

## Limited dispersal by Nazca boobies *Sula granti*

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We documented natal and breeding dispersal at several spatial scales by Galápagos Nazca boobies *Sula granti*, a wide-ranging pelagic seabird. We found exceptionally low degrees of both types of dispersal despite these birds' vagility. Median natal dispersal distances were 26 m and 105 m for males and females, respectively. Median breeding dispersal distances for both sexes were 0 m. No natal or breeding dispersals occurred from our study site at Punta Cevallos, Isla Española to six other colonies in the Galápagos, but we did document four long-distance natal dispersals from Punta Cevallos to islands near the South American coast. Recaptures and dead recoveries of ringed birds showed long distance non-breeding movements to the Central American coast and elsewhere in the eastern Pacific, contrasting with the very limited dispersal to breeding sites.

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Natal and breeding dispersal are important life history traits, affecting source-sink dynamics, gene flow, and other population-level phenomena. Seabirds typically range widely during their normal foraging movements, yet natal dispersal (from natal nest site to first breeding site; Greenwood and Harvey 1982) in seabirds is generally short distance, with many birds settling within a few hundred meters of their natal site (e.g. Osorio-Beristain and Drummond 1993, Aebischer 1995, Spear et al. 1998). Breeding dispersal (between breeding attempts; Greenwood and Harvey 1982) occurs, but typically from site to site within colonies, and not on larger scales (Spendelov et al. 1995, Danchin et al. 1998). Low natal and breeding dispersal may thus restrict gene flow and colonization ability in otherwise highly mobile organisms such as seabirds.

Phylogeographic studies of bird taxa have relied on the traditional model of vicariance-driven differentiation (Mayr 1963, 1970). However, Irwin (2002) recently analyzed cases of phylogeographic breaks without apparent barriers to gene flow, and concluded that the likelihood of observing such breaks in distribution increases as individual dispersal distance decreases. This emphasis on dispersal distance as a pre-zygotic isolating mechanism may illuminate recent phylogeographic pat-

terns in boobies (Family Sulidae). Masked boobies *Sula dactylatra* and Nazca boobies (*S. granti*; AOU 2000) are sister taxa of the eastern tropical Pacific that diverged ~500,000 years ago, apparently without any physical barriers to gene flow (Friesen and Anderson 1997, Friesen et al. 2002, Steeves et al. 2003). Nazca boobies nest primarily on the Galápagos Islands and Malpelo Island, in the eastern equatorial Pacific, while masked boobies nest throughout the rest of the tropical Pacific, including the Revillagigedo Islands off the Mexican coast and on Clipperton Island, NE of Galápagos. In this paper we characterize natal and breeding dispersal in Nazca boobies and evaluate the potential for low dispersal to restrict gene flow to and from populations of masked boobies.

### Methods

#### Ringling and recapture

We have studied the breeding biology and demography of Nazca boobies since 1984 at a breeding colony at Punta Cevallos, Isla Española, Galápagos Islands (1°20' S, 89°40' W; Fig. 1). Breeding at this site is seasonal,

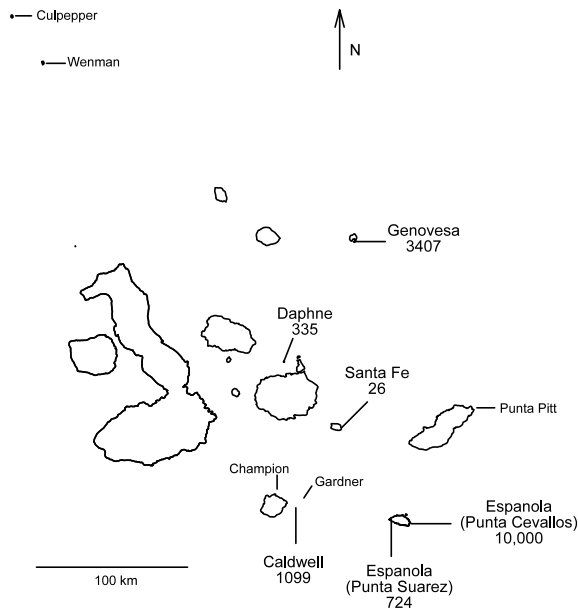


Fig. 1. Nazca booby colonies in the Galápagos Islands. Island names with estimated population sizes (adjusted as described in Methods) beneath were searched for ringed birds. Approximate population sizes of other islands: Champion, < 50; Gardner and Punta Pitt, 100–200 each; Culpepper and Wenman, 1000–several thousand each (Nelson 1978, Anderson unpubl. data).

with laying in Oct.–Jan. and most fledging completed by June of the next year. We refer to breeding seasons by the year in which the season began. Nesting occurred in a series of subcolonies in coastal habitat and we studied birds in three subcolonies (No. 1, 2 and 3; Fig. 2). Subsets of the Punta Cevallos population were ringed every breeding season (except 1988) since 1984.

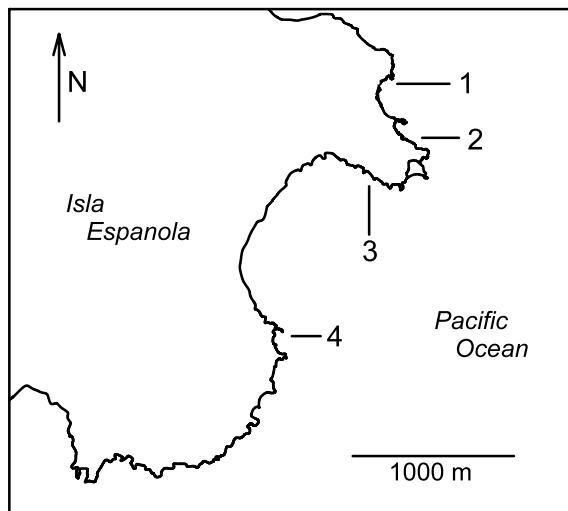


Fig. 2. Nazca booby subcolonies in the eastern region of Punta Cevallos, Isla Española. Subcolonies 1–3 were surveyed for ringed birds (see text); subcolony 4 was not surveyed.

In all seasons (except 1989 and 1990), we or our assistants marked juvenile birds ( $\geq 40$  d post-hatching) with aluminum or steel leg rings. Adults were ringed in 1984–1985, 1987, and 1992–1994. In total, 4,948 chicks and 1,928 adults were ringed between 1984 and 1999. Of these, 1,680 nestlings and 1,090 adults were initially marked with aluminum rings. We added a steel ring to birds carrying aluminum rings when they were first recaptured after 1992 since some aluminum rings were noticeably worn. We estimated ring retention rates in 128 birds marked 6–10 years earlier with two aluminum rings and in 45 birds marked 7.5 years earlier with two steel rings. The proportion of rings retained over 7.5 years was calculated as:

$$z/(z + 1/2w)$$

where  $z$  = no. of double-ringed birds still wearing two rings and  $w$  = no. of double-ringed birds now wearing only one. Per year ring retention rate was estimated by solving for  $x$  in the expression:

$$x^y = a$$

where  $x$  = per year retention rate for years of interest (assumed constant across years),  $y$  = number of years between double-ringing and resighting, and  $a$  = proportion of birds bearing two rings after  $y$  years.

Presence in the colony was assessed through whole-colony recapture surveys on 5–10 consecutive nights at the beginning of each annual breeding season. We conducted surveys at night because the density of birds is higher at night, and birds are easier to capture at night than during the day. Birds were caught by hand and given a temporary spray paint mark (i.e. recaptured without “replacement” in a given year). We estimated the efficiency of the recapture surveys for the years in which most dispersal data were collected (1994–1998) using the ratio of actual number of birds caught to the estimate of the ringed population size from a removal model in Program CAPTURE (Otis et al. 1978). We assumed that the ringed birds represented a closed population since both natal philopatry and breeding site fidelity were very high, and few birds from this colony were seen in surveys elsewhere in Galápagos (see Results).

### Estimating dispersal distances

During the breeding seasons between 1983–1985 and 1991–1998, breeding data were collected for every ringed bird in the three subcolonies at Punta Cevallos, including the location of each nest site. We collected location data at two levels of precision. From 1983–1993, we plotted the locations of nests in subcolony 1 only on a Cartesian coordinate map of the Punta

Table 1. Recapture survey efficiency for four recapture surveys at the beginning of the breeding season. Efficiency is ratio of number of ringed birds caught to the CAPTURE estimate of actual number of ringed birds.

Year of survey	Duration (days)	# Ringed birds recaptured	CAPTURE estimate of # ringed birds	Efficiency
1994	5	1,223	1223 ± 0.72	1.0
1995	5	1,432	1441 ± 4.76	0.994
1996	6	1,569	1578 ± 4.73	0.994
1997	7	1,610	1611 ± 1.82	0.999

Cevallos area with a precision of 5 m. From 1994–1998 we used a more accurate map, with a precision of 1 m, providing nest locations in subcolonies 1, 2 and 3. We refer to these nest locations with 1 and 5 m precisions as “high precision”. Until 1994, we noted in which subcolony ringed birds nested during annual ring recapture surveys (“subcolony precision”), to complement the high precision data from subcolony 1. We used subcolony and high precision data for separate estimates of natal dispersal distance.

To detect dispersal to other sites in the Galápagos, we visited Nazca booby breeding colonies on four other islands (Caldwell, Daphne, Genovesa, and Santa Fé) and the colony at Punta Suárez, the west end of Isla Española (Punta Cevallos is at the east end) in December 1998. At Caldwell, Daphne, and the west side of Genovesa, we checked each bird for rings over 2–5 consecutive nights, and estimated our recapture efficiency by marking every bird found on each of 2–3 consecutive nights in a subsection of each colony. We estimated the actual population size of each subsection with a removal model, again using Program CAPTURE. As with the data from the Punta Cevallos population, we estimated the recapture efficiency for that colony as the ratio of actual number of birds caught in the subsection to the CAPTURE estimate of the subsection’s population size. We estimated the total population size of these colonies by counting all birds present on the first night, and dividing that number by the recapture efficiency for that colony.

At Santa Fé, Punta Suárez, and the east side of Genovesa, we checked each colony on one night only. For Santa Fé, we adjusted the total population size using the mean recapture efficiency from the Caldwell, west Genovesa and Daphne colonies, and for east Genovesa we made the same adjustment using the mean recapture efficiency for west Genovesa, and for Punta Suárez we made the same adjustment using the mean recapture efficiency for Punta Cevallos (located at the opposite end of the same island). Finally, we increased the estimate of total population size for east Genovesa by 15% and for west Genovesa by 7.5%, based on our subjective estimates of the fraction of birds in inaccessible locations. At each of these Nazca booby colonies we checked the bill color of birds present to detect immigration of masked boobies. During each breeding season since 1983 (excluding 1988) we searched the Punta Cevallos colony for birds with *dactylatra* phenotypes.

To detect dispersal to Punta Cevallos, we ringed 250 near-fledgling chicks in the Genovesa colony in December 1998 and then checked subsequent annual ring recapture surveys at Punta Cevallos for their presence.

Ring recoveries of non-breeding birds present outside Galápagos were compiled from band returns directly to us, and from returns sent to the US Bird Banding Laboratory (Laurel, MD).

### Statistical analyses

Statistical analyses were performed with Statistica (v. 5.5; StatSoft, Inc. 1999). Parametric tests of significance were conducted when assumptions were met. In other cases (e.g. strongly left-skewed frequency distributions of dispersal distance) we used non-parametric methods. All statistical inferences are based on P-values from two-tailed tests. Calculations of binomial confidence intervals followed Zar (1999).

## Results

### Ringling and recapture efficiencies

The estimated per year retention rate for aluminum rings aged 6–10 years (rings that had already survived 6–10 years of wear on a bird) was 0.982. The retention rate for 8 year-old stainless steel rings was 1.

At Punta Cevallos, initial visits to an area produced the majority of recaptures and subsequent surveys yielded a regularly diminishing number of recaptures. Modeling efforts using CAPTURE indicated that an average of 4.8 (range 0–14) ringed birds were missed per annual survey at the Punta Cevallos colony. Efficiencies ranged from 0.994–1.000 (Table 1). On Genovesa, Caldwell, and Daphne, efficiencies from less exhaustive counts were 0.751, 0.644, and 0.473, respectively. Total nighttime counts at each colony were adjusted using these efficiencies (Fig. 1; see Methods).

### Natal dispersal within the Punta Cevallos area

Nazca boobies at Punta Cevallos nest within 40 m (typically within 15 m) of the coastal cliff (Townsend et al. 2002) and rarely fly across land (pers. obs.), so

dispersal within the Punta Cevallos area is essentially linear along the coastline. Of 119 birds with high precision natal and first breeding locations, median natal dispersal distance of females (105 m, range 3–1293 m) exceeded that of males (26 m, range 1–1161 m; Mann-Whitney U-test = 854,  $N_1 = 42$ ,  $N_2 = 77$ ,  $P < 0.0001$ ; Fig. 3a). Most natal dispersal distances were less than 256 m, and within this group, females dispersed significantly farther (median = 57 m) from their natal nest than did males (median = 19 m; Mann-Whitney U-test = 364,  $N_1 = 34$ ,  $N_2 = 51$ ,  $P < 0.0001$ ). Among 525 birds providing data with subcolony precision, 122 of 284 females (0.43) settled outside their natal subcolony, while only 74 of 241 males (0.31) did so ( $G = 8.43$ ,  $df = 1$ ,  $P < 0.005$ ).

### Breeding dispersal within the Punta Cevallos area

We analyzed only high precision data on breeding dispersal, since only one of 198 breeding dispersals (0.5%) was between subcolonies. That male moved 388 m between consecutive breeding attempts. All other breeding dispersals were to nearby nest sites, within 25 m of the bird's previous site (Fig. 3b).

We calculated the mean breeding dispersal distance for each bird during the years 1995–99 and then the

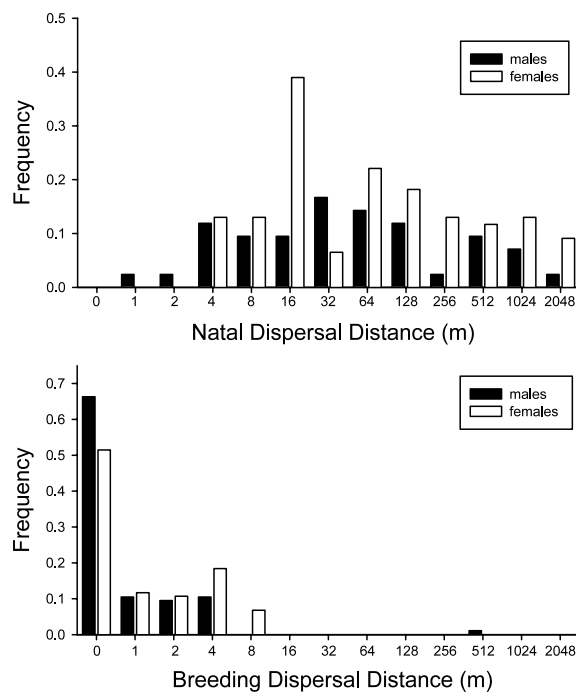


Fig. 3. a) Natal dispersal distances of 42 male and 77 female Nazca boobies. Omitting three natal dispersals to the South American coast, the maximum natal dispersal was 1293 m. b) Mean annual breeding dispersal distances of 94 male and 103 female Nazca boobies across the period 1994–95 to 1998–99. The maximum dispersal distance was 388 m.

median of these values by sex. Females dispersed farther than males did (Mann-Whitney U-test = 3853.5,  $N_1 = 94$ ,  $N_2 = 103$ ,  $P = 0.005$ ), although the median was zero for both sexes. For birds that did move between sites, the median of these values for females (2.7 m) exceeded that for males (1.7 m; Mann-Whitney U-test = 504.5,  $N_1 = 32$ ,  $N_2 = 50$ ,  $P = 0.005$ ). The proportion of breeding seasons in which a bird changed nest sites during 1995–99 did not vary by sex (63.5% of males and 52.5% of females did not move at all in a typical year;  $G = 5.76$ ,  $df = 4$ ,  $P = 0.23$ ). The ringed population's age structure provided many breeders < 5 years old ("younger" birds) and > 8 years old ("older" birds), but not birds 5–8 years old. Younger birds dispersed farther (median = 5.2 m) than did older birds (median = 0.0; Mann-Whitney U-test = 156,  $N_1 = 13$ ,  $N_2 = 76$ ,  $P < 0.0001$ ). Similarly, a larger proportion of younger breeding birds (0.85) dispersed than of older breeding birds (0.25;  $G = 15.09$ ,  $df = 1$ ,  $P < 0.0001$ ).

### Dispersal beyond the Punta Cevallos area

We detected no permanent emigrants during recapture surveys within the Galápagos Archipelago but outside the Punta Cevallos colony in 1998. Two ringed birds were recaptured during these surveys, and in both cases, they were apparently non-breeding visitors, roosting at the edge of the colony with other non-breeders. One of them was recaptured 14 km away at Punta Suárez, at the western end of Española, and had been recorded during a recapture survey at Punta Cevallos six days earlier. This bird was apparently based at Punta Cevallos, since it has been recorded in every annual ring recapture survey there from 1997 to 2001. The second bird was recaptured on Genovesa in the northeastern part of the archipelago, 200 km from its natal colony, and was seen seven days later back at Punta Cevallos. This bird then bred at Punta Cevallos in the following year. No ringed birds were recaptured at Islas Caldwell, Daphne, or Santa Fé. These five sites, plus Punta Cevallos, comprise most Nazca booby breeding colonies in the eastern Galápagos. We did not survey the small colonies on Islas Gardner, Champion, San Cristobal (Punta Pitt), nor the large colonies on Islas Wenman and Culpepper, to the northwest of the main island group (Fig. 1).

Between 1985 and 1999 we determined the breeding site of 755 Nazca boobies ringed as nestlings at Punta Cevallos. Four birds ringed at Punta Cevallos were recaptured breeding outside the Galápagos Archipelago during whole-island ring recapture surveys: one male and one female at Isla de la Plata in mid-1998 (858 km from Punta Cevallos; V. Cano, pers. comm.) off the Ecuadorian coast and two other unsexed birds at Isla Lobos de Afuera in early 2000 (1155 km from Punta Cevallos; J. Figueroa pers. comm.; Fig. 4) off the

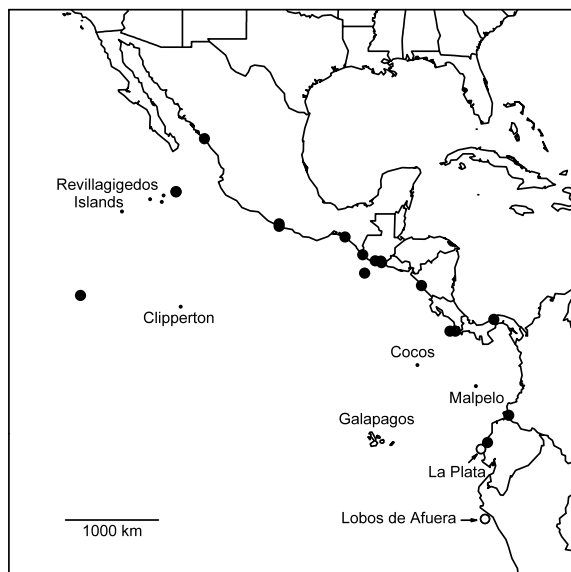


Fig. 4. Nazca boobies ringed as residents of Isla Española and resighted alive as breeders in a colony outside Galápagos (open circles), or resighted alive or recovered dead away from breeding colonies outside Galápagos (closed circles). Nazca boobies breed on Galápagos, Malpelo, La Plata, Lobos de Fuera, and in small numbers on the Revillagigedos and Clipperton. Masked boobies breed on the Revillagigedos and Clipperton.

Peruvian coast. All four birds were ringed as nestlings and never recaptured at Punta Cevallos, so these represent natal dispersals. The estimated probability of natal dispersal to another colony was 0.0040 (95% CI = 0.0008–0.0194). This estimate was confounded by unequal sampling effort: Punta Cevallos was sampled annually, the other Galápagos sites in late 1998 only, Isla de La Plata approximately annually, and the Peruvian islands in early 2000 only. To standardize sampling effort, we assumed that each of these four birds had dispersed to its present location before the time of our ring recapture survey in December 1998. During the 1998 breeding season, 316 birds ringed as nestlings at Punta Cevallos bred at Punta Cevallos. Thus, our most realistic estimate of natal dispersal outside the breeding colony was 4/316 (0.013; 95% CI = 0.0035–0.0318). While we did not search two large remote colonies (> 1,000 birds, Wenman and Culpepper; Fig. 1) and several small colonies (< 200 birds, other colonies without population size estimates in Fig. 1), we found no natal dispersals to the islands that we did search. Since the islands that we did search include most of the breeding birds within the main archipelago (excluding Wenman and Culpepper) and a representative selection of island sizes, population sizes, and distances from Punta Cevallos, we assume that dispersal to these other sites was also zero.

Above we reported that no permanent emigrants were detected at other colonies within the Galápagos, and neither we nor our collaborators detected breeding dispersals to sites outside Galápagos. A total of 1,845 ringed adults had bred at least twice at Punta Cevallos up to 1999, and so could have dispersed away from Punta Cevallos between breeding attempts, but did not. Our data thus indicate that the probability of dispersing to a different colony between breeding seasons is 0 (95% CI = 0–0.002).

#### Range of birds outside Galápagos

We have received ring returns outside Galápagos from 17 Nazca boobies ringed by us in Galápagos in addition to the four that bred on the South American coastal islands, and one additional return from a bird banded on Isla Española before our study (M. Harris pers. comm.). Five returns were of birds that landed on fishing boats at sea, and the others were from coastal areas of Mexico and Central and South America (Fig. 4). One of the coastal recoveries was from the Caribbean mouth of the Panama Canal. Fourteen birds were pre-breeding sub-adults ( $\leq 3$  yrs old) and four were breeding-age adults between 7–22 years old. Of the four adults, three were not breeding at Punta Cevallos at the time that they were recovered, although one had bred there regularly in previous years; the breeding history of the fourth adult is not known.

#### Discussion

Galápagos Nazca boobies present a paradoxical pattern of dispersal. In comparison to data available from other colonial seabirds, in which the probabilities of natal dispersal to a different population range from 1–90% (reviewed by Frederiksen and Petersen 2000), our study population disperses as infrequently as the most philopatric species (wandering albatross *Diomedea exulans*; Croxall and Rothery 1991, Inchausti and Weimerskirch 2002). Breeding dispersal appears to be rare also. On the other hand, we documented natal dispersal of Nazca boobies to islands near the South American coast. While these dispersals are within the breeding range of Nazca boobies, they show that rare individuals from Punta Cevallos do make long distance dispersals on a scale that could extend into the breeding range of masked boobies. Thus, natal philopatry and breeding nest site fidelity severely limit gene flow, but do not preclude it. Sub-adult birds vacate the Galápagos from fledging until at least age 3 (Huyvaert and Anderson unpubl. data), and some breeding-age birds are not seen at the breeding colony for periods of many months. Ring returns indicate that the ocean north of Galápagos is an important destination for these absent

birds, taking them into the breeding range of masked boobies at Clipperton and the Revillagigedos Islands (Fig. 4). Our principal result is that the mobility of Nazca boobies is  $10^3$ – $10^4$  times greater than their usual natal and breeding dispersal: at least some Nazca boobies visit the home range of masked boobies 2000–3000 km from Galápagos, yet generally nest within 500 m of their natal nest site.

Interbreeding by Nazca and masked boobies would probably produce viable offspring, since masked boobies evidently produce adult, breeding offspring with brown boobies *S. leucogaster* (Dorward 1962, Nelson 1978, p. 814), and masked and Nazca boobies have a lesser genetic distance than masked and brown boobies do (Friesen and Anderson 1997). Unfortunately, little is known of the breeding biology of these species at the few sites of breeding sympatry, and what is known indicates porous pre-mating isolation at joint breeding sites. On Clipperton Island (Fig. 4), 12 or more Nazca boobies nested with a masked booby population that was over 400 times larger, and while all Nazca boobies bred homotypically, a thirteenth bird appeared to be a hybrid offspring (Pitman and Jehl 1998). On San Benedicto Island in the Revillagigedos (Fig. 4), Howell and Webb (1990) found four Nazca boobies present and two of these four breeding, and at least one of these two bred with a masked booby. An apparent hybrid adult was seen on San Benedicto the previous year (Pitman and Jehl 1998). We can tentatively conclude that Nazca boobies nesting within the masked booby range breed heterotypically at an appreciable frequency.

The opportunity for such heterotypic mate choice is limited, but not precluded, by low dispersal of each species into the other's range limits, since we documented rare long-distance natal dispersals of 858 km (two cases) and 1155 km (two cases) (although within the Nazca booby range). Natal dispersal on this scale could place Punta Cevallos Nazca boobies at the nearest masked booby breeding site (Clipperton, 2300 km away), and ring recoveries show that Galápagos Nazca boobies make pre-breeding and non-breeding movements well into the masked booby breeding range (Fig. 4; see also Roberson 1998). However, data from Clipperton indicate that many more Nazca boobies enter the masked booby range than breed there: the twelve breeders were accompanied by approximately 138 non-breeders (Pitman and Jehl 1998). This suggests that Nazca boobies may frequently move into the masked booby range, but seldom actually breed there due to the high philopatry that we have demonstrated. The available data suggest that the positive assortative mating reported by Pitman and Jehl (1998) is incomplete, and high philopatry is a more important (but also incomplete) factor restricting gene flow between Nazca and masked boobies.

The high degree of fidelity to the natal colony remains to be explained, given the high vagility of these birds. A number of hypotheses exist to explain variation in avian natal and breeding dispersal, involving ecologically-determined reproductive success at local vs. distant sites (e.g. Danchin et al. 1998), socially-determined competitive abilities (e.g. Van der Jeugd 2001), inbreeding considerations (Shields 1987, Crnokrak and Roff 1999), and other factors (Greenwood and Harvey 1982, Paradis et al. 1998). Most of these factors operate at a small spatial scale, such as within the breeding colony, and so may well apply to the remarkably low dispersal documented in this study. Local adaptation to Galápagos conditions, involving such factors, may have favored philopatry. The Galápagos Islands support a high degree of seabird endemism, with four endemic species (Galápagos petrel *Pterodroma phaeopygia*, Browne et al. 1997; flightless cormorant *Nannopterum harrisi*, Galápagos penguin *Spheniscus mendiculus*, and lava gull *Larus fuliginosus*) and six endemic subspecies among the 19 seabird species breeding there (Harris 1984). Virtually all waved albatrosses *Phoebastria irrorata* (Anderson and Cruz 1998) and swallow-tailed gulls *Creagrus furcatus* (Pitman et al. 1995) breed in Galápagos, and considering them endemic, 63% of Galápagos seabird taxa are endemic at the subspecies level or above, the highest for any archipelago (Snow and Nelson 1984). Approximately 99% of the Nazca boobies breed in Galápagos and on nearby Malpelo Island (Pitman et al. 1995, Anderson et al. unpubl. data), further highlighting the special taxonomic isolation of the archipelago's seabird fauna.

Adaptation to local conditions has been invoked to explain the insular nature of the Galápagos seabirds (Snow and Nelson 1984), and may illuminate the very low degree of dispersal by Nazca boobies. The oceanographic and climatological setting of Galápagos is unusual for tropical islands, with lower water temperatures and local upwelling (Wyrтки 1965, Feldman et al. 1984, Feldman 1986). While these conditions could explain local adaptation by Galápagos endemics (Snow and Nelson 1984), Nazca boobies breed in approximately equal numbers in Galápagos and on Malpelo, which has a more typically tropical environment (Wyrтки 1965). The Galápagos and Malpelo Nazca boobies share two notable features of their environment: a rocky, volcanic nesting substrate with significant topography, and high density nesting with conspecifics in large colonies. In these two respects, Nazca boobies differ from most populations of masked boobies, which typically nest in dispersed, small colonies (Nelson 1978, but see Pitman and Jehl 1998 for a notable exception) and on flat substrates (Pitman and Jehl 1998), often atolls (Nelson 1978). We suspect that local adaptation to these social and abiotic conditions drives the evolution of minimal dispersal, and also of the site-specific soft body part colors (Pitman and Jehl

1998) used in courtship that differentiate Nazca and masked boobies. We also hypothesize that adaptation to these conditions drove the initial differentiation of the two current species.

Limited dispersal should lead to significant population genetic structure within breeding colonies, with attendant spatial proximity to kin, especially siblings, half-sibs, and cousins that are not recognizable as nestmate kin. Interactions with kin could have both positive (e.g. cooperative behavior) and negative consequences (e.g. expression of deleterious recessive alleles via inbreeding) for individual fitness (Waser 1993). In the case of Punta Cevallos Nazca boobies, the relationship of dispersal distance to nesting density may make breeding between kin unlikely. Inter-nest distances average 2.7 m (Anderson 1993) so sons and daughters settling at their median natal dispersal distances (26 and 105 m, respectively) are approximately 10 and 39 nest sites, respectively, from their natal nest. Since established adults show low breeding dispersal, sons should typically breed at least 10 sites from their mother, and daughters at least 39 sites from their father. Brothers and sisters should typically be separated by at least 29 nest sites. Close kin in this species are thus separated by considerably larger numbers of breeding sites than are some other bird species with known low levels of inbreeding (e.g. Woolfenden and Fitzpatrick 1984, Arcese 1989), making close inbreeding unlikely.

Nazca booby females dispersed farther than males did, as is the case in most bird species (Greenwood and Harvey 1982, Clarke et al. 1997). In taxa with resource-defense based mating systems, males typically show higher philopatry than females do (Greenwood 1980). Male Nazca boobies defend specific nest sites from intruders throughout the breeding season, beginning with long periods of display and territory occupation at the breeding season's initiation, and contrary to Nelson's (1978) data from other colonies, aggressive disputes at nest sites are common at Punta Cevallos, often causing bloody injuries. Females, then, may be choosing males that have premium nest sites and males with superior sites may be reluctant to move from them.

In birds, natal dispersal tends to be more frequent and of longer distance than breeding dispersal (Greenwood and Harvey 1982), and this was the case for Nazca boobies in this study. Median natal dispersal distances were 26 m for males and 105 m for females, and only 0.4% of adults moved more than 25 m between breeding attempts. Breeding dispersal of young birds was more frequent and over longer distances than that of old birds: 35% of breeding dispersals by birds < 5 yrs old, but only 1% of birds > 8 yrs old, exceeded 10 m. Why young birds disperse to a greater extent than older birds do is uncertain but, in many species, young birds may initially use marginal habitat

to breed, and later disperse to better sites (Greenwood and Harvey 1982). However, site tenacity may confer benefits, because familiarity with a site could aid the owner when challenged for the resource (Greenwood and Harvey 1982). Site tenacity also is positively associated with mate retention in Nazca boobies, and thereby with reproductive success (Vinueza and Anderson, unpubl. data). The costs and benefits of site tenacity may well differ for young and established birds, if established birds occupy premium nest sites earlier in the season, preventing young, first-time breeders from using a preferred site.

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