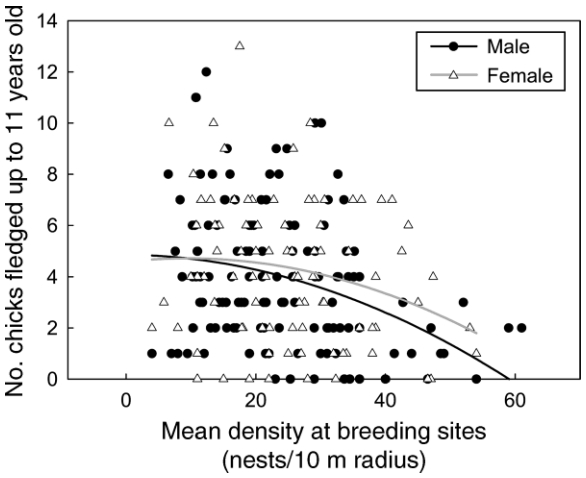


FIG. 4. Relationship between total number of chicks fledged up to age 11 years (127 males and 88 females of the 1994 cohort) and mean density across all of each male's or female's successive breeding sites.

long-distance dispersers and weakest in short-distance dispersers (Fig. 3C, D). In both males and females, local density at the current breeding site varied with CDPS (LMEs: males, L. ratio = 647.66, df = 1, $P < 0.001$; females, L. ratio = 552.43, df = 1, $P < 0.001$) and breeding dispersal distance (males, L. ratio = 44.65, df = 1, $P < 0.001$; females, L. ratio = 46.23, df = 1, $P < 0.001$), while taking annual effects into account (males, L. ratio = 448.67, df = 9, $P < 0.001$; females, L. ratio = 486.91, df = 9, $P < 0.001$). The interaction between CDPS and breeding dispersal distance was significant in both males and females (males, L. ratio = 269.16, df = 1, $P < 0.001$; females, L. ratio = 309.29, df = 1, $P < 0.001$).

Relationship between local density and long-term reproductive success

Total number of chicks fledged in all breeding attempts up to 11 years old decreased as mean density at the breeding sites increased, in both males and females marked as fledglings in 1994 (Fig. 4; GLMs: males, deviance = 33.60, df = 1, $P < 0.001$; females, deviance = 7.65, df = 1, $P < 0.01$).

DISCUSSION

We found both positive and negative density-dependent dispersal in the same colony, yielding an overall U-shaped relationship between density and dispersal distance. In males, the U-shaped relationship between density and dispersal distance appeared in both natal and breeding dispersal. However in females, the U-shaped relationship appeared only for breeding dispersal. In general (except for female natal dispersal), our data indicate positive density-dependent dispersal at moderate to high densities, with individuals moving to lower density patches; and negative density-dependent dispersal at low to moderate densities, with individuals moving to higher density patches. The farther a bird dispersed, the greater the change in local density. In environments where density is heterogeneous, it is inevitable that greater dispersal results in greater change in density over some scales of possible dispersal distance. Nonetheless, it was important to confirm that the density-dependent dispersal distances of the boobies did indeed carry them to patches of more moderate density, since this is required by the hypothesis. These results confirm the predictions of the U-shaped relationship between density and dispersal distance in a population showing wide spatial variation in patch density. While a number of studies of avian and mammalian species have shown either positive or negative effects of temporal or spatial variation in density on dispersal (Table 1), this is the first to test and confirm the simultaneous presence of both patterns in a single population.

This booby's tendency to disperse from low-density patches to higher density patches implies that the positive effects of inhabiting a moderate density site outweigh the dispersal costs, as suggested for other bird species (Oro and Pradel 2000, Serrano et al. 2001, 2003, Forero et al. 2002, Cam et al. 2004). Costs of dispersal for boobies probably do not include the increased energy expenditure and mortality risk incurred when animals disperse between populations (Gandon and Michalakis 2001); their within-population dispersal could involve challenges associated with settlement in an unfamiliar neighborhood and successful persistence there. Breeding close to conspecifics could increase the fitness of Blue-Footed Boobies in several ways. Both males and females could enjoy increased opportunities for pairing and for extra-pair relationships (see Wagner 1993, Wagner et al. 2000 for the "hidden lek hypothesis"), which are rife in the study colony and usually involve territorial neighbors (Osorio-Beristain and Drummond 1998). Also, defense against egg-stealing Heermann's Gulls (*Larus heermanni*), chick-predating milk snakes (*Lampropeltis triangulum*), and food-stealing gulls and spiny iguanas (*Ctenosaura similis*) is probably enhanced by the presumed improved ability of groups of neighbors to detect intruders and the observed tendency of neighbors to attack intruders simultaneously (Drummond et al. 1986, Rodríguez and Drummond 2000). At the proximate level, longer distance movement from natal or previous breeding sites with currently low density toward denser patches possibly results from conspecific attraction, the tendency to settle near conspecific territory holders (Stamps 1994). Conspecific attraction can carry animals to habitat that is suitable for occupation (conspecific cueing; Stamps 1987, 1994), and the behavioral responses involved could be calibrated to promote settlement in patches where density is moderate (Serrano et al. 2003, 2005). For instance, it has been suggested that individuals could be attracted to areas where conspecifics have previously been successful (Danchin et al. 1998).



PLATE 1. A pair of Blue-footed Boobies on Isla Isabel, Nayarít, off the Pacific coast of Mexico. Photo credit: S.-Y. Kim.

Negative effects of density that favor dispersing from high-density patches to lower density patches are likely to include more frequent fighting with neighbors, as well as increased risk of cuckoldry by male neighbors, egg-dumping by female neighbors (Osorio-Beristain et al. 2006), parasitism of parental care by neighbors' chicks (surreptitious adoptees; H. Drummond, *unpublished data*), and attacks by neighbors on offspring that trespass on their territories (Drummond et al. 1986). Movement from high-density patches to lower density patches possibly results from two processes: avoidance of competitive interactions at denser patches (Ens et al. 1995) and competitive exclusion from denser patches by more competitive breeders (Sutherland 1996, Negro et al. 1997, Paradis et al. 1998, Travis et al. 1999). Exclusion could explain why the positive relationship between density and dispersal distance is clearer in males than in females. Male boobies should face greater competition for breeding sites and mates than females because males are more responsible for territory establishment (Nelson 1978, Stamps et al. 2002; cf. Greenwood 1980) and because males outnumber females both at hatching (Torres and Drummond 1999) and at breeding (R. Torres and H. Drummond, *unpublished data*). Presumably, establishing a territory in a dense area is more difficult for male first-time breeders than for female first-time breeders, who showed only a negative relationship between density and natal dispersal distance.

The significant U-shaped relationship observed in female breeding dispersal distance could be at least partly due to faithful females following their mates and consequently showing the males' density dependent pattern. The positive density effect is weaker in females than in males, possibly because many females nested with new mates close to the females' own previous sites and were not constrained by their former mates' dispersal.

Analysis of the 1994 cohort showed that in both sexes, the higher the mean density of the patches used by an individual over its lifetime (up to age 11 years), the fewer fledglings it produced. Increased competition and interference at high densities may have reduced reproductive success (Sutherland 1996). It is also possible that individuals breeding at high densities might have to queue for more years before their first reproduction and consequently make fewer reproductive attempts by age 11 years than those at low densities. However, the

expected positive relationship between density and fitness at low to moderate densities was not observed. Tentatively, we attribute absence of this latter effect to a sampling problem described in the methods. Exclusion of birds that never in their (possibly brief) lives managed to find a partner or establish or hatch a clutch would result in overestimation of mean reproductive success of birds in low density areas if such individuals mostly attempted to settle in low-density areas.

Density dependence of life-history traits and evolutionary strategies has been frequently discussed and tested in the context of behavioral and ecological studies and conservation issues (Sutherland 1996). Ecologists now argue that Allee effects (Allee 1951) and conspecific attraction have received far less attention than they deserve and must be integrated with our understanding of the effects of conspecific competitors on the fitness and life-history strategies of individuals (Stamps 1994, Stephens and Sutherland 1999, Greene and Stamps 2001). Our findings go some way toward understanding how complex negative and positive effects of conspecifics on fitness can shape the spatial distribution patterns of populations and the behavioral mechanisms that underlie them. Further understanding will require taking into account the costs of dispersal (Travis et al. 1999, Greene and Stamps 2001). In the case of vagile but highly philopatric species like the Blue-footed Booby, these costs may largely account for most individuals moving no farther than several meters between successive nest sites and apparently ignoring hectares of demonstrably suitable habitat throughout their adult lives.

To understand how simultaneous positive and negative density-dependent dispersal has evolved, we must also explore the fitness consequences of patch density and dispersal distance through more extensive sampling. This will require experiments that take into account long-term benefits and proximate costs of dispersal, as well as differences among individuals in age, life history, and competitiveness. We have a poor grasp of how population variables such as density influence individual decision making, spatial distributions, and life histories, and how these in turn affect population dynamics (Hanski 2003, Stamps 2003). The Blue-footed Booby's U-shaped pattern of density-dependent dispersal distances may tend to make the density distribution of the population more homogeneous (Sutherland 1996, Travis et al. 1999, Hanski 2003) and increase mean individual fitness.

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