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NATAL DISPERSAL AND DEFERRED BREEDING IN THE BLUE-FOOTED BOOBY

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ABSTRACT.—Male Blue-footed Boobies (*Sula nebouxii*) first nested at an age of two to six years ($\bar{x} = 4.7$), and females a little earlier at one to six years ($\bar{x} = 3.6$). Both sexes nested selectively close to the natal site in their first reproduction (males 24.1 m, females 28.3 m) and similarly close to the natal site in their second reproduction, despite displacement from first to second site. First sites of both sexes were similarly close to the natal site and the parents' current site, and parents dispersed only 26.2 m between hatching and first reproduction of their offspring. Throughout their lives, both sexes may tend to nest close to the natal site and, hence, close to kin. Nonetheless, given high nest density in the colony (0.0356 nests/m^2) and high variance in natal dispersal (males, SD = 33.1 m; females, SD = 35.2 m), inbreeding and social interactions with kin are unlikely to result. Overall, these results do not support the hypothesis that philopatry in some marine birds and other animals functions to achieve an optimal balance between inbreeding and outbreeding. *Received 3 October 1991, accepted 28 May 1992.*

THE DISTANCE moved by a bird from the nest site where it hatched to the nest site of its own first reproduction (natal dispersal) may have an important influence on gene flow between and within populations, and on the evolution of social behavior (e.g. Mayr 1963, Greenwood et al. 1979a). Limited dispersal (philopatry) is common in birds and, in most species, females disperse farther than males (Greenwood et al. 1978, Greenwood 1983). It has been proposed that limited dispersal and mate choice function to ensure a moderate level of inbreeding (optimal inbreeding/outbreeding; Shields 1982, 1983, Bateson 1982, 1983), to conserve coadapted gene complexes, or to maintain adaptation to local conditions (but see Ralls et al. 1986).

Colonial marine birds often breed in dense congregations of small territories that appear bare and homogeneous and are used only for raising offspring. In contrast, territories of the more frequently studied terrestrial species are large, complex and used also for feeding. Intuitively, previous experience of a nest territory is less likely to benefit a colonial marine bird than many passerines and other birds that can learn about the distribution of food, refuges, and dangers in a territory and its vicinity (e.g. Greenwood and Harvey 1976, Eden 1987). Consequently, Shields (1982, 1983) interpreted limited natal dispersal in the Laysan Albatross (*Diomedea immutabilis*; Fisher 1976) as evidence of selection for breeding with kin. In the present study we assessed whether the pattern of natal and breeding dispersal of Blue-footed Boobies (*Sula nebouxii*) is such as to promote interactions and matings with kin.

Most species of the Sulidae (gannets and boobies) are known to disperse or migrate over great distances from the natal colony. However, most individuals probably establish their first nest in the same colony a few years later (Nelson 1978). If these long-lived birds show long-term attachment to the natal site, cooperative or competitive associations with kin could result. In order to investigate this possibility, we described the natal and breeding dispersal (movement between sites of successive breeding attempts) of both sexes of the Blue-footed Booby and related dispersal to colony nest density. We also evaluated whether boobies continue to disperse away from the natal site after their first reproduction and whether offspring nest near their parents.

Our data are the first quantifications of natal dispersal and age of first reproduction in the Sulidae based on marked nestlings. Natal dispersal of individual marine birds within colonies has rarely been measured and has not previously been related to dispersal of kin or nest density.

The Blue-footed Booby nests colonially on tropical Pacific islands on ground that is bare or studded with trees or boulders, and not steeply inclined. Males establish nesting territories and females, which are 27% heavier, choose among males (Nelson 1978). Both sexes incubate the clutch of one to three eggs during 41 days and feed the brood during 18 weeks or more (Nelson 1978).

METHODS

The seven-year study (1982–1988) was made at the colony on Isla Isabel, Mexico (21°52′N, 105°54′W), that had more than 400 breeding pairs of Blue-footed Boobies in two subcolonies (Fig. 1). Territory diameters on the island vary from about 2 m in the egg stage to about 4 m when chicks become mobile (Osorno and Gonzalez 1987). Nests are several meters apart in much of the colony, but there are clumps of nests where nearest neighbors are on average 2 m apart (Castillo and Chavez-Peon 1983).

A 15,000-m^2 section of forest was divided into plots of roughly 20 × 20 m defined by the trees at their corners. The study area encompassed dense nesting areas near the forest edge, as well as sparse areas in the forest interior (Fig. 1). It was mapped with precision and the marker trees were numbered permanently to serve as reference points for recording the distance (nearest 10 cm) and direction (nearest 2°) of the center of each nest site.

During March to June every year from 1982 through 1988, we marked every nest (scrape containing eggs or chicks) with a numbered peg up until the time most chicks in the colony fledged. We inspected nests: every three days in 1982, 1984 and 1987; every four days in 1983; daily in 1985; every six days in 1986; and during two isolated visits, late in the hatching period and early in the fledging period, in 1988. Chick sex was not known, but adults were reliably sexed by vocalization (males whistle and females grunt; Nelson 1978).

Birds were individually marked using three colored PVC bands. During 1982 through 1985 we banded all chicks that reached six weeks of age; during 1987 and 1988 we banded only six-week-old chicks from broods that started out with two chicks. During 1982 and 1983, we banded all nesting adults; in 1984 we banded only adults whose mate was already banded. The numbers of chicks and adults, respectively, marked in each year were: (1982) 130, 237; (1983) 14, 170; (1984) 194, 18; (1985) 57, 0; (1986) 0, 0; (1987) 94, 0; and (1988) 158, 0. Uneven selection of chicks and adults for banding in different years was due to shortage of personnel and bands. It should not introduce any systematic bias because: (1) to estimate ages and proportions of chicks that nest in the colony, we used only the large cohort of chicks marked in 1982, which had the longest period to start breeding (cohorts of other years were included only for estimating range of ages and estimating dispersal distances); and (2) the chicks from two-chick broods in the last two years did not attempt reproduction, and are mentioned only for completeness. Failure to band some adults should only have the effect of reducing some sample sizes in analyses of dispersal.

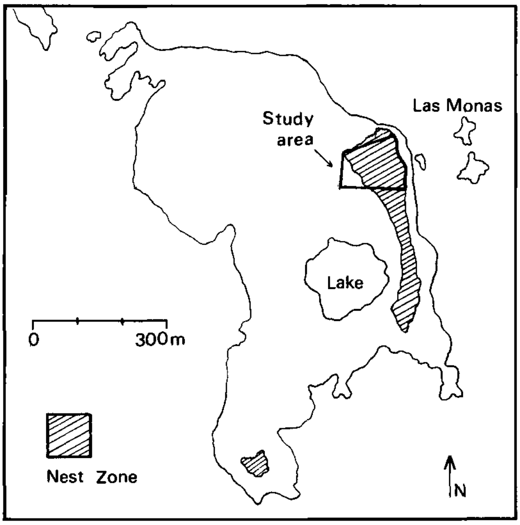

Fig. 1. Isla Isabel, showing two Blue-footed Booby subcolonies and study area near Las Monas sea stacks.

In every year we noted and verified the band numbers of both adults at every marked nest. To detect marked birds possibly nesting outside the study area, the whole colony was scanned with binoculars roughly twice a month during every breeding season. In addition, in every breeding season we spent several weeks conducting behavioral observations and experiments in the colony outside the study area, which gave extensive opportunity to detect adults with bands.

First breeders making a random choice among available nest sites could nest "close" to the natal site by chance. Therefore, we calculated an expected dispersal distance for each bird under the null hypothesis that it was equally likely to settle on any of the sites used in the same year by its peers, namely first breeders of the same sex. Expected dispersal was the mean of the distances between each bird's natal nest site and the first nests of all recorded peers (it could not be calculated for two males in 1987 and 1988 because there were no known peers). This is a conservative test, since it excludes peers with natal sites outside the study area.

RESULTS

Of 130 chicks marked in 1982, 23.1% had attempted reproduction (were recorded with eggs or chicks) by 1988, comprising 9 males and 21 females. In 1988 only one male and one female of this cohort nested for the first time, implying that recruitment of both sexes was ending after six years. Female bias in recruitment from the

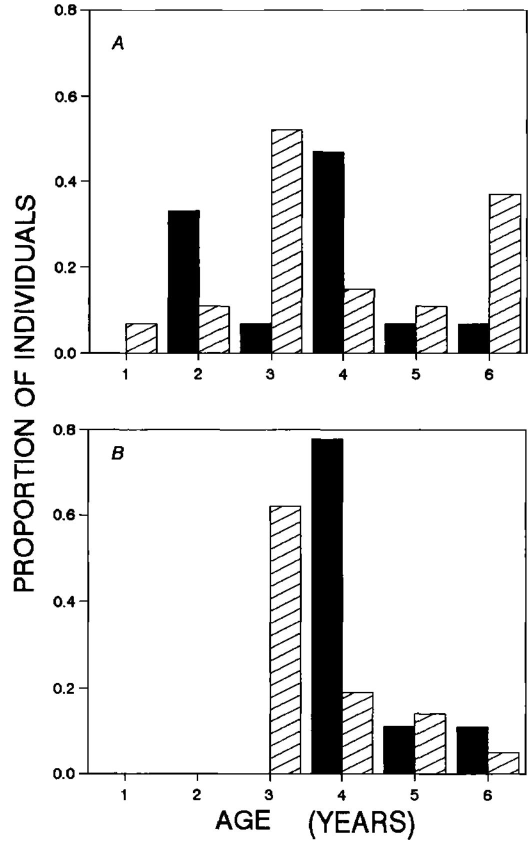

Fig. 2. Age of first reproductive attempt of males (solid bars) and females (shaded bars) fledged: (A) during 1982-1986 (15 males and 27 males); and (B) in 1982 (9 males and 21 females).

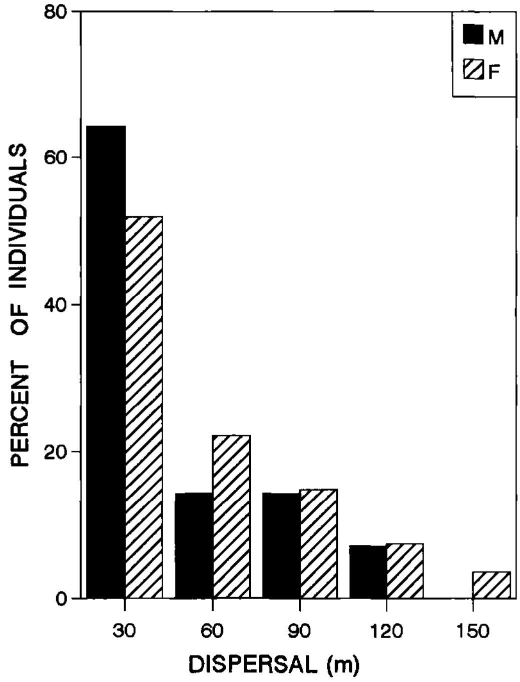

Fig. 3. Natal dispersal for 14 males (M) and 27 females (F) grouped in 30-m intervals.

1982 cohort into the breeding population was not significant ($G = 2.45$, $df = 1$, $P > 0.05$). Six females and six males banded as chicks after 1982 also attempted reproduction during the study.

In the 1982 cohort, first reproduction by females was significantly earlier than by males (Mann-Whitney test, $U = 45$, $P = 0.01$; Fig. 2); females of this cohort nested first at three to six years ($\bar{x} = 3.6 \pm$ SD of 0.90, $n = 21$) and males at four to six years ($\bar{x} = 4.7 \pm 0.90$, $n = 9$). Based on chicks banded in all years, the range of ages of first reproduction was one to six years for females and two to six years for males (Fig. 2). In 1982 and 1983, there was a severe El Niño oceanographic event, which may have discouraged the 1982 cohort from nesting in their first two years.

All first nests of males and females that we found were in the natal subcolony and located in or adjacent to the study area (including the nest of one male that was not mapped through oversight). Males and females, respectively, nested at a median distance of 24.1 m ($\bar{x} = 33.1 \pm 33.1$ m, $n = 14$) and 28.3 m ($\bar{x} = 40.8 \pm 35.2$ m, $n = 27$) from the natal site. There was no significant difference in the mean natal dispersal of the sexes ($P = 0.36$, $z = -0.907$, Mann-Whitney test), and the ranges of their dispersal distances were similar, with males dispersing 2.0 to 110.8 m and females 4.1 to 149.8 m (Fig. 3).

The mean expected dispersal distance for males was 45.6 m, and 10 of 12 moved less than their individual expected distance ($P < 0.02$, one-tailed sign test); the mean expected distance for females was 45.2 m, and 21 of 27 were closer than expected ($P = 0.06$). Hence, within the natal subcolony males and, perhaps, also females nested closer to their natal site than would be expected by chance.

Did each successive breeding attempt involve progressive dispersal away from the natal site? Thirteen birds marked as chicks nested twice during the study—five males and eight females that nested in the natal subcolony in two suc-

Table 1. Distance (m) moved away from natal site for first and second breeding attempts.

	Natal site to		First nest to second nest
	First nest	Second nest	
	Males ($n = 5$)		
Median	21.9	29.6	54.7
Mean	33.2	33.9	43.3
SD	44.6	18.0	18.4
	Females ($n = 8$)		
Median	27.9	30.9	18.9
Mean	47.1	44.5	28.5
SD	49.9	36.4	35.0

cessive years. The distance between the natal site and the second site for both sexes was similar to the distance between the natal site and the first site, despite substantial movement between first and second sites (Table 1).

We also examined the distance between first breeders' nest sites and their parents' current nest sites, using the 21 birds that nested for the first time in a year when one or both parents also nested. These first nesters selected sites that on average were at similar distances from their natal and parental sites (Fig. 4). Sites of the seven males were an average 47.4 ± 43.0 m from the parental site and 38.4 ± 29.5 m from the natal site (median = 34.1, 32.3, respectively; $P = 0.40$, $T = 9$, Wilcoxon test). Sites of the 14 females were an average 28.2 ± 20.4 m from the parental site and 32.6 ± 26.3 m from the natal site (median = 26.0, 23.7, respectively; $P = 0.43$, $T = 65$). Parents themselves showed limited breeding dispersal; when chicks first nested, their parents were nesting an average 26.2 ± 21.2 m ($n = 21$) from the site where the chicks were hatched.

During 1982 to 1986, mean nest density for the study area (excepting five interior plots that never held a nest) was 0.0356 ± 0.0068 nests per m^2. Hence, within a male or female's median radius of natal dispersal there were on average 65 or 90 nests, respectively, in the season he/she nested.

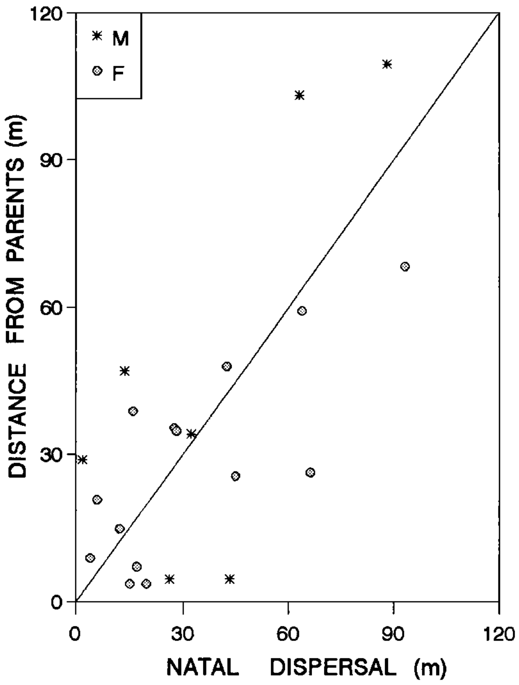

Fig. 4. Natal dispersal and proximity of parents. Distance from bird's first nest site to: (1) its natal site; and (2) its parents' current site. Male (M) and female (F) birds. Birds above diagonal nearer to natal site; birds below diagonal closer to parents' site.

Discussion

Female Blue-footed Boobies first nested at one to six years, and males at two to six years. Therefore, deferred breeding in this species shows high individual variation similar to that reported for some other marine birds (e.g. Mills 1989, Wooller et al. 1989). Even females fledged in the same season varied by as much as three years and males by as much as two years. There was no apparent shortage of nest sites in the colony, and it is unlikely that both sexes have to postpone breeding simply for lack of potential partners. More likely, all boobies delay reproduction at least until they have acquired advanced foraging skills (Nelson 1977). High variation in age of first breeding attempt could reflect great individual variation in physical condition or foraging skills or, alternatively, different strategies for maximizing breeding success over a long lifetime. Males may delay one year longer than females on average because delayed maturity or intrasexual competition prevent them mating earlier, but there are no data in support of this supposition.

Outside the study area, the checks twice weekly and incidental checks during experiments may not have been sufficient to detect all nests of marked birds, but finding none at all outside the study area indicates there were probably very few. We cannot tell whether some chicks nested on other islands, which were not monitored. In the North Atlantic Gannet (*S. b. bassanus*), the only sulid whose natal dispersal has been studied, 95% of chicks that returned to breed went to their group of origin (Nelson 1978). Therefore, we suspect that natal dispersal of Blue-footed Boobies to other colonies is on a small scale, and that mortality accounts for most chicks that did not return to Isla Isabel. If this is correct, then both sexes of this booby are highly philopatric and roughly three-fourths of nestlings that survive to at least six weeks of age die before attempting reproduction one to six years later. However, this proportion is very approximate, being based on a single cohort of chicks that fledged just months before the severe El Niño event of 1982–1983. El Niño events occur every few years in the Pacific, and they can seriously prejudice the reproduction and survival of marine birds (e.g. Schreiber and Schreiber 1984).

If the only factor influencing breeding dispersal was the last site occupied, then boobies on average should stray progressively farther from the natal site with each successive breeding attempt. On average this did not happen; hence, the breeding dispersal of both sexes probably was influenced by cues from the natal site itself, or habitat features or clumps of nests near the natal site. Clumps of nests could arise from conspecific attraction or common response to spatial variation in habitat. Equal proximity to parents' current site and natal site could arise through social attraction between parents and offspring or, more simply, through parents and offspring responding similarly to the same habitat features or clumps of nests.

The limited natal dispersal and breeding dispersal of both chicks and parents indicate that both sexes nest close to the natal site during many years. At first glance, this should lead to spatial association of relatives within the subcolony. However, given that the median natal dispersal of males and females carried them past an average 65 or 90 nests, respectively, and that both sexes showed relatively high variance in natal dispersal, close relatives probably pair infrequently (unless mate choice favors relatives). There is no reason to expect that parent–offspring and full-sib pairings exceed the low frequencies of 0.0 to 3.2% estimated for most other species of birds (Ralls et al. 1986), and indeed no such pairings were detected. Consequently, it is unlikely that limited dispersal either functions to achieve optimal inbreeding/outbreeding or incidentally leads to moderate inbreeding (note contrary conclusions for Laysan Albatross in Shields 1982). Similarly, this limited dispersal should not lead to kin-selected behavioral cooperation among neighboring pairs (discussed in Greenwood et al 1979b).

Then what, if any, is the function of limited dispersal in the Blue-footed Booby? Nesting near the natal site may be beneficial because that site is of good quality, as proven by the chick's own successful fledging (Ghiselin 1974, cf. Ashmole 1962), or even because habitat familiarity helps a first breeder (Lack 1954, Greenwood 1980). The terrain in the colony is heterogeneous, with trees, shrubs, bare ground, grass and rocks, implying variation in site quality. For example, particular locations vary in the proximity and suitability of spots for taking off and landing (difficult maneuvers for boobies) and may be subject to different probabilities of predation by milk snakes (*Lampropeltis triangulum*), a common cause of chick deaths on Isla Isabel (Drummond et al. 1986, 1991). Areas where breeding is risky because of factors which cannot readily be assessed before egg laying (e.g. predation and parasitism) may be best avoided by relying on the earlier experience of one's parents.

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