

TESTING THE FEEDING-NICHE PARTITIONING HYPOTHESIS IN THE
SEXUALLY DIMORPHIC BLUE-FOOTED BOOBY

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“.....The dive of a single Booby, like that of the Hawk, is always a notable exhibition of skill, strength and perfection of the winged fisherman’s art. Only a person rarely gifted in the use of words could adequately describe it. How, then, can one hope to paint a pen-picture of a thousands of Boobies diving, of a skyful of Boobies, which, in endless stream, poured downwards into the sea? It was a curtain of darts, a barrage of birds.....This spectacle, the most surprising evolution I have ever seen in bird life, was witnessed repeatedly during the day.....”

Dr. Frank M. Chapman, Nov 1918

in Bird Islands of Peru, pag 64

(Robert C. Murphy 1925)

ABSTRACT

The feeding-niche partitioning hypothesis predicts that sexual size dimorphism in birds evolved as a result of disruptive selection between sexes to avoid food competition. I tested this hypothesis on breeding Blue-footed Boobies (*Sula nebouxi*) on Isla Lobos de Tierra, Perú, where females are 31% heavier than males. Dietary analysis was determined from regurgitations and foraging behavior was examined using dataloggers in 2002 and 2003. Bearing ($60 - 120^\circ$) and mean maximum foraging distances (19 - 54 km), diet composition ($>79\%$ Peruvian Anchovies, *Engraulis ringens*), time of arrival (mainly before dusk), number of trips per day (1 - 2), and proportion of travel time (83 - 89%) was similar between sexes. Females consumed larger (mean = 12.5 ± 1.4 cm) Peruvian anchovies than males (mean = 11.9 ± 1.6 cm), but no differences in size were found in three other prey species. Overall, females brought 1.5 times more food to the nest than males (range of mean of crop mass = 80 - 109 g). A higher number of females than males departed by mid-morning and dives were deeper around noon than at other times. Females dove deeper (mean = 4.5 ± 1.7 m) than males (mean = 3.5 ± 1.5 m). The lack of spatial and temporal segregation as well as similarities in diet composition between sexes may be explained in terms of the flocking behavior of birds at sea. It is also likely that intersexual similarities may be the result of optimal food conditions during the study period. An analysis of maximum dive depth and body mass of males and females revealed that heavier birds attained deeper depths, but the effects of sex per se and body mass were difficult to separate because the studied birds did not overlap in size. Further sex-specific comparisons of diving behavior among individuals of similar size are

necessary to elucidate the effects of body mass in promoting feeding segregation in the water column.

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The Díaz family in Piura and my uncle Eduardo Carranza in Lambayeque always offered their houses to keep our gear when we were stuck in the mainland. Mr. Juan Amaya in Parachique brought drinking water to the Island when our reserves started to run off and Joanna Alfaro did persuasive arrangements in the fishermen village of

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CHAPTER 1

INTRODUCTION AND METHODS

INTRODUCTION

Sexual size dimorphism is widespread in the animal kingdom, but the direction and degree on how sexes differ in size varies considerably among and within taxa. For instance, females are larger than males in many species of insects, spiders, anuran amphibians and fishes, whereas the reverse pattern is usually found in reptiles, birds and mammals (e.g., Andersson 1994). Similarly, a wide spectrum of sexual dimorphism in size can be found within a taxon such as teleost fishes. Most deep-sea ceratioid anglerfish males are several times smaller than females (Pietsch 1976), whereas in some species of protogynous coral-reef fish, the male is generally the larger sex (Warner 1984).

Two main hypotheses have been proposed to explain the evolution of sexual size dimorphism in animals: (1) sexual selection and (2) intra-specific niche divergence. The sexual selection hypothesis predicts that differences in traits between males and females evolved either by competition for access to mates, generally determined by contests, or by choice for high quality mates (Darwin 1871). The intra-specific niche divergence hypothesis or ecological model proposes that sexual dimorphism evolved through disruptive selection of the sexes to avoid food competition (feeding niche segregation, Darwin 1871), to divide ecological or social roles (dimorphic niche, Slatkin 1984), or to occupy different habitats (bimodal niche, Schoener 1967). Empirical and genetic studies suggest that these hypotheses are plausible in explaining the evolution of sexual dimorphism in body size and morphology (Hedrik and Temeles 1989). Nevertheless, all these processes may act simultaneously or sequentially, hiding the relative importance of each mechanism acting over a single species (Shine 1989).

There are innumerable examples where the degree and direction of sexual dimorphism in body size is unequivocally predicted by the theory of sexual selection. For example, it has been suggested that sexual selection is the major evolutionary force responsible for the strong sexual size dimorphism in Northern Elephant Seals (*Mirounga leonina*) in Baja California and Marine Iguanas (*Amblyrhynchus cristatus*) of the Galapagos Islands because large males have a higher mating success and greater endurance rivalry than small males (LeBoeuf 1974, Wikelski and Trillmich 1997).

Conversely, the intra-specific niche divergence hypothesis has received less attention because it has been difficult to test (Shine 1989). Even if true, it cannot predict the direction of size differences between sexes, and in most cases, the distinction between origin and maintenance of the dimorphism has remained unclear. Thus, ecological differences may help maintain sexual size dimorphism even though that dimorphism originated through the action of sexual selection (Slatkin 1984).

The predictive value and parsimony of the sexual selection approach has overshadowed the ecological model; however there are numerous studies demonstrating a relationship between sexual dimorphism in size and differential foraging behavior (e.g., Selander 1966, Schoener 1967). For instance, the sexual differences in bill size and tongue structure in the Hispaniola Woodpecker (*Melanerpes striatus*) have an ecological significance in adapting the sexes to reduce food competition, with large males occupying different subniches than females (Selander 1966). The disparity of body size in many predatory birds is explained in terms of the disproportionate distribution of labor between sexes: large females are more efficient in incubating and guarding the nest, and cope easily with fasting, whereas small males are engaged more in feeding activities

because they are agile enough to capture prey more efficiently (Andersson and Norberg 1981). Likewise, sexual size differences in the Lizard (*Anolis conspersus*), are associated with structural differences in habitat: adult males tend to occupy larger and higher perches than females (Schoener 1967).

Although reversed size dimorphism (RSD: females larger than males) is common in several animal taxa (Ralls 1976, Jehl and Murray 1986, Andersson 1994), it is rare among seabirds (Fairbain and Shine 1993); only being found in frigatebirds (Fregatidae), skuas and jaegers (Stercorariidae) and boobies (Sulidae). Several hypotheses have been proposed to explain why females are larger than males: higher fecundity, better parental care, assortative mating, or dominance in contests over resources (e.g., Andersson 1994). Blue-footed Boobies (*Sula nebouxii*) are tropical seabirds displaying marked sexual size dimorphism. Females are 30%-32% heavier and 5%-10% larger than males, and therefore it is a suitable species for testing the intra-specific niche divergence hypothesis. Based on this disparity, Nelson (1978) proposed that in early stages of the chick-rearing period, males may go on foraging trips of short durations to shallow inshore waters, whereas females may spend more time at the nest, feed far away from the colony and deliver food to their chicks less often than males (Nelson 1978).

The origin and maintenance of RSD in the Blue-footed Booby has not been explored and is beyond the scope of this study. Instead, I will examine whether the differences in body size between females and males, regardless of the direction of the dimorphism, may reduce intersexual competition for food at Isla Lobos de Tierra, Peru. Blue-footed Boobies are plunge-divers and the access of greater depths depends on the free-falling speed, height, angle of impact with the sea surface and body mass. I predict

that both sexes will either 1) not overlap in the foraging areas 2) feed on different prey, 3) feed on the same prey, but of different sizes, 4) forage at different time of the day or 5) dive at different depths. The diet composition and foraging behavior will be determined in a group of known-sex breeding birds carrying small data loggers. These devices recorded foraging routes, diving behavior and at-sea activities so, that multiple datasets can be examined.

This thesis is divided into six chapters. A description of the study site and methods are given in this chapter to avoid redundancy as the protocols for nest observations, attachment of devices, datalogger deployment and data analysis were similar throughout. In Chapter 2, the effect of instrumentation on the breeding and foraging performance of the birds is examined. Monitoring of instrumented birds is crucial to identify any adverse effect on behavior and survival and also to obtain reliable data on foraging performance. Bearing and maximum foraging distances are described in Chapter 3. Because food type is relevant in the analysis of intra-specific competition, I analyzed diet composition, prey size and crop mass in Chapter 4. In Chapter 5, I presented information on the timing of foraging, the duration and number of feeding trips per day as well as the time allocated to different at-sea activities such as traveling, resting on the sea surface and diving. Finally, dive depth, dive duration, and number of dives per trips are discussed in Chapter 6.

Study area.- Lobos de Tierra (6°24'S, 80°51'W, Fig. 1) is a remote, desert island, characterized by extensive plains with small, gravel hills < 80 m in elevation. Extensive sand beaches are found primarily on the eastern side. Between the low hills are irregular,

narrow, rocky valleys unsuitable for nesting birds. This island is the largest along the Peruvian coast, with an area estimated to be 1,426 Ha (9 x 3 km). Warm tropical waters from the north and west and cold upwelling waters from the south and east surround the island. These oceanographic front boundaries change both seasonally and among years, affecting the number (Guillén 1991) and diet composition of Blue-footed Boobies (Janhcke and Goya 2000). Average sea surface temperature during the study period varied from 17-18°C in June-July 2002 to 22-23°C in January-February 2003 (Proyecto de Aprovechamiento y Extracción del Guano de las Islas, PROABONOS, unpubl. data). Lobos de Tierra currently is protected and administered by PROABONOS, a government agency in charge of the exploitation and commercialization of guano.

Lobos de Tierra supports 150,000 - 200,000 breeding pairs of Blue-footed Boobies (C. Zavalaga, unpubl. data). Other sympatric species that nest on the island include the Peruvian Booby (*Sula variegata*; 1,000 - 5,000 pairs), Peruvian Pelican (*Pelecanus thagus*; 25,000 - 50,000), Kelp Gull (*Larus dominicanu*; 100 - 200 pairs), Red-legged Cormorant (*Phalacrocorax gaimardi*; 15 - 20 pairs), Nazca Booby (*Sula granti*; 5 - 10 pairs) and Humboldt Penguin (*Spheniscus humboldti*; 2 - 10 pairs).

Blue-footed Boobies occur in the tropical eastern Pacific Ocean (Murphy 1936, Nelson 1978). They breed in discrete insular colonies located mainly in the Gulf of Baja California, the Galápagos Archipelago, the Gulf of Panama and northern Perú (Nelson 1978). The largest single colony occurs on Isla Lobos de Tierra, a region still under the influence of the cold nutrient-rich Humboldt Current (Murphy 1936). The southernmost breeding colony of Blue-footed Boobies is located on Isla Lobos de Afuera (6°45'S), 60 km south of Isla Lobos de Tierra.

To judge by the breeding status of the birds in 2002 and 2003, Blue-footed Boobies bred year round on Isla Lobos de Tierra, but a hatching peak occurred by the end of December 2002 (C. Zavalaga, unpubl. data). Two to three eggs are normally laid per clutch and chicks hatch asynchronously after 6 weeks of incubation (Nelson 1978). Brood reduction is facultative and can occur when food conditions are unfavorable (Drummond et al. 1991). The most common brood size is two chicks, but nests with three chicks are also found. Chicks fledge when 12-14 weeks old (Nelson 1978).

Blue-footed Boobies capture their prey by plunge-diving from heights < 30 m (Anderson and Ricklefs 1987). Dives are generally shallow and last no longer than 5 s (Duffy 1987). In Perú, they feed mainly on Peruvian Anchovies (*Engraulis ringens*), but other inshore prey can be ingested when anchovy supply is reduced (Jahncke and Goya 2000). Main predators are feral cats and dogs. Occasionally, Kelp Gulls and Turkey Vultures (*Cathartes aura jota*) also prey upon eggs and chicks.

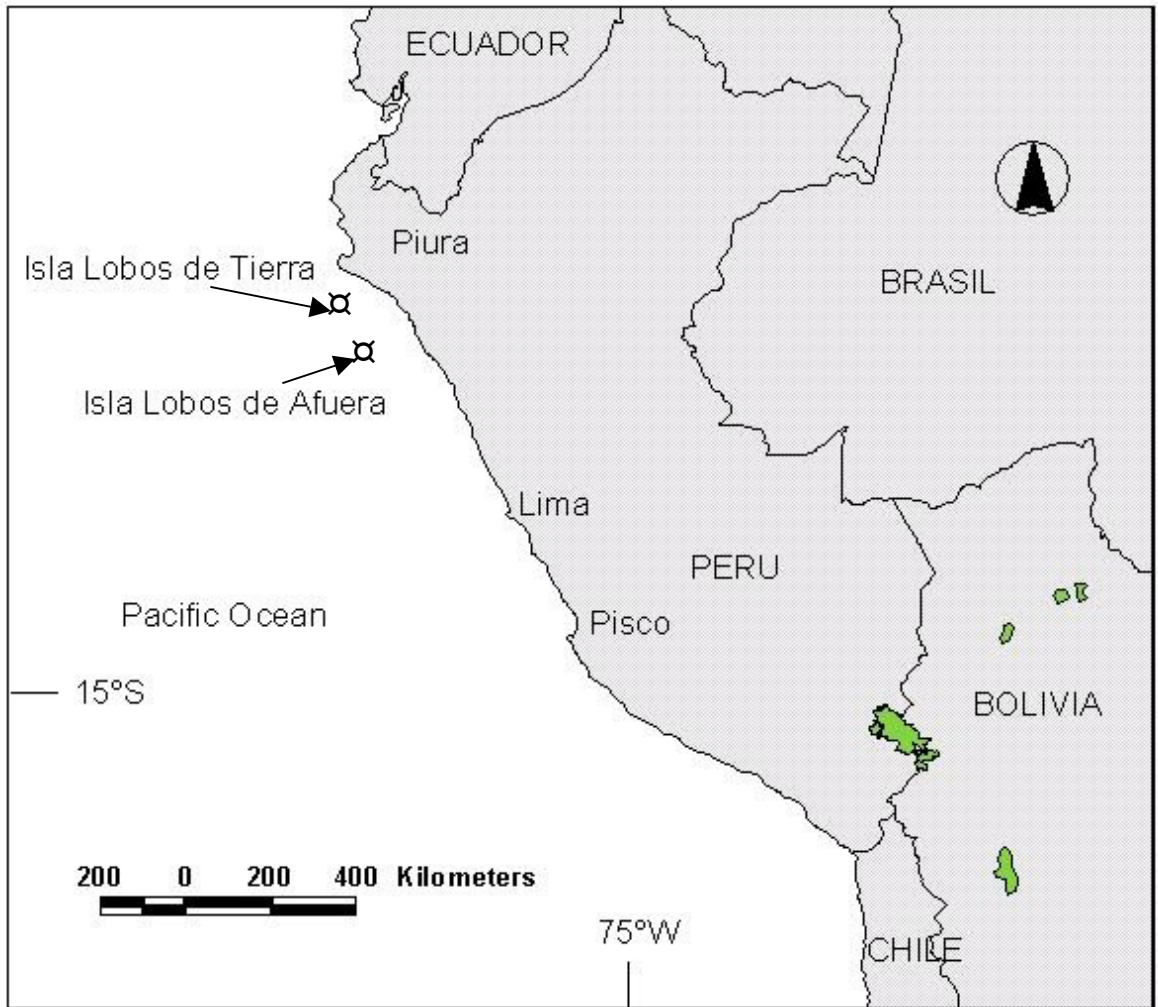


Figure 1. Location of Isla Lobos de Tierra.

The degree of sexual dimorphism in the size of Blue-footed Boobies on Isla Lobos de Tierra is similar to that found at other colonies (Nelson 1978, Guerra and Drummond 1995), with females being 31% heavier and 6 - 9% larger than males (Table 1). In 2003, I counted the number of molted tail feathers of all studied birds. Overall, females and males were at similar stages of the molting cycle (females: mean = 2.07 ± 1.76 , range = 0 - 7, $n = 81$; males: mean = 2.16 ± 1.69 , range = 0 - 5, $n = 55$; t -test, $t = 0.29$, $P = 0.76$).

Study period.- This study was conducted on Isla Lobos de Tierra during two seasons: winter (28 June – 21 July 2002) and summer (25 January - 27 February 2003). Fieldwork in 2002 took place in one sub-colony called “El Once” (150-200 nests in July 2002), located 3.5 km south of the island’s guard houses. In 2003, two sub-colonies were selected: El Once (1,200 – 1,500 nests in January 2003) and “La Base” (300 – 400 nests in January 2003) located a few meters behind the guard houses.

In 2002 most of the breeding population was engaged in courtship and nest establishment, with 67% of the studied birds engaged in incubation and the remaining attending chicks < 2 weeks old. In 2003, conditions were different as almost all chicks had hatched, and 91% of the studied birds were rearing small to medium-sized chicks (mass range: 100 – 1400 g). Therefore, the winter survey period focused on the incubation period, whereas the summer survey period focused on rearing. Likewise, oceanographic conditions were different between seasons, with colder waters around Lobos de Tierra in winter than in the summer (Peruvian Marine Research Institute, IMARPE, unpubl. data). This difference is important as the foraging behavior of birds

changes according to the energetic demands of the breeding cycle and the spatial distribution of prey (e.g., Weimerskirch et al. 1997).

METHODS

Data loggers.- Foraging activities of Blue-footed Boobies were determined with two types of miniature bird-borne data loggers: (1) flight sensor and depth-meter recorders (FSD) and (2) flight sensor and compass recorders (FSC). These devices are not commercially produced, but are manufactured by the Istituto di Elaborazione dell'Informazione, C.N.R., Pisa, Italy. Their reliability and accuracy have been successfully tested in several studies on the foraging behavior of free-ranging seabirds such as Northern Gannets (*Sula bassana*; Garthe et al. 2000, Lewis et al. 2002), Thick-billed Murres (*Uria lomvia*; Benvenuti et al. 1998, Benvenuti et al. 2002, Falk et al. 2002), Razorbills (*Alca torda*; Dall'Antonia et al. 2001, Benvenuti et al. 2001), Cory's shearwaters (*Calonectris diomedea*; Dall'Antonia et al. 1995) and Black-legged Kittiwakes (*Rissa tridactyla*; Daunt et al. 2002).

Table 1. Morphometric data and molting stage of Blue-footed Boobies (110 females, 120 males) on Isla Lobos de Tierra, Perú in 2002 and 2003. Means are expressed \pm s.d. and range is given in parentheses. Statistical test: Z-test for comparisons of means.

Measurements	Females	Males	Z - Test	P
Body mass (g)	1730 \pm 118 (1350 – 2000)	1323 \pm 82 (1125 – 1500)	31.31	< 0.001
Culmen length (cm)	10.66 \pm 0.32 (9.88 – 11.45)	9.90 \pm 0.24 (9.16 – 10.43)	20.41	< 0.001
Tarsometatarsus length (cm)	5.77 \pm 0.25 (4.30 – 6.23)	5.30 \pm 0.14 (4.86 – 5.66)	18.49	< 0.001
Wing chord (cm)	43.41 \pm 1.07 (40.4 – 46.6)	40.87 \pm 0.97 (38.2 – 43.8)	17.98	< 0.001

Both devices were equipped with a small, modified microphone (flight sensor) with a membrane activated by body movements and wing flapping, so different at-sea activities such as resting on the sea surface and traveling could be recognized by changes in the intensity and frequency of signals: (1) traveling flight, with strong signals characterized by stable intensity and frequency, and (2) swimming or resting on the sea surface, characterized by weak signals of low intensity (Fig. 2). Additionally, when the flight sensor was coupled to the depth-meter, diving activities also could be identified (Fig. 2). Data from the flight sensors were used to determine the time budget of at-sea activities, the timing of arrivals and departures, and consequently the duration of feeding trips (Chapter 5).

In the FSD, the flight sensor was coupled to a depth meter with an operative range of 0 - 70 m, and 1-m resolution. The memory capacity was 128 Kb, and the recording time interval was set at 6 s for the flight sensor and 2 s for the depth meter. At this rate, the logger could continuously store data for 2.3 days. The external width of the streamlined container was 22 - 33 mm, height 13 - 18.5 mm, and total length 80 mm. The instruments, including the waterproof container and batteries, weighed 28 g (about 1.5% of the bird's body mass). For the analysis of dive depth, all records < 1 m were excluded because they may account for "bathing splashes" immersions (Falk et al. 2002). The FSDs were used to determine dive depth, dive duration, timing of dives and number of dives per trip (Chapter 6).

The FSC was supplied with a flight sensor and a compass. This device recorded the bird's time budget during a feeding trip and changes in the direction of the main axis of the bird's body with respect to geomagnetic north. Because the compass was fitted to a

transducer to convert from angular to electrical resistance values, any change in bearing during the flight was recorded. Temporal changes in bearing were transformed into spatial vectors by multiplying the bird's estimated flight speed by the time spent in a particular bearing, and therefore the routes are approximate representations of the birds' spatial distribution. The routes provide information about the spatial strategy (straight or circuitous path), directional preferences for feeding, and the approximate foraging range. Flight-path reconstruction was possible because Blue-footed Boobies have a sufficiently constant flight speed (39.1 km/h, Anderson and Ricklefs 1987). The bird's velocity with respect to the ground was then corrected by considering wind speed and direction measured hourly on a summit of a hill 30 m in elevation, an altitude similar to the flight altitude of Blue-footed Boobies (Anderson and Ricklefs 1987). The error associated to wind drift is likely minimal as trade winds along the Peruvian coast generally blow from the southeast (Bakun 1987).

The memory capacity of the FSD was 128 Kb, and the recording time interval was set at 6 s for the flight sensor and the compass, so the logger could store data for 4.5 days. The FSC, including the waterproof container and other components, weighed 29 g and was 23 mm in width, 14-19 mm in height and 97 mm in total length. Because changes from horizontal positions (e.g., during plunging) cause angular changes in the compass, FSCs were calibrated *in situ* to compensate any deviations for horizontal displacement.

Flight sensors, compasses and depth meters were synchronized to an internal timer, so recording the exact "on" time of each instrument identified the timing of each

at-sea activity. Flight, dive and spatial data were analyzed by a special software application, VISUA 3 (designed by A. Ribolini, IEI, CNR, Pisa).

Device attachment.- All birds were captured at their nests using a monofilament noose attached to a 3-m aluminum pole. Low nest density (inter-nest distance usually > 1 m) permitted random sampling, both in the periphery and the center of the colony, without disturbing neighboring nests. Overall, 32 birds in 2002 and 78 in 2003 were fitted with data loggers (Table 2). However, because some devices failed to record data or fell off during deployment, I only obtained reliable data from 20 birds in 2002 and 64 in 2003. To avoid any possible data dependence between pairs, only one individual per nest was selected in most of the cases.

The FSDs were attached underneath the base of the two longest central tail feathers using Tesa tape. As pointed out by Anderson and Ricklefs (1987), boobies press their feet against the ventral base of the tail feather while plunging, which protects the logger against the shock of impact with the sea surface. This attachment method usually took less than 5 min. from recapture to release. The FSCs were not attached to the tail feathers, but to the lower bird's back (just above the uropygeal gland) because the compass needed to be located along the main axis of the bird's body. I also used Tesa tape to attach the FSCs, and this procedure took 10-15 minutes from capture to release. The majority of birds resumed brooding immediately upon release, but some birds flew to the sea for bathing and returned to their nests within 5 min. Boobies were recaptured in their nests either the same day after completing one feeding trip or between one to four days later (mode = 1 day).

After bird restraining, the device was retrieved, the adult and their chicks weighed with a spring balance, measured with a caliper (culmen length, tarsometatarsus) or ruler (wing chord), painted on their breast feathers with a red dye (rhodamine B) for females and yellow dye (picric acid) for males, and marked with a numbered aluminum ring (only in 2003). Sex of adults was determined by body size (females 30% heavier than males), pupil size and shape (larger and more irregular in females) and calls (whistles in males, grunts in females, Nelson 1978). The information collected by the devices was downloaded in the field via a serial port to a portable computer.

Nest observations. – Direct observations of nest attendance were necessary for two reasons: (1) to determine the timing and the duration of feeding trips of non-instrumented birds for comparisons on the duration of feeding trips, breeding success and mass increment rate of chicks between instrumented and non-instrumented birds, and (2) to capture instrumented birds upon their return. Both groups were observed simultaneously and when differences on foraging parameters were not detected, data were pooled in order to increase sample size and power of statistical tests.

In 2003, it was not possible to study both sub-colonies simultaneously because of the limitation in the number of observers. Thus, La Base sub-colony was monitored from 25 January to 7 February and again between 22 and 27 February, whereas birds at El Once sub-colony were observed from 10 to 18 February. All observations were undertaken between dawn and dusk (0630-1830 h in 2002 and 0600-1900 h in 2003). Twenty-nine nests in 2002 and 44 in 2003 were marked with numbered stones and the presence/absence of each bird was checked every 30 minutes by walking around the

colony periphery (5 - 10 m away the nests). Non-instrumented birds were not captured, but marked with a small brush placed at the end of a 3 m pole.

Foraging trip duration of non-instrumented birds was defined as the time elapsed between departure and arrival to and from the nest. Not all changeovers could be observed as some birds left and arrived at the nest before and after dusk. Information from instrumented birds revealed that birds did not forage during dark hours, but 27% and 11% of the departures in 2002 and 2003, respectively, occurred before the start of nest observations. Likewise, 28% and 19% of the arrivals occurred after dusk. Because data from the devices showed that more than 50 - 60% of the departures and arrivals occurred within the 30 minutes prior to the start and within 30 minutes after the end of the observation period, I assumed that unobserved departures occurred at 0600 h in 2002 and 0530 h in 2003, whereas unobserved arrivals took place at 1900 h in 2002 and 1930 h in 2003.

Table 2. Number of Blue-footed Boobies fitted with data loggers, number of non-instrumented birds used for observations of nest attendance, and number of regurgitations obtained from both instrumented and non-instrumented birds of each sex at Lobos de Tierra in 2002 and 2003.

	2002		2003	
	Females	Males	Females	Males
Birds instrumented with FSD	9	9	27	30
Birds instrumented with FSC	7	7	12	9
Non-instrumented birds	15	13	30	32
Regurgitations (instrumented)	7	14	29	26
Regurgitations (non-instrumented.)	56	45	89	59

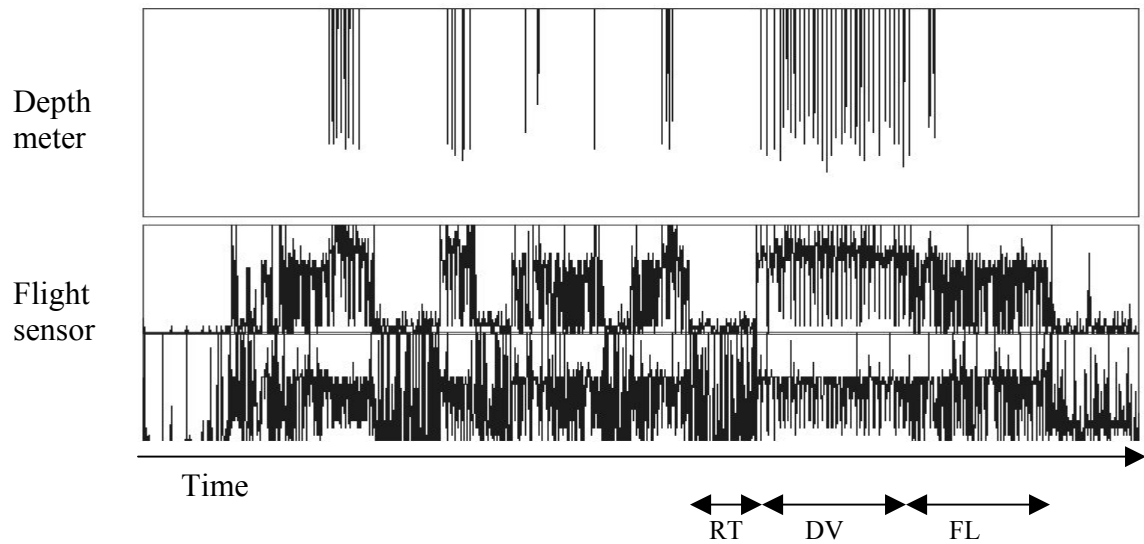


Figure 2. Intensity and frequency of signals from a flight sensor/depth meter recorder attached to a female Blue-footed Booby that left the nest at 0905 h and returned at 1346 h. The graph shows the three main at-sea activities: RT = resting on the sea surface, DV = diving, and FL = flying. The strongest signals from the flight sensors in the lower graph coincide with the diving activity in the upper graph.

Chick measurements and survival.- To detect any adverse effect of instrumentation on chick growth and breeding success, nestlings from single and two-chick broods from instrumented and control parents were marked and weighed with a spring balance to the nearest 10 g. Only small and medium sized chicks (100 – 1200 g) were selected and marked with a numbered fiber-tape band around the humerus. This range of chick size corresponded to the linear part of body-mass growth (Drummond et al. 1991), and chick growth rate was expressed as the mass increment divided by the time interval between two successive measurements. After 7-14 days of the first measurement, chicks were re-weighed and the tape removed.

Dietary analysis. - Sex-specific differences in diet composition, prey size and crop mass were assessed by analysis of stomach contents from induced regurgitations of 72 instrumented and 216 non-instrumented birds in both years (Table2). Stomach samples from instrumented birds were obtained in both sub-colonies immediately after returning from a feeding trip. Additionally, regurgitations from five non-instrumented known-sex adults (but unknown breeding status) were collected daily throughout the study period. These birds were chosen at random and captured during the night between 1930 – 2100 h either in the periphery of the breeding sites or on beaches.

A non-invasive method for collection of stomach contents was preferred as Blue-footed Boobies regurgitate spontaneously by holding them upside down and by pressing gently on their bellies until all the food is passed (presence of bile). Samples were collected in plastic bags and analyzed either the same day or the next morning. Diet

composition was expressed as percentage by mass (mass of a particular prey item/mass of the regurgitation).

Fish length was assessed either by direct measurement of intact fish (accuracy ± 1 mm), or in the case of partially digested Peruvian Anchovies, by measurements of the sagittal otolith extracted from the head (accuracy ± 0.01 mm). The initial anchovy length was estimated using otolith length-fish length equations (fish length in cm = $0.798 + 3.33$ otolith length in mm; Castillo et al. 1999). Because there were no significant differences in diet composition between instrumented and non-instrumented birds (see Chapter 2), data from both groups were pooled for further analyses. However, mean mass of regurgitations was calculated only from instrumented birds in order to eliminate any bias associated to partial digestion of food after returning to the island.

Data analysis.- For comparisons of spatial distribution at sea, foraging routes were reduced to two main variables: (1) bearing of the outmost foraging point, and (2) the maximum distance (the furthest point away from the nest). Flight orientation was measured in angles and as such, it could not be considered a linear variable. I compared bearings of feeding trips between sexes and seasons, and estimated means and s.d. by using circular statistic analysis (Batschelet 1981). To evaluate whether flight orientation and dispersion was not at random, the Rayleigh test was used. Flight orientation between sexes and seasons was compared using the Mardia-Watson Wheeler test (Batschelet 1981). Flight orientations from birds with more than one trip were averaged to avoid pseudo-replication. Locations of birds and a local coastline map (extracted from <http://rimmer.ngdc.noaa.gov/coast/>), were overlaid into a Universal Transverse Mercator

projection using ArcGIS 8.3. Most of the data collected either from the instruments or from direct observations (dive depth, number of dives, prey size, length of feeding trips, maximum foraging distance, time allocation of foraging activities and timing of dives) included multiple observations of the same bird, and therefore the data could not be considered independent. To avoid pseudo-replication, I used generalized mixed linear models using restricted maximum-likelihood estimations (REML) for comparisons between sexes and seasons. In these models, sex and season were included as fixed factors and bird identity as a random factor. A Generalized Mixed Model (GMM) with a link=logit procedure was used to test differences in the number of feeding trips/day because values were best described by a binomial distribution (1 or >1; more than 2 trips/bird/day were rare). For single observations per bird (crop mass of instrumented birds) a generalized linear model (GLM) was used for comparisons. When required, data was normalized using logarithmic or arcsin transformations. Chi-square, Fisher's exact test, or Z-test were used for comparisons of proportions between independent groups, but other non-parametric tests were used for comparisons of medians (Mann-Whitney U-test) and distributions (Kolmogorov-Smirnov for two samples) when sample size was small and not normally distributed (Sokal and Rohlf 1995). Inter-sexual differences in the diversity of prey items in the diet were examined using the *t*-test for the Shannon-Weiner index of diversity [$H = -\sum p \cdot \log p$] (Zar 1984). Linear regression was performed to examine relationships between two variables, but the Spearman rank correlation coefficient was preferred when sample size was small (Zar 1984). In order to control for any possible effect of sex on adult body mass, the analysis of covariance (ANCOVA) was performed when a relationship between body mass and maximum dive depth was

examined. Means are expressed ± 1 s.d., except as otherwise indicated. I chose to define marginal significance at $0.05 < P < 0.10$, in addition to the traditional definition of significance at $P < 0.05$. All statistical analyses were performed using SAS version 8.2.

CHAPTER 2

EFFECTS OF INSTRUMENTATION ON BREEDING AND FORAGING PERFORMANCE

INTRODUCTION

Recent advances in miniaturization of electronics have permitted the production of different devices small enough to be attached to free-ranging birds. Radio transmitters, satellite transmitters and data loggers are among the most representative (Wilson et al. 2002). They have been extensively used on birds in order to explore detailed aspects of foraging behavior such as the duration of foraging trips (Weimerskirch et al. 1993, Taylor et al. 2001), time allocation of at-sea activities (Quintana 2001, Falk et al. 2002), spatial distribution at sea (Weimerskirch et al. 1993, Wood et al. 2000, Falk et al. 2001) and diving behavior (Grémillet et al. 1998, Frere et al. 2002).

Researchers have always been concerned with how these devices affect the foraging and breeding performance of birds. Unfortunately, some devices can increase the energetic expenditure of instrumented birds because of drag (Culik and Wilson 1991), and in extreme cases, decrease survival. Indirect measurements also have shown that these devices affect nesting success (Watanuki et al. 1992), behavior of instrumented birds on land (Wilson and Wilson 1989), diving performance (Wilson 1989), and duration of foraging trips (Taylor et al. 2001). Thus, to minimize the impacts of instrumentation, several factors need to be evaluated such as size and shape of instruments, attachment method, deployment period, position of the device, among others. Furthermore, a method used successfully in one species may be useless in another as a consequence of the bird's foraging method (e.g., diving vs. surface seizing), body size, sex, behavior (e.g., timid vs. human tolerant species) or breeding status. All these variables should be taken into consideration to reduce any adverse effect on the bird's behavior and to obtain reliable data on the bird's foraging performance.

In this chapter, I evaluate the effects of bird-borne data loggers used in this study by comparing 1) chick survival, 2) body mass increment of chicks, c) diet composition, 3) prey mass of adults and 4) duration of foraging trips between instrumented and non-instrumented birds. When possible, I also examine the effect of sex and season on these variables. This comparison was a prerequisite for further analysis of sex-specific foraging behavior of Blue-footed Boobies on Isla Lobos de Tierra, Perú.

RESULTS

Apparently, capture and attachment of the devices had no adverse effect on the bird's behavior. Unlike other procedures, the use of Tesa tape was the most adequate method for device attachment in this study because it could be applied quickly and minimal damage to feather structure. The majority of birds resumed incubation or brooding immediately after release. No discomfort or increase in preening activities was observed, and birds did not abandon their nests when approached for recapture. In 2002, five devices fell off during deployment and only one of 34 birds was never seen again after attachment. In 2003, only one device fell off and all instrumented birds ($n = 78$) were recaptured.

The proportion of successful nests (expressed as the number of pairs that did not abandon their nests during a period of at least two weeks) was similar between instrumented (86%, $n = 77$) and non-instrumented boobies (87%, $n = 47$; $\chi^2 = 0.01$, $P =$

0.91, $df = 1$; both years pooled). All instrumented pairs that failed ($n = 11$) abandoned their nests days after device recovery.

In 2003, the growth rate of siblings from two-chick broods of instrumented parents was lower (A chicks: 24.2 ± 8.0 g/d, $n = 15$; B chicks: 24.6 ± 8.4 g/d, $n = 15$) than that of control chicks (A chicks: 31.4 ± 11.4 g/d, $n = 19$; B chicks: 36.38 ± 16.0 g/d, $n = 18$; t -test for A and B chicks, $P < 0.05$). When singleton chicks are compared, no difference in growth rate was found (non-instrumented: 32.2 ± 12.1 g/d, $n = 22$; instrumented: 34.8 ± 18.2 g/d, $n = 10$; t -test, $t = 0.69$, $P > 0.05$).

The proportion of anchovy in the diet was similar between instrumented (96%, $n = 72$) and non-instrumented (88%, $n = 216$) birds (Z -test for proportions, $Z = 1.94$, $P < 0.05$; both years pooled). Likewise, the mean crop mass was similar between groups (Z -test, $Z = 0.03$, $P = 0.855$, $n = 267$; both years pooled).

In 2003, the devices did not have adverse effects on the duration of feeding trips of breeders (REML, $F_{1,745} = 0.48$, $P = 0.4873$). Likewise, females and males spent a similar amount of time foraging (REM, $F_{1,100} = 0.54$, $P = 0.463$) and the interaction of instruments and sex was not significant (REML, $F_{1,745} = 0.89$, $P = 0.344$). A similar result of the effect of instrumentation and sex was found in 2002. However, a significant interaction of sex by instrument (REML, $F_{1,259} = 15.2$, $P = 0.001$) indicated that males fitted with data loggers spent more time at sea (mean = 6.08 ± 3.65 h, $n = 16$) than non-instrumented males (mean = 3.89 ± 2.16 , $n = 128$; Tukey test, $q = 4.64$, $P < 0.05$, all other comparisons, $P > 0.05$).

DISCUSSION

The devices used in this study had no negative effects on the dive depth of Northern Gannets (*Morus bassana*; Garthe et al. 2003), adult body-mass variation and breeding success of Razorbills (*Alca torda*; Benvenuti et al. 2001), foraging locations of Thick-billed Murres (*Uria lomvia*; Falk et al. 2002) and trip duration in Black-legged Kittiwakes (*Rissa tridactyla*; Daunt et al. 2002).

Blue-footed Boobies were highly tolerant to human presence. Most of the birds came back to their nests immediately after handling and remained in their nests even when approached for recapture. Data loggers weighed < 1.5% of the bird's body weight and were attached either underneath the tail feathers or in the lower back to reduce the bird's impact on the sea surface during plunge-diving. Likewise, they were only deployed for a short period of time, usually less than 2 days, decreasing the risks of long-term effects on body condition.

Instrumentation did not affect the diet composition and amount of food brought to the nest. The survival of chicks with parents fitted with devices was similar to those of non-instrumented parents. Siblings from two-chick broods of instrumented parents grew slower than control chicks, but single chicks from one-chick broods grew as fast as control chicks. Previous studies have demonstrated that Blue-footed Booby parents provisioned two-chick broods at roughly double the mass-specific rate to single chicks (Anderson and Ricklefs 1992). Consequently, if energy demands are higher in larger broods, a lower growth rate of senior and junior chicks within a brood suggest that instrument attachment may affect the food delivery rate. Other variables such as chick

sex ratio within a brood (Torres and Drummond 1999) could be involved, but this effect was difficult to determine in the field. It is also likely that depriving chicks of at least one meal (one regurgitation obtained during adult recapture) had an adverse effect on the rate of mass increase in two-chick broods during 1-2 week sample intervals. Handling and instrumentation did not affect the at-sea activities of parents, but it could have altered the behavior of parents on the ground, as they would be more alert in their nests and pay less attention to their chicks after being captured.

Instrument attachment affected the foraging trip length of males only in 2002. Males fitted with data loggers spent on average 2 h longer at sea than non-instrumented birds. These differences were not found in females in the same season or between sexes in 2003. As discussed in the following chapters, birds foraged at greater distances and spent more time foraging in 2002 than in 2003. These differences may be associated with the distribution of their main prey. Blue-footed Booby males are 31% lighter than females and the added mass of the recorder may increase foraging effort of males when food conditions are not optimal.

In conclusion, data loggers used in this study had no adverse effect on the foraging behavior of Blue-footed Boobies when food was apparently abundant. However, under poor food conditions the foraging efficiency of instrumented males may decrease as a consequence of an increased wing loading. Although at-sea activities may not be affected, chick provisioning and the behavior of adults could be altered due to manipulation.

CHAPTER 3

FLIGHT ORIENTATION AND MAXIMUM FORAGING DISTANCE

INTRODUCTION

The segregation of foraging areas seems to be a plausible explanation for reducing intersexual food competition of satellite-tracked Wandering Albatrosses (*Diomedea exulans*; Weimerskirch et al. 1993), Northern Giant Petrels (*Macronectes halli*; Gonzáles-Solís et al. 2000) and Adélie Penguins (*Pygoscelis adeliae*, Clarke et al. 1998). There is evidence that breeding Blue-footed Boobies on Isla Lobos de Tierra return to their colonies from specific directions (Duffy 1987), and on Isla Isabela at the Galápagos Archipelago, radio-tracked brooding birds fed mainly to the east and north-east of the island up to 30 km offshore, suggesting that they do not forage at random (Anderson and Ricklefs 1987). However, the spatial distribution at sea between males and females in this species has not yet been examined and it is necessary to elucidate whether partitioning of feeding niche may occur.

In this chapter, I examine the hypothesis of intersexual segregation of feeding areas as a mechanism to reduce food competition in the Blue-footed Booby on Isla Lobos de Tierra. I will determine the orientation of foraging trips as well as the maximum foraging range of incubating and brooding known-sex birds during two field seasons.

RESULTS

Information on 58 foraging routes from 26 breeding birds fitted with FSC were obtained in both years (9 birds in 2002 and 17 birds in 2003). Routes are categorized in two main groups: straight (Fig. 3A, 3B) and circuitous (Fig. 3C, 3D). Both consisted of 1) a straight

outbound flight, 2) a main foraging area with frequent changes of bearing and 3) a straight inbound flight. The main difference between both strategies was the duration of each flight sector, with outbound and inbound flights longer for straight routes than in circuitous routes. Seventy-one percent of females foraged using a straight route, while 42% percent of males preferred a circuitous trip; however, these differences were not significant (Fisher's exact test, $P = 0.126$).

Directions of the outmost foraging point in 2002 were not randomly distributed (Rayleigh test, vector length $VL = 0.682$, $n = 9$, $P = 0.011$), but the birds were flying mainly to the southeast (mean = $123^\circ \pm 46^\circ$, $n = 9$; Fig. 4A). Mean bearing between sexes was similar (Mardia-Watson-Wheeler test, $B = 0.28$, $P > 0.05$; Table 3), but the dispersion of flight directions was higher in males (Rayleigh test, $VL = 0.563$, $P = 0.215$). Small sample size for females ($n = 4$) did not allow a statistical test, but the mean vector length ($VL = 0.834$) suggests a high aggregation for a particular direction (Table 3).

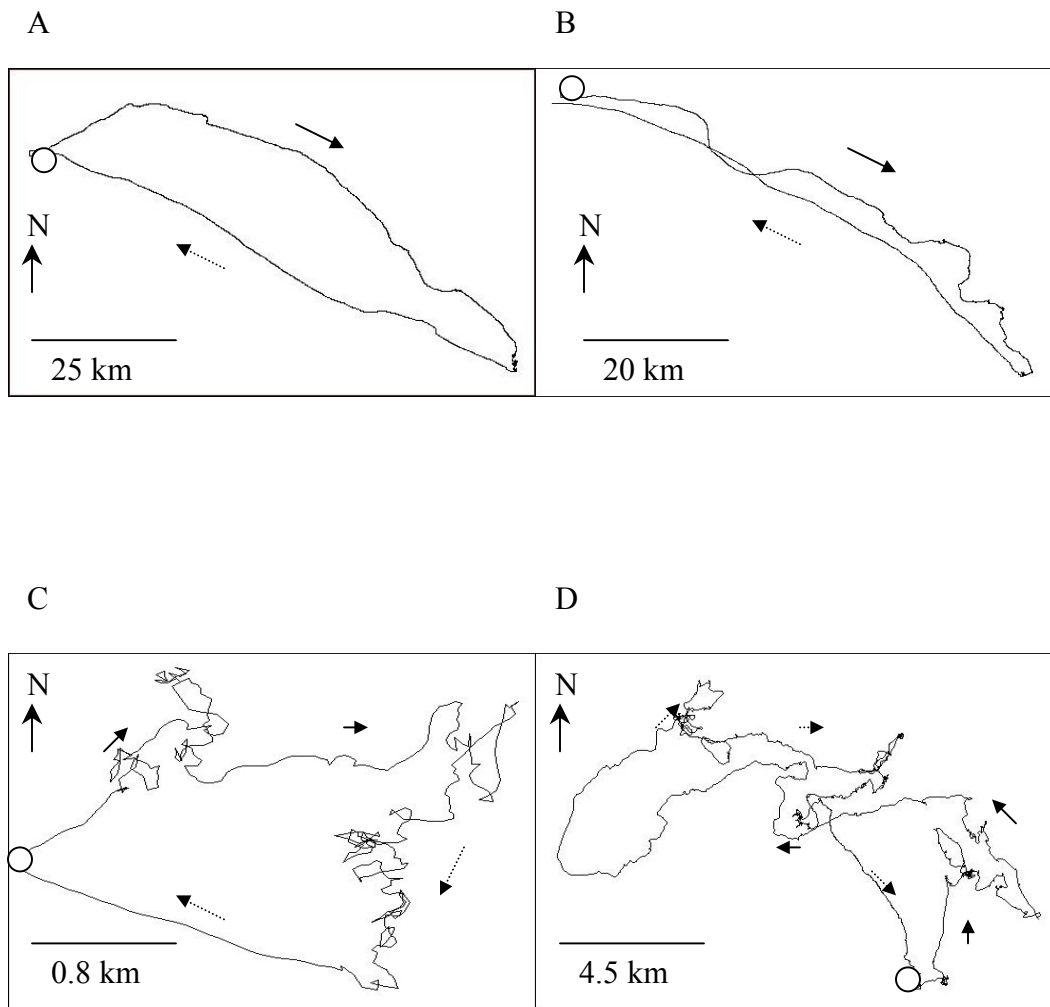


Figure 3. Foraging routes of Blue-footed Boobies breeding at Isla Lobos de Tierra. Straight routes (A, B) were undertaken by two females, and circuitous routes (C, D) by two males. The circle indicates the breeding colony and the bold and dashed arrows show the outbound and inbound flights, respectively.

Similarly, mean flight orientation for all birds in 2003 was not random (Rayleigh test, $VL = 0.596$, $P = 0.001$). They were feeding mainly to the east (mean = $76^\circ \pm 52^\circ$) and closer to the island (Fig. 4B). Mean bearing in 2003 differed significantly from 2002 (Mardia-Watson-Wheeler test, $\chi^2 = 8.40$, $n = 30$, $P = 0.005$, Table 3). Again, there were no significant differences in the mean flight direction between sexes (Mardia-Watson-Wheeler test, $B = 7.96$, $P > 0.05$), but females were more oriented to the east (Rayleigh test, $VL = 0.70$, $P = 0.005$; Table 3) than males (Rayleigh test, $VL = 0.480$, $P = 0.204$). Thus, for both years males and females had similar flight directional preferences, but dispersion was higher in males than in females.

Birds foraged at greater distances in 2002 (mean = 50.32 ± 27.42 km, $n = 17$; Fig. 4A) than in 2003 (mean = 35.70 ± 29.12 km, $n = 41$; Fig. 4B), but this difference was marginally significant (log-transformed max. distance, REML, $F_{1,22} = 3.50$, $P = 0.074$). Sex-specific differences in the maximum foraging distance were not significant (log-transformed max distance, REML, $F_{1,22} = 1.84$, $P = 0.188$; Table 3, Fig. 5), with a marginal interaction between sex and season (REML, $F_{1,22} = 3.16$, $P = 0.089$), indicating that males traveled longer distances in 2002, but shorter distances in 2003 (Table 3).

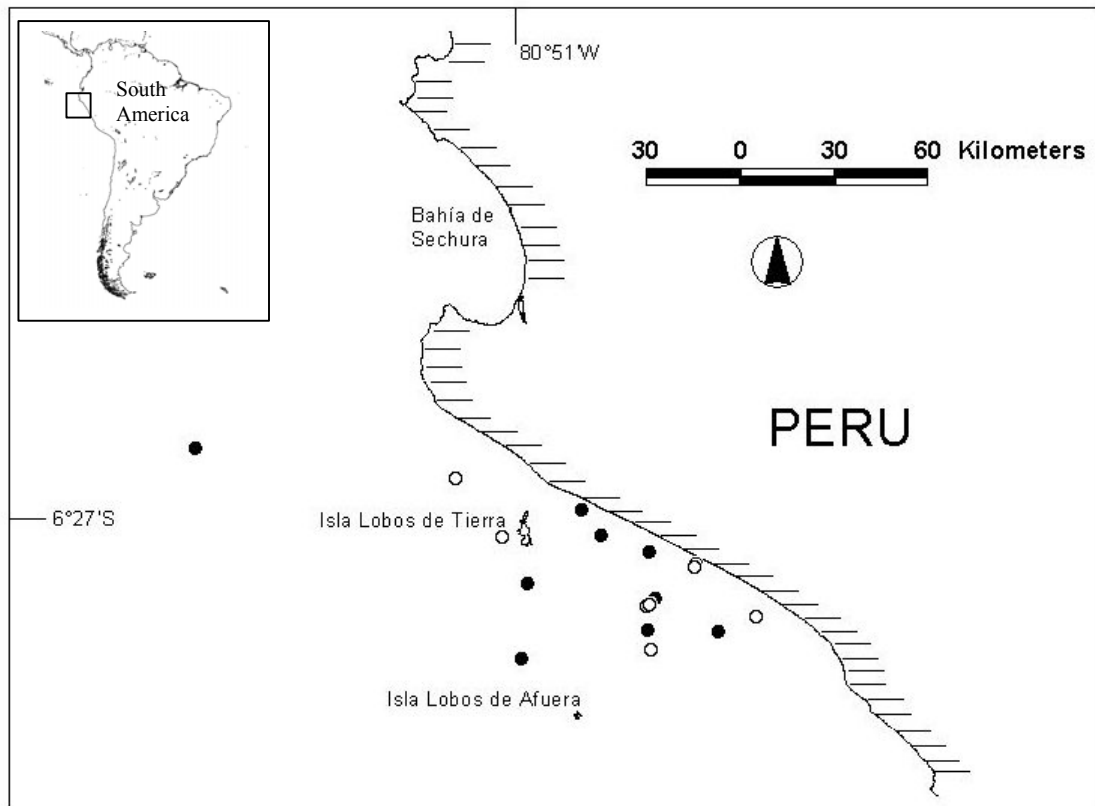


Figure 4A. At-sea spatial distribution of Blue-footed Boobies from 17 trips made by 4 females (solid circles) and 5 males (open circles) in 2002.

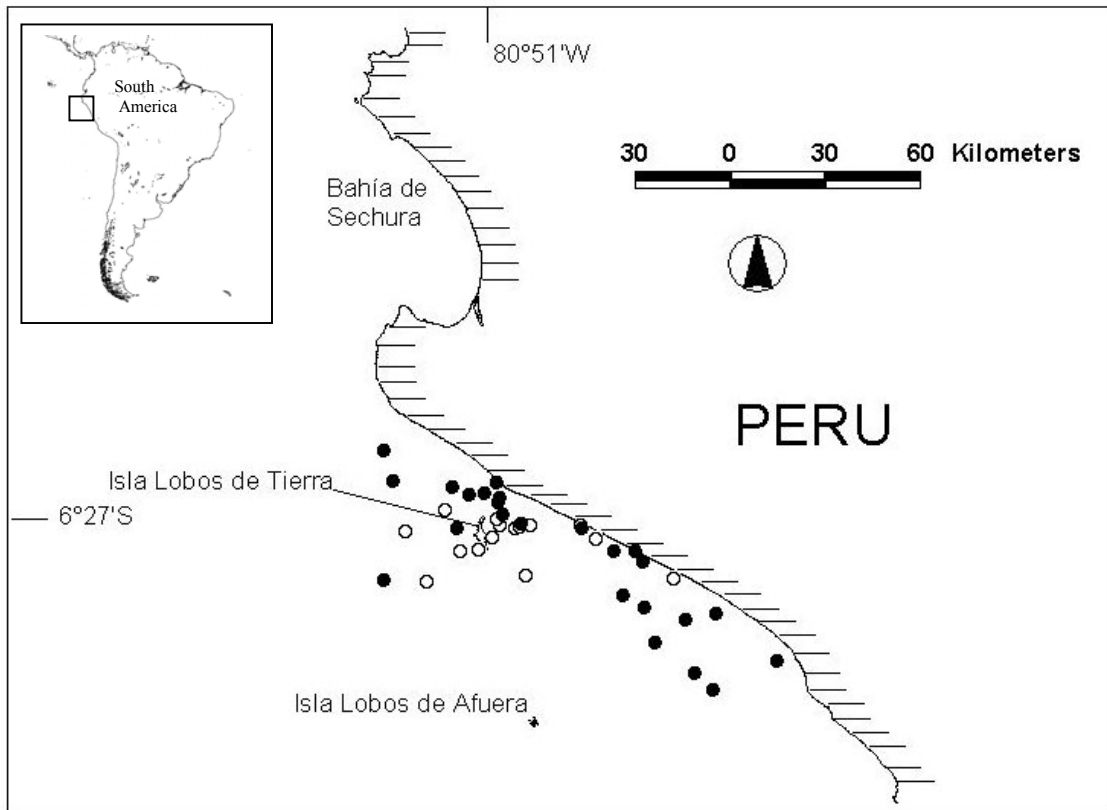


Figure 4B. At-sea spatial distribution of Blue-footed Boobies from 41 trips made by 10 females (solid circles) and 7 males (open circle) in 2003.

Table 3. Flight direction and maximum foraging distance by sex of breeding Blue-footed Boobies at Isla Lobos de Tierra, Perú, in 2002 and 2003.

	2002		2003	
	Females	Males	Females	Males
Bearing (°)				
Mean ± SD	120 ± 33	128 ± 54	84 ± 45	60 ± 58
Range	65 - 159	93 - 268	26 - 340	58 - 300
Number of birds	4	5	10	7
Maximum Distance (km)				
Mean ± SD	47 ± 30	54 ± 26	45 ± 31	19 ± 17
Range	16 - 109	8 - 94	8 - 102	3 - 63
Number of trips	9	8	26	15

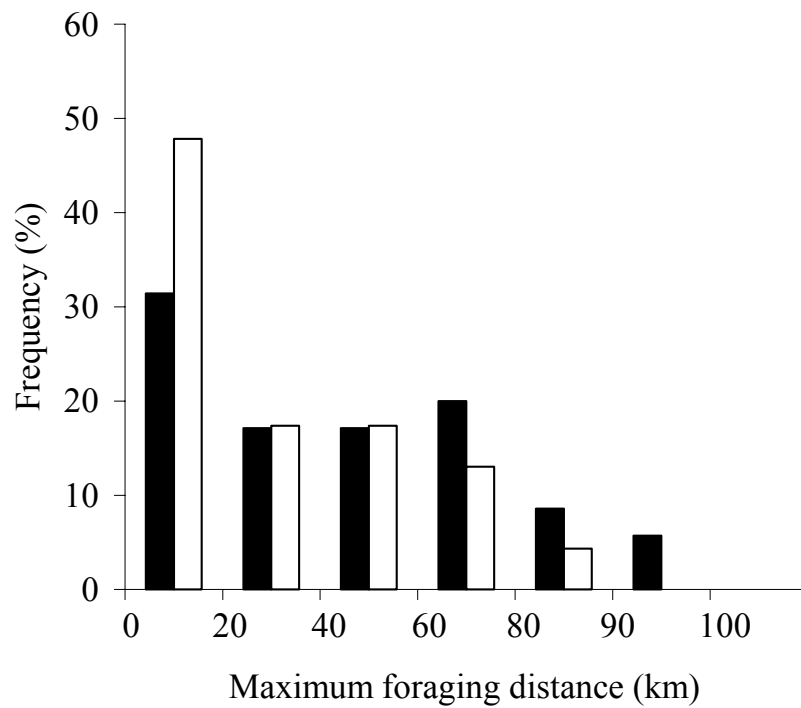


Figure 5. Distribution of maximum foraging distance from 58 trips of 15 female (solid bars) and 12 male (open bars) Blue-footed Boobies fitted with flight sensors and data loggers at Isla Lobos de Tierra in 2002 and 2003 (data for both years were pooled).

DISCUSSION

The results obtained in this study do not support the hypothesis of intersexual segregation of feeding areas in the Blue-footed Booby. Females traveled longer distances than males in 2003, but shorter distances than males in 2002. Both sexes usually foraged 30-55 km from the island and were predominantly oriented to the east or southeast where cold, upwelling waters of the Humboldt Current are found. Flight orientation of males was more dispersed than females, while females were more oriented to some specific feeding grounds. Males made predominantly circuitous routes while females tended to fly straight to a specific area, suggesting that males are more erratic in searching for food. However, there is no evidence that males feed close to the island in shallower waters and females search for food at further distances.

Some authors have suggested that intersexual spatial segregation of some species of seabirds is the result of competitive exclusion of feeding areas. For instance, male Northern Giant Petrels feed chiefly on penguin and seal carcasses on beaches while females consume a greater proportion of krill, squid and fish offshore. This segregation may avoid competition for food and reduce intraspecific aggressions as larger males can better defend feeding territories and establish dominance at carrion (González-Solís et al. 2000). Likewise, the dominance of the relatively larger Wandering Albatross on the feeding grounds, at the edge of the Crozet island shelf, may force the relatively smaller female to feed farther north in pelagic waters during the brooding period (Weimerskirch et al. 1993). The intersexual differences of foraging areas in Adélie Penguins during the guarding period may be a consequence of the initial parental role division during early

stages of the reproductive cycle. Male Adélie Penguins put more of their reproductive effort into a courtship and incubation than their mates (Chapell et al. 1993), which is compensated later by shorter and more inshore trips (Clarke et al. 1998). Likewise, Gilardi (1992) suggested that the division of parental roles in the Brown Booby (*Sula leucogaster*), may explain why females, which are the larger sex, forage at greater distances than males. Female Brown Boobies feed more often and bring larger amounts of food to their chicks than males because of their increased payload capacity and foraging range. Conversely, males will feed close to the colony to have a quick access to their nests and greater odds for extra-pair copulations (Gilardi 1992). Northern Gannets also exhibit sexual differences in their feeding areas, despite not being sexually dimorphic (Lewis et al. 2002). Possible explanations for these observations have been attributed to differences in the energy or nutrient requirements between sexes as a consequence of molting stage or calcium deficiency of females during egg production (Lewis et al. 2002).

Intersexual segregation of feeding areas as an ultimate factor for the evolution of sexual dimorphism does not apply to Blue-footed Boobies in northern Perú, at least at present, because females and males not only fed upon the same prey (see next chapter), but unlike other more pelagic birds, they foraged at shorter distances from the colony where food supply can be more predictable. However, the division of labor hypothesis in the Blue-footed Booby during the chick-rearing period has not been supported by behavioral observations on Isla Isabela, México (Guerra and Drummond 1995). The molting stage of Blue-footed Boobies during the study period was similar between sexes (Table 1) and it is unlikely that females prefer discrete areas at sea, searching for

calcium-rich prey when an abundant calcium source is available ashore on deposits of mollusk shells (pers. obs.).

If food competition is the driving force for disruptive selection on the sexes, then it is expected that feeding-niche segregation would occur in years when food is scarce. There is some evidence that food supply during the study period was relatively high (pers. obs.). First, a large population of Blue-footed Boobies (over 150,000 breeding pairs) and Peruvian Pelicans (over 20,000 pairs) bred on the island. When conditions are not optimal, pelicans do not attempt to breed or abandon their nests (pers. obs.). Second, the Peruvian Anchovy was the predominant prey in the diet of Blue-footed and Peruvian boobies (C. Zavalaga, unpubl. data). The occurrence of anchovies in the booby's diet indicates favorable conditions (Jahncke and Goya 2000). Third, commercial fishing activities were cancelled between January and March 2003, reducing possible levels of competition for the same anchovy stocks, and fourth, no reproductive failure was observed in any of the seabird species nesting on the island. Thus, a high availability of anchovies around Isla Lobos de Tierra during the study period probably explains not only the occurrence of high numbers of breeding birds, but also the lack of partitioning of foraging areas between sexes.

No differences in bearing and foraging range between sexes also may indicate that birds forage in large flocks and some can be attracted to feeding frenzies while commuting to other areas. Multispecies feeding flocks involving Blue-footed Boobies have been observed in the Galápagos Islands (Mills 1998). Likewise, feeding in large flocks is a common behavior for several endemic seabirds of the Humboldt Current as an adaptation to exploit the patchy distribution of anchovy schools (Duffy 1983), and on

some occasions, Blue-footed Boobies were observed in feeding frenzies a few kilometers from Lobos de Tierra in association with Peruvian Boobies, Peruvian Pelicans, Inca Terns (*Larosterna inca*), and dolphins (pers. obs.).

In conclusion, female and male Blue-footed Boobies did not exhibit a marked at-sea spatial segregation in spite of their sexual size dimorphism. However, the high availability of food during the study period may not have promoted any ecological differentiation between the sexes and similar studies under different oceanographic conditions (inter-annual comparisons in the same colony or comparisons among different localities) are necessary to confirm the results found here. Other proximate factors such as feeding in large flocks or attraction to feeding frenzies also may explain the lack of intersexual spatial segregation of Blue-footed Boobies in northern Perú.

CHAPTER 4

DIET COMPOSITION, PREY SIZE AND FOOD LOAD

INTRODUCTION

There is scant information on the feeding habits of Blue-footed Boobies. Indirect evidence suggests that these birds are generalist predators, consuming flying fish (*Exocoetus* spp.), sardines, anchovies, mackerels and squids (Nelson 1978). The only quantitative dietary analysis of Blue-footed Boobies was conducted on Isla Lobos de Tierra, northern Perú (Jahncke and Goya 2000). Here, they feed extensively on Peruvian Anchovies when available, but can switch to other more coastal fishes in years of oceanographic anomalies. Moreover, the feeding niche overlap between Blue-footed, Peruvian and Nazca boobies was considerably high in spite of the marked differences in size among these sympatric species (Jahncke and Goya 2000). It is likely that the three species of boobies forage in different areas to avoid interspecific competition. Thus, Nazca Boobies forage further offshore than Blue-footed Boobies (Anderson and Ricklefs 1987), and the latter feed in a wider area than Peruvian Boobies (Duffy 1987). However, Blue-footed Boobies and Peruvian boobies preyed upon different sizes of Peruvian Anchovies, suggesting size-specific segregation of feeding niches, as Blue-footed Boobies are up to 13% heavier than Peruvian Boobies (Nelson 1978). Although female Blue-footed Boobies on the Galápagos Islands can carry larger food loads than males (Anderson and Ricklefs 1992), it is unknown whether diet composition or separation of prey size distribution operates also at the intraspecific level.

The intersexual feeding niche divergence as a mechanism for the evolution of sexual dimorphism in birds is still controversial and has been overshadowed by the sexual selection hypothesis (see Shine 1989). This controversy rises from contradictory results on diet composition or prey size between both monomorphic and dimorphic

species. For instance, sex-specific differences in diet composition occurred in species either with moderate sexual size dimorphism such as Slaty-backed Gulls (*Larus schistisagus*; Watanuki 1992), Common Murres (*Uria aalga*; Lorentsen and Anker-Nilssen 1999), Magellanic Penguins (*Spheniscus magellanicus*; Forero et al. 2002), Common Terns (*Sterna hirundo*; Wagner and Safina 1989), Crested Auklets (*Aethia cristatella*; Fraser et al. 2002), but it was absent in species with marked sexual dimorphism such as Magnificent Frigatebirds (*Fregata magnificens*; Calixto-Albarrán and Osorno 2000). On the other hand, intersexual differences in mean prey size, but not in diet composition in Roseate Terns (*Sterna dougallii*; Wagner and Safina 1989), Adélie Penguins (*Pygoscelis adeliae*; Ainley and Emison 1972) and Antarctic Shags (*Phalacrocorax bransfieldensis*; Casaux et al. 2001), suggest subtle differences in feeding ecology.

In this chapter, I examine possible intersexual feeding-niche divergence in the dimorphic Blue-footed Booby. Because males and females forage at similar areas, it is likely that the ecological segregation between sexes occurs in the type, size or quantity of food consumed. To test this hypothesis, I investigated the diet composition, prey size and food load from spontaneous regurgitations of known-sex Blue-footed Boobies on Isla Lobos de Tierra, Perú.

RESULTS

Diet.- Blue-footed Boobies fed on 16 species of fish and one species of squid (Table 4), but the Peruvian Anchovy was the most important prey consumed. There was a significant difference in diet composition between seasons, with a lower proportion of anchovies in 2002 (80%) than in 2003 (97%, Z test for proportions, $Z = 3.87$, $P < 0.05$). The diversity of prey items in the diet of females was similar to that of males in 2002 ($H_f = 0.094$, $H_m = 0.139$, t -test, $t = 0.66$, $P > 0.05$) and 2003 ($H_f = 0.572$, $H_m = 0.498$; t -test, $t = 0.937$, $P > 0.05$). Likewise, males and females consumed similar proportions of anchovies either in 2002 (Z -test for proportions, $Z = 11$, $P = 0.61$) or in 2003 ($Z = 15.4$, $P = 0.46$, Table 4).

Adult anchovies (total length ≥ 11 cm) were the target age group preyed upon by Blue-footed Boobies (80% of the total number anchovies consumed were adults). Mean anchovy total length was significantly smaller in 2002 (mean = 11.74 ± 1.48 cm, $n = 930$) than in 2003 (mean = 12.95 ± 1.44 cm, REML, $F_{1,1330} = 202.9$, $P < 0.001$). Females consumed significantly larger anchovies (mean = 12.53 ± 1.52 cm, $n = 856$) than males (mean = 11.89 ± 1.59 cm, $n = 724$, REML, $F_{1,1330} = 5.31$, $P = 0.0214$). There were no significant sex-by-season interaction terms (REML, $F_{1,1330} = 2.08$, $P = 0.149$). Likewise, the total length of Short-finned Butterfish (*Peprilus snyderi*) captured by females (mean = 11.43 ± 1.36 cm, $n = 55$) was larger than that of males (mean = 10.36 ± 1.61 cm, $n = 41$), but unlike anchovies, these differences were not significant (REML, $F_{1,81} = 1.88$, $P = 0.174$). Mixed models analysis for testing size differences in other prey was not attempted because of small sample sizes. However, when the median fish length per regurgitation

was assessed to avoid pseudo-replication, and then these medians compared between sexes, females and males consumed similar sizes of Pacific Bumpers (*Chloroscombrus orqueata*) (Mann-Whitney *U*-test, $U = 11$, $P = 0.83$) and Long-nose Anchovy (*Anchoa nasus*) (Mann-Whitney *U*-test, $U = 2$, $P = 0.10$).

Food load.- In both seasons, females brought larger food loads (2002: mean = 109.2 ± 67.2 g, $n = 10$; 2003: mean = 115.8 ± 79.5 g, $n = 29$) than males (2002: mean = 93.8 ± 45.4 g, $n = 10$; 2003: mean = 79.9 ± 49.7 g, $n = 25$), but these differences were not significant (log-transformed crop mass, GLM, $F_{1,73} = 1.25$, $P = 0.268$). Prey mass also was similar between seasons (GLM, $F_{1,73} = 0.63$, $P = 0.431$, Fig. 6A), and the seasonal effect on prey mass was not different in males and females (GLM, $F_{1,73} = 0.71$, $P = 0.402$). When using data from chick-rearing birds in 2003 only ($n = 54$), the sex-specific differences in food load were marginal (log-transformed food load, GLM, $F_{1,53}$, $P = 0.056$).

When the food load was divided by the adult body mass, the relative food load also was similar between sexes (arcsin ratio GLM, $F_{1,73} = 0.04$, $P = 0.847$, Fig. 6B) and between seasons (GLM, $F_{1,73} = 0.26$, $P = 0.608$). There was no interaction of sex and season affecting the relative food load of birds (GLM, $F_{1,73} = 0.50$, $P = 0.483$).

Table 4. Sex-specific diet composition (expressed as % by mass) for Blue-footed Boobies on Isla Lobos de Tierra in June-July 2002 (females = 63, males = 61) and January-February 2003 (females = 118, males = 85). F = females, M = males.

Prey Species		2002		2003	
		F	M	F	M
Peruvian anchovy	<i>Engraulis ringens</i>	98.0	97.0	78.9	82.5
Short-finned butterflyfish	<i>Peprilus snyderi</i>	---	---	4.9	9.0
Long-nose anchovy	<i>Anchoa nasus</i>	---	0.5	2.5	3.1
Pacific mackerel	<i>Scomber japonicus</i>	---	---	2.0	1.2
Pacific bumper	<i>Chloroscombrus orqueata</i>	---	---	2.7	0.7
Horse mackerel	<i>Trachurus murphyi</i>	---	---	2.9	---
Squid	<i>Loligo gayi</i>	---	0.7	1.2	0.5
Peruvian banded croaker	<i>Palaronchurus peruanus</i>	---	---	1.2	---
Peruvian weakfish	<i>Cynoscion analis</i>	---	---	1.0	1.2
Striped mullet	<i>Mugil cephalus</i>	---	---	0.8	---
Palm ruff	<i>Seriolella violacea</i>	---	---	0.8	---
South Pacific sauri	<i>Scomberesox saurus scombroides</i>	2.0	---	0.8	1.6
Starry butterflyfish	<i>Stromateus stellatus</i>	---	---	0.2	---
Gulf gurnard	<i>Bellator gymnothetus</i>	---	---	---	0.1
Peruvian silverside	<i>Odontesthes regia regia</i>	0.1	---	---	0.1
Blue bobo	<i>Polydactylus approximans</i>	---	0.9	---	---
Bighead tilefish	<i>Caulolatilus affinis</i>	---	0.7	---	---

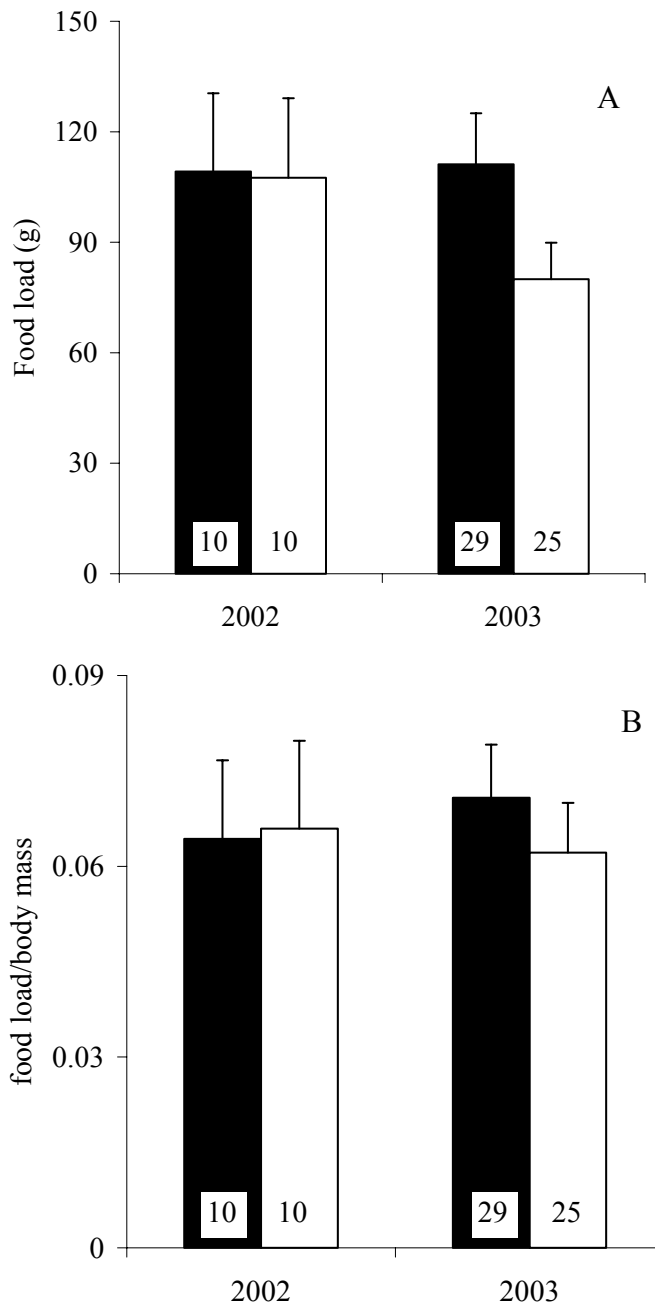


Figure 6. Mean absolute (A) and relative (B) food load (± 1 SE) of female (solid bars) and male (open bars) Blue-footed Boobies in 2002 and 2003 at Lobos de Tierra Island, Perú. Sample size is given at the bottom of the bars.

DISCUSSION

Diet composition and prey diversity were similar between female and male Blue-footed Boobies, and therefore differences in body size do not demonstrate any advantages to avoid inter-sexual competition for food type. Because of these similarities in prey type, it is likely that food quality consumed by females and males, in terms of specific caloric content, also was similar. I did not observe any qualitative differences in the breeding condition of prey consumed by males and females (e.g., gonad development). The sex-specific differences in the diet of other dimorphic seabird species seem to be related more to the segregation of the feeding areas (Wagner and Safina 1989, Weimerskirch et al. 1997, Clarke et al. 1998, González-Solís et al. 2000) or partitioning of foraging times (Croxall and Lishman 1987, Favero et al. 1998, Fraser et al. 2002) than the selection of particular prey.

It has been suggested previously (Chapter 3) that the lack of feeding area segregation between male and female Blue-footed Boobies on Isla Lobos de Tierra could be related to the formation of feeding flocks conspicuous enough to attract birds from different locations. Also, food availability during the study period may have been above the species threshold value that would promote intraspecific competition. The same proximate factors may explain the similarities in diet composition between sexes. Nevertheless, females consumed larger anchovies than did males. Because there was overlap in the time (see Chapter 5) and location of foraging between male and female Blue-footed Boobies, it is likely that they feed upon the same anchovy schools. It seems that anchovies within a school are heterogeneous in length and that the capture of

different fish sizes between sexes may be the result of spatial stratification of the prey once it is disrupted during multiple dive-plunging by the flock. Female Blue-footed Boobies can dive deeper and longer than males (see Chapter 6) and consequently, they could capture larger fish in deeper waters or could pursue them underwater by wing and foot propulsion. This explanation is just speculative as it is unknown whether Peruvian Anchovies of different ages or sizes are not randomly distributed within a school.

A 7% larger bill in females relative to males (Table 1) may allow them to capture and handle larger prey more efficiently, as may occur in the Antarctic Shag (*Phalacrocorax bransfieldensis*; Favero et al. 1998). The difference of anchovy mean size consumed by females and males was only 0.7 cm, but even small differences in food features may become a strong selection pressure for changes in body size of the consumers when competition for food is severe, as occurred in Medium Ground Finches (*Geospiza fortis*, Boag and Grant 1981). Why prey size selection occurred only in Peruvian Anchovies and not in other prey is unknown, but it may be related to interspecific differences in the aggregation behavior of fish.

On Isla Española in the Galápagos Archipelago, food load of female Blue-footed Boobies was more than three times that of males (Anderson and Ricklefs 1992), whereas on Isla Lobos de Tierra this difference was not significant and only 1.5 times higher. It is likely that this disparity between localities results from the energetic demands of the adults. The breeding adults sampled in Galápagos were rearing large nestlings (>1000 g) during the peak of provisioning rate (Anderson and Ricklefs 1992). On Isla Lobos de Tierra, birds were mostly provisioning small, medium-sized chicks (100 - 1000 g) when the daily food intake was lower (Anderson and Ricklefs 1992). The larger food loads of

females seem to be related to their size as the intersexual ratio of food load (1.5) is similar to the ratio of female to male body mass (1.3 - 1.4). Indeed, when the food load is standardized according to body mass, the relative food load is similar between sexes suggesting that during the study period female and male Blue-footed Boobies foraged until a certain mass-load threshold was attained.

The results of this study partially support the hypothesis of feeding-niche partitioning as a mechanism to reduce intraspecific competition. Diet composition was similar between sexes, but Peruvian Anchovy size consumed by females was slightly larger than those consumed by males. No differences in prey sizes were found in three other prey species. The differences in anchovy length may be the result of a size-related stratification of anchovies within a school, prey handling efficiency and the capability of Blue-footed females to dive deeper and longer than males. Accordingly, multiple plunging of birds over a school will depolarize it, larger anchovies may refuge in relatively deeper waters and heavier females will capture them either while surfacing or by underwater pursuit. Food load was 1.5 times larger in females than in males as a consequence of the disparity in body mass, but this difference was not significant. Because the relative crop mass is similar between sexes, it is suggested that Blue-footed Boobies on Isla Lobos de Tierra forage until a certain mass load threshold is reached.

CHAPTER 5

TIMING OF FORAGING, FORAGING TRIP DURATION AND TIME ALLOCATION OF AT-SEA ACTIVITIES

INTRODUCTION

The type of parental care that has evolved in a species varies widely within the Class Aves (Clutton-Brock 1991). Biparental care is found in all seabirds, but the extent on parental investment is not always equally shared between the sexes. Nest attendance is unevenly allocated at different stages of the breeding cycle in Emperor Penguins (*Aptenodytes forsteri*; Williams 1995) and Macaroni Penguins (*Eudyptes chrysolophus*; Barlow and Croxall 2002) or foraging takes place at different times of the day during chick brooding in the Thick-billed Murre (*Uria lomvia*; Jones et al. 2002). In other seabirds, mates share duties equally during incubation or chick rearing, although the energetic input to their chicks may differ (Weimerskirch et al. 1997). There are many anatomical, physiological, behavioral and ecological factors that explain the partitioning of incubation or brooding duties between mates in some species of seabirds (see Clutton-Brock 1991). Nevertheless, the temporal pattern of foraging activities has been poorly described in seabird species with marked sexual dimorphism.

It has been suggested that reversed size dimorphism of Blue-footed Boobies has evolved as a mechanism to reduce food competition (Nelson 1978). However, I have demonstrated that there was no feeding niche partitioning in this species when the at-sea distribution and diet composition was compared between females and males (Chapters 3 and 4). If a temporal rather than spatial segregation reduces intersexual competition for food in the Blue-footed Booby, it would be expected to find differences either in the (1) timing of foraging, (2) foraging trip length, (3) number of trips per day or (4) time budget of at-sea activities.

To assess these foraging variables, I monitored the departure and arrival times by direct observations of breeding birds. Simultaneously, I attached flight sensors in a group of birds to examine time allocation of different activities at sea.

RESULTS

Timing and duration of foraging trips.- Activity recorders revealed that Blue-footed Boobies foraged only during daylight hours and spent the night in their nests (sunrise and sunset during the study period varied between 0640 - 1835 h in June-July 2002 and 0650 - 1901 h in January-February 2003). Only 13% of the trips started before sunrise, generally during twilight, whereas 14% of the trips were completed after sunset, but no later than 2030 h. Only one bird spent the night resting on the sea surface close to the island after completing its foraging trip.

When the time of the day was split into five equal periods, the number of departures in each time period was significantly different between sexes in 2002 ($F_{1,24} = 4.89$, $P = 0.037$) and marginally different in 2003 (REML, $F_{1,80} = 3.65$, $P = 0.06$) because females departed more often by mid-morning than did males (Fig. 7). Conversely, the pattern of departures was similar between males and females in both seasons (2002: REML, $F_{1,24} = 2.57$, $P = 0.122$; 2003: REML, $F_{1,80} = 0.50$, $P = 0.482$, Fig. 8).

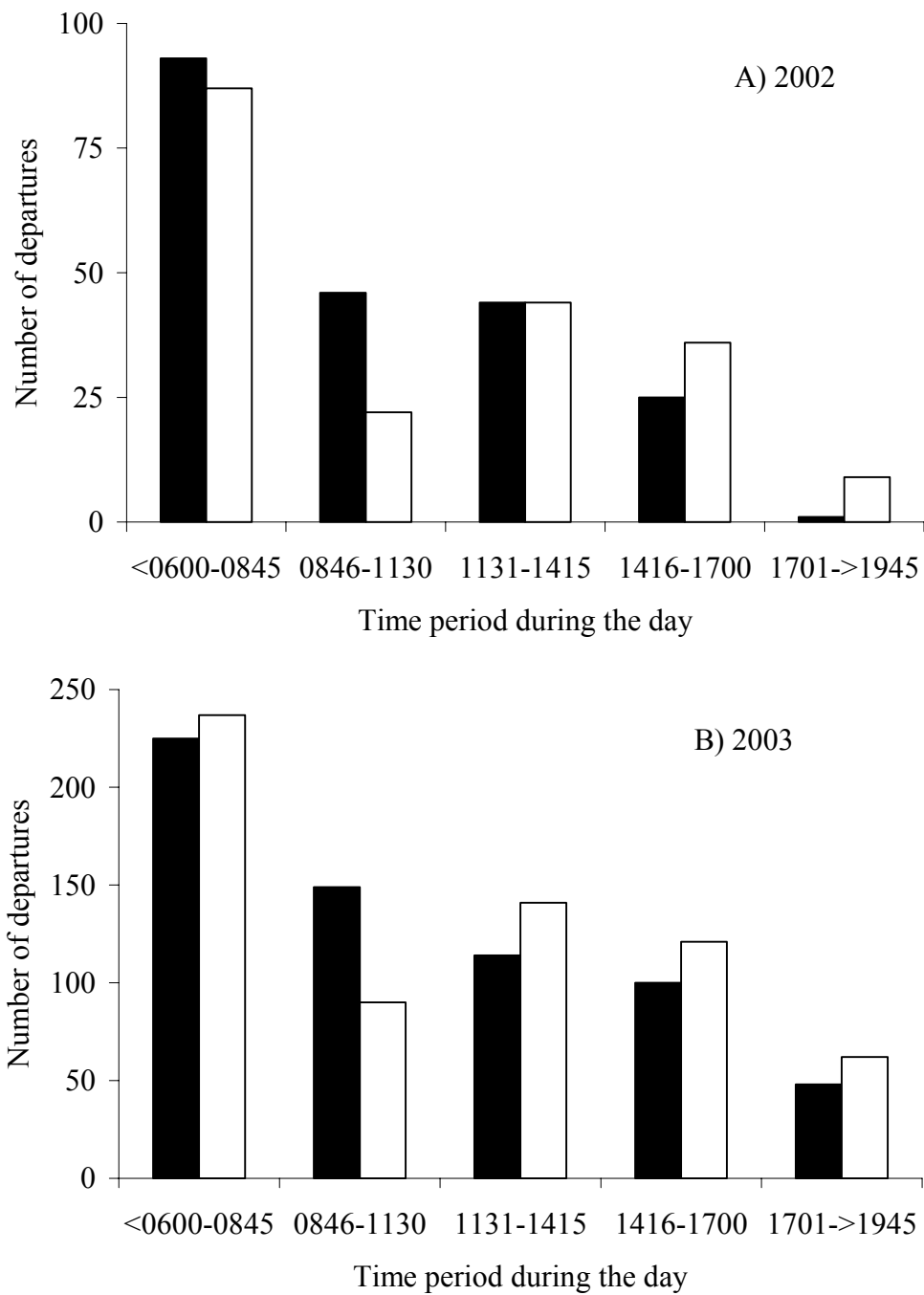


Figure 7. Timing of departures of 13 Blue-footed Booby pairs ($n = 407$ trips) in 2002 (A) and 41 pairs ($n = 1287$ trips) in 2003 (B). Females and males are represented by solid and open bars, respectively.

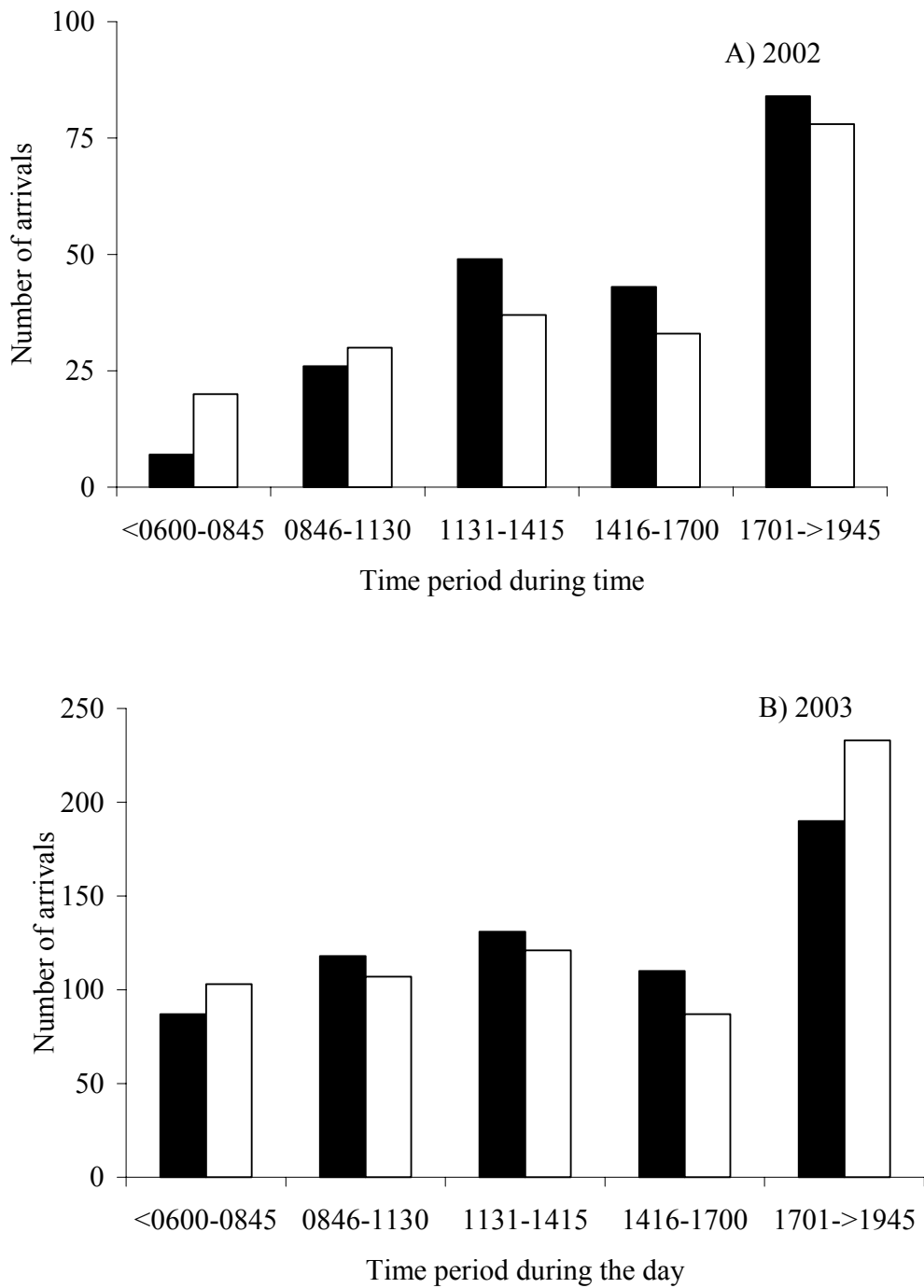


Figure 8. Timing of arrivals of 13 Blue-footed Booby pairs ($n = 407$ trips) in 2002 (A) and 41 pairs ($n = 1287$ trips) in 2003 (B). Females and males are represented by solid and open bars respectively.

It was not possible to estimate how many trips each instrumented bird could complete in a day because most of the devices were retrieved after one feeding trip. However, the number of trips determined from data loggers of birds fitted with devices for more than 3 days ($n = 8$ birds) and the number of trips determined simultaneously by nest attendance observations of the same birds was exactly the same (range: 1 - 3 trips per day). Thus, to examine sex-specific differences in the number of trips per day, I used data from direct observations of marked non-instrumented birds, where the nest changeovers were known ($n = 57$ birds). Overall, the number of feeding trips per day was significantly lower in 2002 (mean = 1.2 ± 0.39 , $n = 345$) than in 2003 (mean = 1.73 ± 0.68 , $n = 742$), but it was similar between males and females (GMM, link=logit, $\chi^2 = 1.75$, $P = 0.185$; Table 5). No significant interaction of sex by year in the number of trips per day was found (REML, $F_{1,113} = 0.51$, $P = 0.475$).

Foraging trip durations were highly variable, ranging from 0.38 to 14 h during the study period (Fig. 9). The feeding trips were significantly longer in 2002 (mean = 4.07 ± 0.20 h, $n = 298$) than in 2003 (mean = 2.50 ± 0.19 h, $n = 849$; REML log (x+1)-transformed trip duration, $F_{1,1007} = 82.12$, $P < 0.0001$; Fig. 9). The difference in the duration of feeding trips between females and males was marginally significant (REML, log (x+1)-transformed trip duration, $F_{1,1007} = 3.31$, $P = 0.07$, Table 5, Fig. 9). Likewise, differences between sexes by season in the duration of feeding trips also was marginal (REML, $F_{1,1007} = 2.97$, $P = 0.085$), indicating that females tended to spend more time at sea than did males in 2002, but in 2003 feeding trips of males were longer (Table 5, Fig. 9).

Table 5. Number of trips per day and duration of foraging trips of Blue-footed Boobies on Isla Lobos de Tierra. Values are means \pm 1 s.d., range (number of trips).

Parameters	2002		2003	
	F	M	F	M
No. trips/day per bird	1.18 \pm 0.4	1.17 \pm 0.39	1.70 \pm 0.69	1.75 \pm 0.68
	1 - 3 (178)	1 - 3 (167)	1 - 4 (372)	1 - 5 (370)
Trip duration (h)	5.12 \pm 2.78	4.13 \pm 2.46	2.88 \pm 2.05	2.91 \pm 1.99
	0.5 - 13 (154)	1 - 13.5 (144)	0.4 - 12 (446)	0.4 - 14 (403)

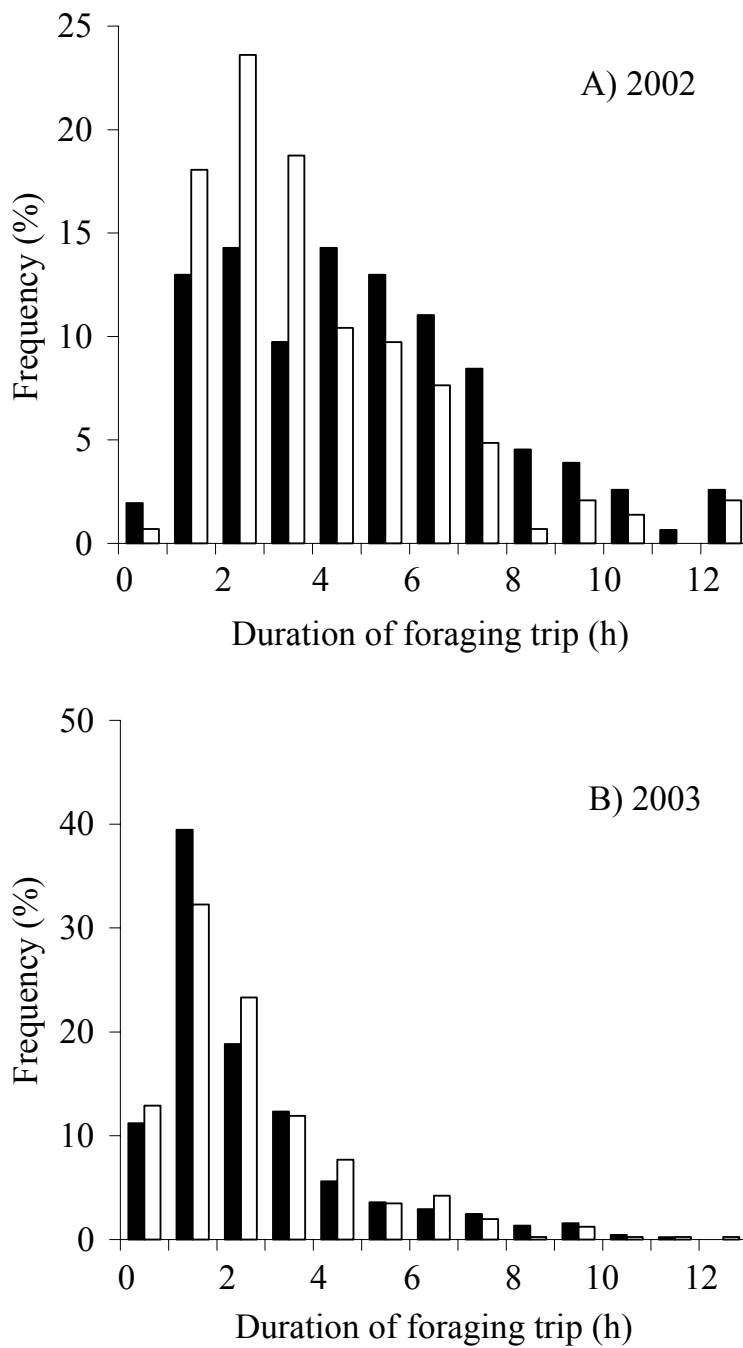


Figure 9. Distribution of the duration of foraging trips of 24 pairs Blue-footed Boobies ($n = 298$ trips) in 2002 (A) and 58 pairs ($n = 849$ trips) in 2003 (B). Females are represented by solid bars and males by open bars.

Time allocation of foraging activities.- There was high variation in the travel time from colony departure to the first dive in a feeding trip (mean = 23.0 ± 23.3 min., range: 1 - 143 min., $n = 93$) or from the last dive to the arrival at the nest (mean = 27.1 ± 21.8 min., range = 1 - 115, $n = 93$). However, the majority of Blue-footed Boobies began plunge-diving shortly after leaving the colony, with 44% of first dives occurring within the first 15 min. after departure. Thirty-one and 65% of the last dives were completed 15 and 20 min. prior to the arrival at the nest, respectively. When diving activity is compared to the proportion of total time spent foraging, it is clear that the birds were engaged in feeding activities during the entire trip, except the first 5% and last 10% period of the total trip duration, when they were leaving and returning to the island, respectively (Fig. 10). The temporal patterns of diving activity were similar both between seasons (Kolmogorov-Smirnov, $D = 0.077$, $P < 0.0001$) and between sexes (Kolmogorov-Smirnov, $D = 0.052$, $P < 0.05$, Fig. 10).

Overall, Blue-footed Boobies spent a higher proportion of their foraging time traveling and searching for food (83 - 89%), whereas resting on the sea surface and diving accounted for 8 - 13% and 3 - 6%, respectively. Data from 94 trips by 46 birds showed that the proportion of travel time was similar between sexes (arcsin transformed REML, travel time, $F_{1,42} = 0.52$, $P = 0.475$, Fig. 11) and seasons (arcsin transformed REML, travel time, $F_{1,48} = 0.02$, $P = 0.876$).

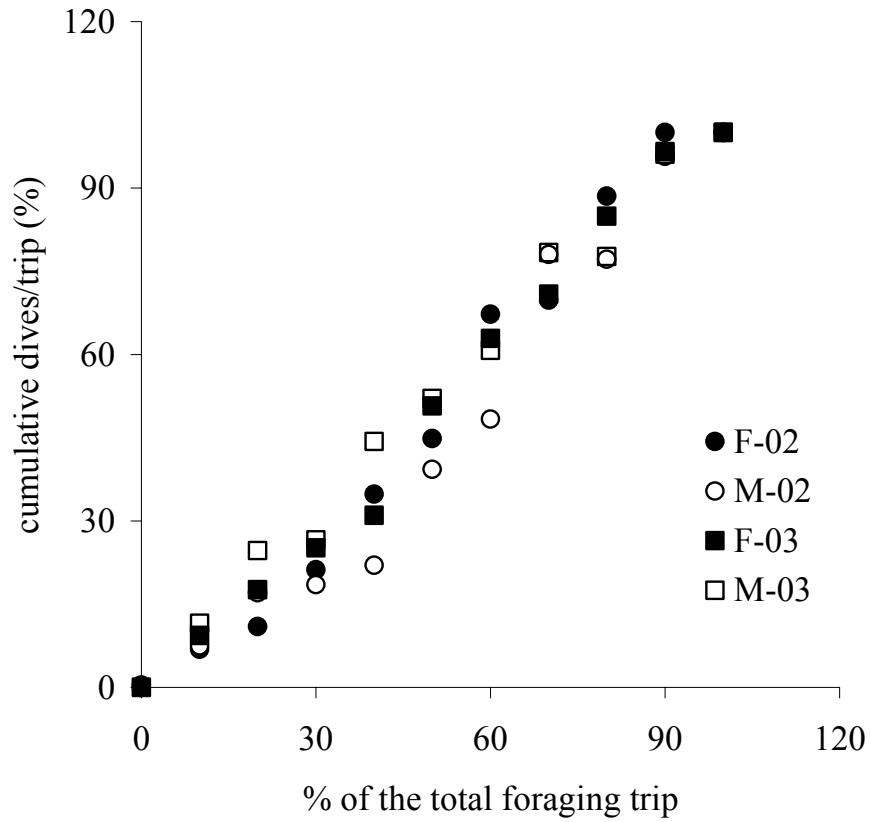


Figure 10. Cumulative number of dives made during a feeding trip in relation to the flight time for 8 (3 females, 5 males) and 37 (16 females, 21 males) instrumented Blue-footed Boobies breeding on Isla Lobos de Tierra in 2002 and 2003, respectively.

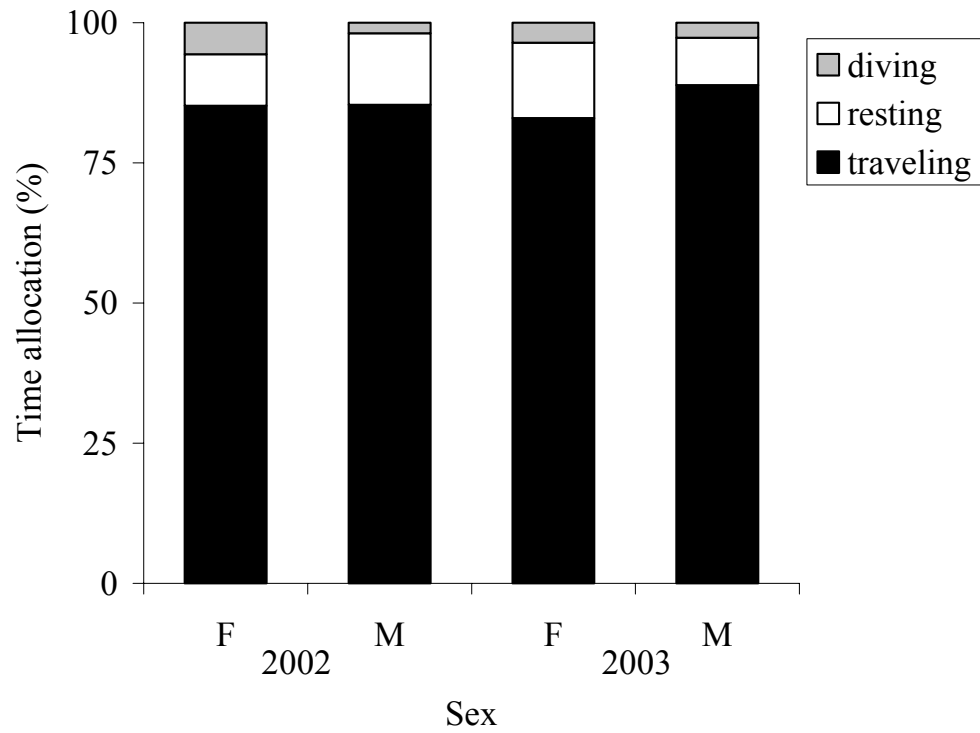


Figure 11. Time allocation (mean percentage) of three major at-sea activities (diving, resting on the sea surface and traveling) of 9 (4 females, 5 males) and 37 (17 females, 20 males) Blue-footed Boobies breeding on Isla Lobos de Tierra in 2002 and 2003, respectively.

DISCUSSION

Blue-footed Boobies on Isla Lobos de Tierra are diurnal foragers. Some birds could leave and return to their nests during twilight or before and after dusk, but feeding activities were not recorded during the night. Departures occurred chiefly after dawn and decreased steadily during the day, whereas the arrivals exhibited an opposite trend. The number of departures by mid-morning was higher in females than in males. It is interesting to observe that this pattern seemed to be fixed, regardless the breeding status or season. I hypothesize that this difference is the result of a higher accessibility of females to anchovies around midday, when the visibility in the water column is the highest. Females can attain deeper dives than males (Chapter 6), and consequently they could have access to anchovies that are deeper during the hours of high visibility. Thus, male probability of capturing prey in deeper waters around midday might be lower than that of females, and most males will remain in their nests during this period of time or will feed later in the day.

The diurnal vertical migration is a common behavior of Peruvian Anchovies, with schools remaining in deeper waters during the daylight and in shallower waters during twilight and night (Jordán 1971). It is likely that there are no sexual differences in the timing of foraging when the boobies feed on prey without rhythmic vertical movements because there would be no advantages to either sex. However, there could be advantages in foraging at different times of the day in species that are sexually dimorphic. In the Galápagos, male Blue-footed Boobies foraged later in the day than did females (Anderson and Ricklefs 1992), suggesting again that males could feed more efficiently

when prey are near the surface. A distinct difference in the diurnal timing of foraging is found in Thick-billed Murres, where males forage during midday and females during the dawn and dusk hours (Jones et al. 2002). This temporal segregation might benefit both sexes because females can expend less energy (and recover readily after the costs of egg production) by feeding on prey that migrate to shallow waters during dusk and dawn, while males will forage by shorter periods during the daylight, but will gain by spending more time in the nest before the lengthy period of uniparental care at sea (Jones et al. 2002). Such a division of labor is absent in the Blue-footed Booby, and therefore anatomical or behavioral rather than physiological constraints seem to be the most important factors for the observed temporal partitioning of foraging activities on Isla Lobos de Tierra.

The duration and number of feeding trips per day by either sex was similar within each season, but female Blue-footed Boobies could bring 1.5 times as much food as males during intermediate stages of the chick-rearing period (this study, Chapter 3), suggesting that females on Isla Lobos de Tierra may be more efficient foragers. In fact, female Blue-footed Boobies foraged 2 times more efficiently than males at the Galápagos (Anderson and Ricklefs 1992). Likewise, females fed their chicks more often than did males and the mass of food provided by females was greater than males until the chicks were at least 35 days old (Guerra and Drummond 1995). Foraging trips were highly variable not only between individuals but also within individuals, indicating that food distribution was unpredictable. Nevertheless, in pelagic seabirds, mates compensate for the allocation of resources between reproduction and survival by alternating trips of short and long duration when a threshold in adult body mass (Weimerskirch et al. 1997, Clarke

2001) or chick body condition (Baduini 2002) is reached. The duration of feeding trips of Macaroni Penguins was similar between sexes during the crèche period, but the larger males fed the chicks at a lower rate than females to recover the weight lost during the guarding period (Barlow and Croxall 2002). This alternation of foraging trips may also occur in the Blue-footed Booby, as they are able to regulate their body condition with changes of foraging effort (Velando and Alonso-Alvarez 2003). A more detailed analysis of feeding trips, coupled with regular weighing of adults and their chicks, is necessary to elucidate how adult body condition or chick mass regulates the duration and number of feeding trips in the Blue-footed Booby.

The proportion of time spent traveling and the diving activity during a foraging trip was similar between sexes, suggesting that flocking may be a common behavior of Blue-footed Boobies when searching for food. Unlike the more pelagic Northern Gannet (*Morus bassana*; Garthe et al. 1999, 2003), Blue-footed Boobies do not rest on the sea surface for long periods because their trips are shorter and they feed relatively closer to their colonies.

CHAPTER 6

DIVING BEHAVIOR

INTRODUCTION

Plunge-diving is the feeding technique used by all sulids to get their food (Nelson 1978). Once prey is located from the air, they plunge downwards at high speeds, entering the water at different angles. Cape Gannets (*Sula capensis*; Adams and Walter 1993), Atlantic Gannets (*Morus bassanus*; Garthe et al. 2000) and Red-footed Boobies (*Sula sula*; Le Corre 1997) can pursue their prey by swimming beneath the surface, using their feet and wings, but the depth they obtain depends mainly on the momentum gained during the plunge. Accordingly, it is expected that within the Sulidae, maximum dive depths would be positively related to body mass. For instance, the 3.0-kg Atlantic Gannet attained depths up to 22 m (Garthe et al. 2000), whereas maximum dive depth of the 0.9-kg Red-footed Booby was only 9.7 m (Le Corre 1997). It is likely that this relationship also occurs intraspecifically in species with pronounced sexual dimorphism in size, such as the Blue-footed Booby.

Interspecific allometric equations relating dive depth to body mass have been described for diving seabirds such as penguins, alcids and cormorants (see Schreer and Kovacs 1997), but intraspecific sexual comparisons of dive depths have been less studied (Walker and Boersma 2003) and conclusions on what factors limit dive depths still are not clear. For instance, the relatively larger male of Humboldt Penguins (*Spheniscus humboldti*; Taylor et al. 2002) and Japanese Cormorants (*Phalacrocorax capillatus*; Watanuki et al. 1996) dive deeper than the female. On the other hand, males and females in dimorphic Shags (*Phalacrocorax aristotelis*; Wanless et al. 1991) dive to similar depths, whereas in the monomorphic Atlantic Gannet, females dive deeper (Lewis et al. 2002), suggesting that factors other than body mass may limit dive depths between sexes.

In this chapter, I examine the sex-specific diving capabilities of Blue-footed boobies breeding on Isla Lobos de Tierra. Because diving depths in other birds are related to body mass, I expect that Blue-footed Booby females attain deeper dives than males.

RESULTS

The depth, duration and number of dives per trip were assessed from 51 birds (females = 23, males = 28) fitted with depth meters and flight sensors. One female Blue-footed Booby attained a maximum depth of 22 m with immersion time of 39 s (Table 6). However, the majority of dives were shallow (90% of dives < 6 m, Fig. 12A) and short (87% of dives < 10 s, Fig. 12B). Only dive depth was compared between sexes as it was significantly correlated to dive duration (Pearson correlation, $r = 0.69$, $P < 0.001$). Dive depths were similar in 2002 and 2003 (log transformed dive depths REML, $F_{1,4082} = 2.58$, $P = 0.108$, Table 6), but females dove significantly deeper than males (log transformed dive depths REML, $F_{1,47} = 10.33$ $P = 0.002$, Table 6).

There were significant seasonal differences in the total number of plunge-dives a bird performed per trip (log-transformed REML, $F_{1,55} = 5.62$, $P = 0.021$), with a higher number in 2002 than in 2003 (Table 6). Males dove a greater number of times per trip than did females, but these differences were not significant (REML, $F_{1,47} = 1.06$, $P = 0.308$). No interaction between sex and year in the dive depth was found (REML, $F_{1,55} = 0.72$, $P = 0.399$).

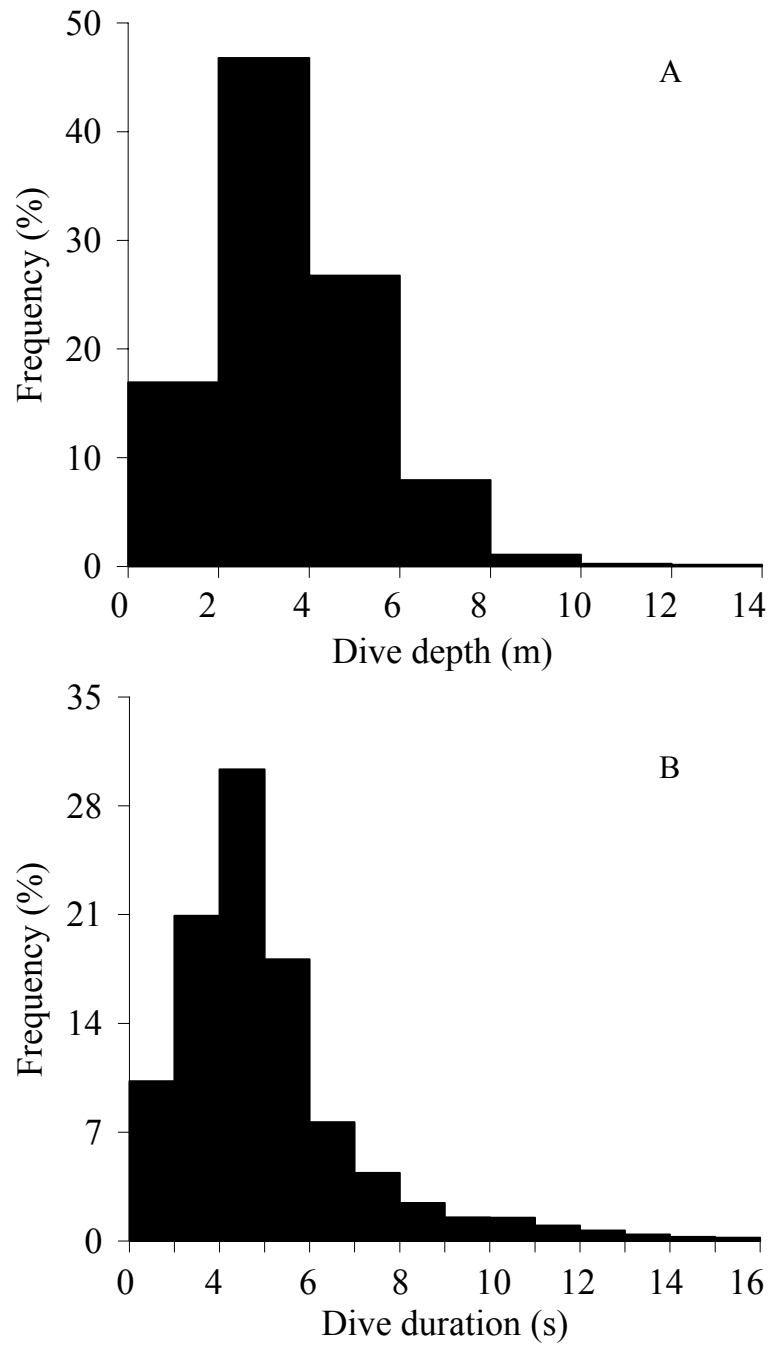


Figure 12. Dive depth (A) and dive duration (B) distributions of 51 Blue-footed Boobies at Lobos de Tierra Island (number of dives = 4133) in 2002 and 2003.

The mean dive attained by Blue-footed Boobies not only varied at different times during the day (log transformed, REML, $F_{5,4072} = 5.75$, $P < 0.001$), but the interaction between sex and time of the day on the dive depth was significant (log transformed, REML, $F_{5,4072} = 3.71$, $P = 0.002$). This indicates that females tended to dive deeper around noon than in other time periods, whereas dive depths of males were rather constant during the day (Fig. 13A, 13B). When maximum dive depth of Blue-footed Boobies is compared to body mass, a significant positive correlation was found (Pearson, $R^2 = 0.12$, $n = 51$, $P = 0.007$). However, when the effect of sex is included in the model, there was no significant correlation between body mass and maximum dive depth (ANCOVA, body mass, $F_{1,50} = 2.06$, $P = 0.158$, Fig.14).

Table 6. Dive depth, duration and frequency of dives per trip for 51 Blue-footed Boobies (23 females, 28 males) on Isla Lobos de Tierra. Values are mean \pm 1 s.d., range (sample size).

Parameters	2002		2003	
	F	M	F	M
Dive depth (m)	3.91 \pm 1.46 1 - 11 (510)	3.29 \pm 1.17 1 - 8 (491)	5.07 \pm 1.97 1 - 22 (1489)	3.69 \pm 1.48 1 - 13 (1636)
Dive duration (s)	8.00 \pm 5.0 1.5 - 35 (510)	5.05 \pm 2.93 1.5 - 23 (491)	7.26 \pm 4.60 1 - 39 (1489)	5.66 \pm 3.92 0.5 - 27 (1636)
No. dives per trip	47 \pm 21 18 - 76 (9)	70 \pm 41 7 - 127 (7)	34 \pm 24 2 - 109 (44)	36 \pm 28 3 - 109 (46)

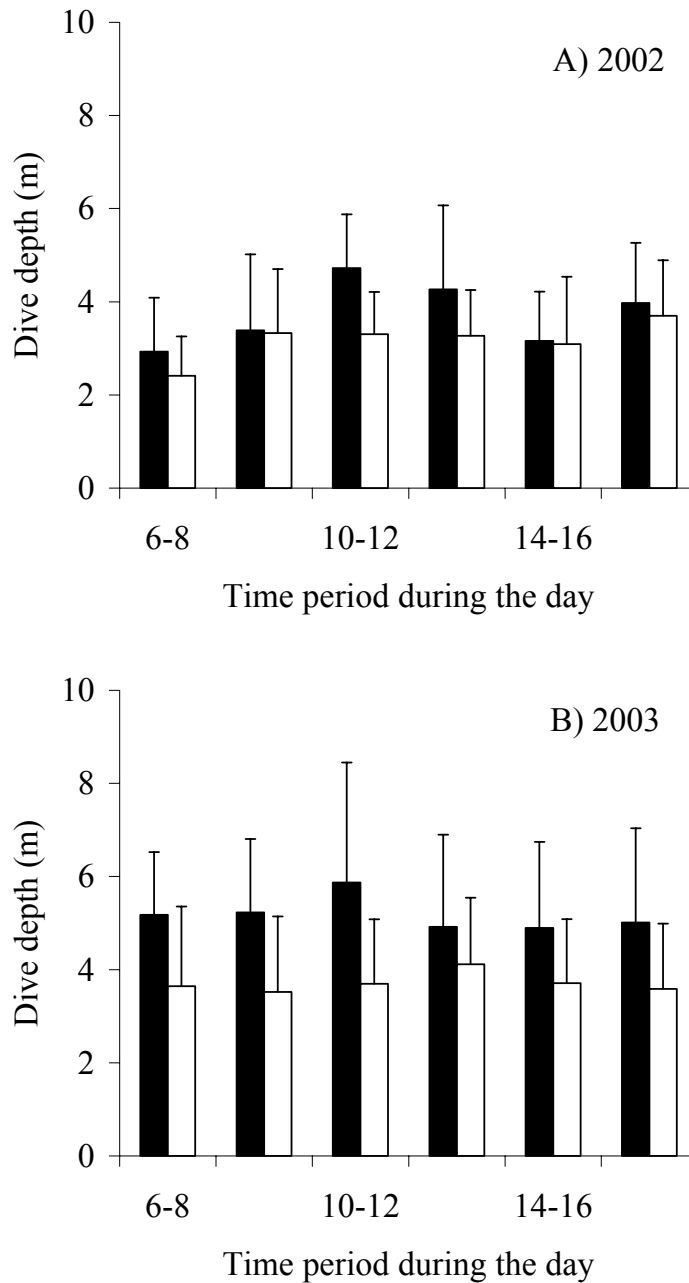


Figure 13. Mean dive depth (± 1 SD) at different time periods of the day for 9 birds (4 females, 5 males) in 2002 (A) and 42 birds (20 females, 22 males) in 2003 (B). Females are represented by solid bars and males by open bars.

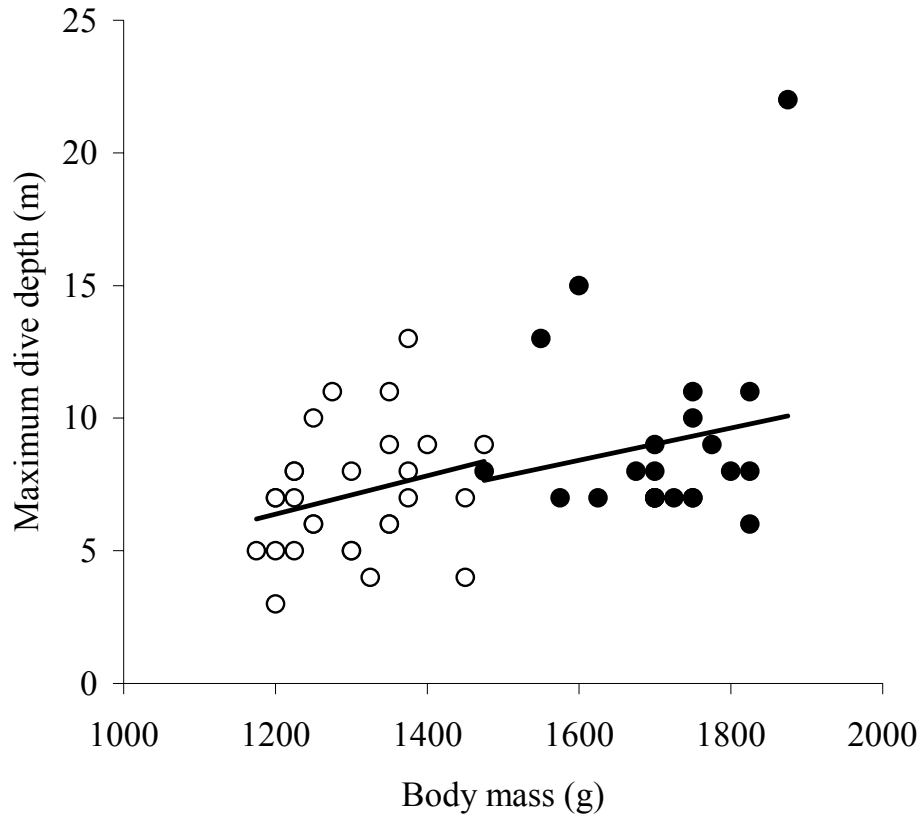


Figure 14. Relationship between the maximum dive depth and body mass of 23 female (solid circles) and 28 male (open circles) Blue-footed Boobies at Isla Lobos de Tierra females: $y = -1.32 + 0.006x$, $R^2 = 0.02$, $P > 0.05$; males: $y = -2.33 + 0.007x$, $R^2 = 0.07$, $P > 0.05$.

DISCUSSION

This study is the first completed on the diving behavior of Blue-footed Boobies. Like all members of the Sulidae, Blue-footed Boobies are shallow divers, exploiting the upper 6 m of the water column. However, some dives were deeper (up to 22 m) indicating that swimming underwater by foot or wing propulsion also may be an important technique to pursue their prey. Body size is one of the most important factors influencing the diving capabilities of seabirds such as penguins, alcids, cormorants (see Schreer and Kovacs 1997) and diving-petrels (Zavalaga and Jahncke 1997). Interspecific allometric comparisons among taxa have revealed that larger species can dive deeper (Schreer and Kovacs 1997) or longer (Boyd and Croxall 1996). The physiological mechanisms regulating diving capabilities of highly specialized diving birds must be different to those exhibited by shallow plunge-divers such as boobies and gannets. The momentum gained during the plunge relies, among other factors, on the bird's body mass, and consequently it may play an important role to control dive depths. Nevertheless, the diving capabilities of Blue-footed Boobies resemble those of the larger Atlantic and Cape gannets, which also can dive up to 22 m (Garthe et al. 2000), suggesting that factors other than body mass can play an important role in limiting dive depths.

Lewis et al. (2002) demonstrated that sex-specific differences in diving behavior might not be mediated by differences in body size because in the monomorphic Northern Gannet, females dive deeper than males. In the dimorphic Blue-footed Booby, females also dive deeper than males suggesting that body mass is an important factor limiting their dive depths. According to this evidence, a main question arises: Are the intersexual

differences in diving depths of sulids related to body mass or to sex per se? The results here suggest that in the Blue-footed Booby the heavier individuals attain deeper dives, but when the effect of sex is taken into consideration, the relationship between body mass and maximum dive depth disappears. Thus, any factor associated to sex other than body mass may explain the differences observed. Lewis et al. (2002) suggested that sexual differences in energy or nutrient requirements (e.g., molt, calcium intake) might lead females to search for particular prey at specific areas and/or depths. These two possible mechanisms do not apply to Blue-footed Boobies at Isla Lobos de Tierra because during the study period the number of molted tail feathers between sexes was similar (Table 1). Likewise, source of calcium for eggshell production is found in unlimited deposits of small mollusk shells on the shore (pers. obs.) and, as occurs in other bird species, females obtain calcium from shells and bones available close to their nests (Graveland and Drent 1997, pers. obs.). Behavioral differences may confer a competitive advantage for one sex over the other while feeding at sea. Blue-footed Booby females are more aggressive than males on land (pers. obs.), but it is unknown whether this aggressiveness is maintained in the feeding flocks and how it can lead to females diving deeper.

The effects of sex and body mass in the Blue-footed Booby are difficult to separate because males and females only marginally overlap in their body masses (Fig.14, Table 1). Therefore, it is likely that both factors are operating simultaneously while feeding at sea. Thus, around noon when the number of females at sea exceed the number of males and the interference competition between sexes is supposed to be the lowest, females dove deeper not as a result of behavioral factors or nutritional requirements, but because they could access fish schools in deeper waters during hours of

higher visibility in the water column. This observation suggests that dive depth may be mediated primarily by body mass.

CONCLUSIONS

The results of this study showed that the orientation to the outermost foraging point, foraging distances, diet composition, diurnal patterns of arrivals to the colony, length and number of feeding trips per day, proportion of travel time as well as number of dives per trip were similar between the sexes. These similarities may be the result of the bird's flocking behavior while feeding on patchily distributed anchovy schools. Feeding frenzies are conspicuous and can attract birds from different directions when commuting to other locations, and consequently, all birds in the flock feed on the same prey. Likewise, similarities on foraging behavior during the study period may be the result of abundant and available food. Intersexual comparisons during seasons of low food supply (e.g., EL Niño) or in colonies located in less productive environments may reveal a feeding niche segregation not found during this study.

Conversely, intersexual segregation occurred once the prey was located as females dove deeper, longer, captured bigger anchovies and consumed larger amounts of food than did males. It is tentative to attribute this ecological divergence to sexual differences in morphometry, as females are 31% heavier and 5-9% larger than males. Indeed, heavier individuals attained greater depths than lighter birds. However, the effect of sex and body mass on maximum dive depths was difficult to separate for two reasons; (1) within a gender, small and large birds dove at similar depths and (2) the distribution of body mass between males and females seldom overlapped. Individuals within the overlapping range of body mass could be selected for future investigations on the hypothesis of diving depth segregation. It also is expected that if sexual dimorphism

evolved as a mechanism to avoid food competition, the breeding success of more dimorphic pairs should be higher than less dimorphic birds. Other explanations such as underwater dominance of one sex over the other and sex-specific nutritional or energetic constraints are unlikely explanations for diving segregation in the Blue-footed Booby, but need to be tested.

LITERATURE CITED

- Adams, N. J., and C. B. Walter. 1993. Maximum diving depths of Cape Gannets. *Condor* 95:734-736.
- Ainley, D. G., and W. B. Emison. 1972. Sexual size dimorphism in Adélie Penguins. *Ibis* 114:267-271.
- Anderson, D. J., and R. E. Ricklefs. 1987. Radio-tracking Masked and Blue-footed boobies (*Sula* spp.) in the Galápagos Islands. *National Geographic Research* 3:152-163.
- Anderson, D. J., and R. E. Ricklefs. 1992. Brood size and food provisioning in Masked and Blue-footed boobies (*Sula* spp.). *Ecology* 73:1363-1374.
- Andersson, M., and R. Å. Norberg. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biological Journal of Linnean Society*. 15:105-130.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton.
- Baduini, C. 2002. Parental provisioning patterns of Wedge-tailed Shearwaters and their relation to chick body condition. *Condor* 104:823-831.
- Bakun, A. 1987. Monthly variability in the ocean habitat off Perú as deduced from maritime observations, 1953 to 1984. Pages 46-74 in *The Peruvian Anchoveta and Its Upwelling Ecosystem: Three Decades of Change*. (D. Pauly and I. Tsukayama, Eds.). ICLARM Studies and Reviews No.15, IMARPE, Lima.
- Barlow, K. E., and J. P. Croxall. 2002. Provisioning behaviour of Macaroni Penguins *Eudyptes chrysolophus*. *Ibis* 144:248-258.

- Batschelet, E. 1981. Circular Statistic in Biology. Academic Press, London.
- Benvenuti, S., F. Bonadonna, L. Dall'Antonia, and G. A. Gudmundsson. 1998. Foraging flights of breeding Thick-billed Murres (*Uria lomvia*) as revealed by bird-borne direction recorders. *Auk* 115:57-66.
- Benvenuti, S., L. Dall'Antonia, and P. Lyings. 2001. Foraging behavior and time allocation of chick-rearing Razorbills *Alca torda* at Gaesholmen, central Baltic Sea. *Ibis* 143:402-412.
- Benvenuti, S., L. Dall'Antonia, and K. Falk. 2002. Diving behaviour differs between incubating and brooding Brünnich's Guillemots, *Uria lomvia*. *Polar Biology* 25:474-478.
- Boag, P. T., and P. R. Grant. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. *Science* 214:82-85.
- Boyd, I. L., and J. P. Croxall. 1996. Dive durations in pinnipeds and seabirds. *Canadian Journal of Zoology* 74:1696-1705.
- Calixto-Albarrán, I., and J-L. Osorno. 2000. The diet of the Magnificent Frigatebird during chick rearing. *Condor* 102:569-576.
- Casaux, R., M. Favero, P. Silva, and A. Baroni. 2001. Sex differences in diving depths and diet of Antarctic Shags at the South Shetland Islands. *Journal of Field Ornithology* 72:22-29.
- Castillo, R., M. Gutierrez, S. Peraltila, and N. Herrera. 1999. Biomasa de los principales recursos pesqueros durante el verano de 1999. Crucero BIC Jose Olaya Balanadra 990203, de Tumbes a Tacna. Informe Instituto del Mar del Perú 147:31-45.

- Catry, P., R. A. Phillips, and R. W. Furness. 1999. Evolution of reversed sexual size dimorphism in skuas and jaegers. *Auk* 116:158-168.
- Clarke, J., B. Manly, K. Kerry, H. Gardner, E. Franchi, S. Corsolini, and S. Focardi. 1998. Sex differences in Adélie Penguin foraging strategies. *Polar Biology* 20:248-258.
- Clarke, J.R. 2001. Partitioning of foraging effort in Adélie Penguins provisioning chicks at Béchervaise Island, Antarctica. *Polar Biology* 24:16-20.
- Clutton-Brock, T. 1991. *The Evolution of Parental Care*. Princeton University Press, Princeton.
- Chapell, M. A., D. N. Janes, V. H. Shoemaker, T. L. Bucher, and S. K. Maloney. 1993. Reproductive effort in Adélie Penguins. *Behavioral Ecology Sociobiology* 33:173-182.
- Croxall, J. P., and G. S. Lishman. 1987. The food and feeding ecology of penguins. Pages 101-131 *in* *Seabirds Feeding Ecology and Role in Marine Ecosystems*. (J. P. Croxall, Ed.). Cambridge University Press, Cambridge.
- Culik, B. M., and R. P. Wilson. 1991. Energetics of underwater swimming in Adélie Penguins (*Pygoscelis adeliae*). *Journal of Comparative Physiology* 161:285-291.
- Dall'Antonia, L., P. Dall'Antonia, S. Benvenuti, P. Ioale, B. Massa, and F. Bonadonna. 1995. The homing behavior of Cory's Shearwater (*Calonectris diomedea*) studied by means of direction recorders. *Journal of Experimental Biology* 198:359-362.
- Dall'Antonia, L., G. A. Gudmundsson, and S. Benvenuti. 2001. Time allocation and foraging patterns of chick-rearing Razorbills in northwest Iceland. *Condor* 103:469-480.

- Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex*. Reprinted by Rand, McNally and Co, Chicago.
- Daunt, F., S. Benvenuti, M. P. Harris, L. Dall'Antonia, D. A. Eiston, and S. Wanless. 2002. Foraging strategies of the Black-legged Kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. *Marine Ecology Series Progress* 245:239-247.
- Drummond, H., J. L. Osorno, R. Torres, C. Garcia, and H. M. Larios. 1991. Sexual size dimorphism and sibling competition: implications for avian sex ratios. *American Naturalist* 138:623-641.
- Duffy, D. C. 1983. The foraging ecology of Peruvian seabirds. *Auk* 100:800-810.
- Duffy, D. C. 1987. Aspects of the ecology of Blue-footed and Peruvian boobies at the limits of their ranges on Isla Lobos de Tierra, Perú. *Colonial Waterbirds* 10:45-49.
- Fairbairn, J., and R. Shine. 1993. Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere. *Oikos* 68:139-145.
- Falk, K., L. Dall'Antonia, and S. Benvenuti. 2001. Mapping pre- and post-fledging foraging locations of Thick-billed Murres in the North Water polynya. *Ecography* 24:625-632.
- Falk, K., S. Benvenuti, L. Dall'Antonia, G. Gilchrist, and K. Kampp. 2002. Foraging behavior of Thick-billed Murres breeding in different sectors of the North Water polynya: an intercolony comparison. *Marine Ecology Progress Series* 231:293-302.
- Favero, M., R. Casaux, and P. Silva. 1998. The diet of the Antarctic Shag during summer at Nelson Island, Antarctica. *Condor* 100:112-118.

- Forero, M. G., K. A. Hobson, G. R. Bortolotti, J. A. Donázar, M. Bertellotti, and G. Blanco. 2002. Food resource utilization by the Magellanic Penguin evaluated through stable-isotope analysis: segregation by sex and age and influence on spring quality. *Marine Ecology Progress Series* 234:289-299.
- Fraser, G. S., I. L. Jones, and F. M. Hunter. 2002. Male-female differences in parental care in monogamous Crested Auklets. *Condor* 104:413-423.
- Frere, E., F. Quintana, and P. Gandini. 2002. Diving behavior of the Red-legged Cormorant in southeastern Patagonia, Argentina. *Condor* 104:440-444.
- Garthe, S., D. Grémillet, and R. W. Furness. 1999. At-sea-activity and foraging efficiency in chick-rearing Northern Gannets *Sula bassana*: a case study in Shetland. *Marine Ecology Progress Series* 185:93-99.
- Garthe, S., S. Benvenuti, and W. A. Montevecchi. 2000. Pursuit plunging by Northern Gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*). *Proceedings of the Royal Society of London B* 267:1717-1722.
- Garthe, S., S. Benvenuti, and W. A. Montevecchi. 2003. Temporal patterns of foraging activities of Northern Gannets, *Morus bassanus*, in the northwest Atlantic Ocean. *Canadian Journal of Zoology* 81:453-461.
- Gilardi, J. D. 1992. Sex-specific foraging distributions of Brown Boobies in the Eastern Tropical Pacific. *Colonial Waterbirds* 15:148-151.
- González-Solís, J., J. P. Croxall, and A. G. Wood. 2000. Sexual dimorphism and sexual segregation in foraging strategies of Northern Giant Petrels, *Macronectes halli*, during incubation. *Oikos* 90:390-398.

- Grant, P. R., and B. R. Grant. 2003. Reversed sexual dimorphism in the beak of a finch. *Ibis* 145:341-343.
- Graveland, J., and R. H. Drent. 1997. Calcium availability limits breeding success of passerines on poor soils. *Journal of Animal Ecology* 66:279-288.
- Grémillet, D., G. Argentin, B. Schulte, and B. M. Culik. 1998. Flexible foraging techniques in breeding cormorants *Phalacrocorax carbo* and shags *Phalacrocorax aristotelis*: benthic or pelagic feeding? *Ibis* 140:113-119.
- Guerra, M., and H. Drummond. 1995. Reversed size dimorphism and parental care: minimal division of labour in the Blue-footed Booby. *Behaviour* 132:479-497.
- Guillén, V. 1991. Población mensual del Camanay (*Sula nebouxii*) en el Perú, durante 1985-86 y 1988-90. *Boletín de Lima* 76:53-58.
- Hedrick, A. V., and E. J. Temeles. 1989. The evolution of sexual dimorphism in animals: hypothesis and tests. *Trends in Ecology and Evolution* 4:136-138.
- Jahncke, J., and E. Goya. 2000. Responses of three booby species to El Niño 1997-1998. *Waterbirds* 23:102-108.
- Jehl, J. R. Jr., and B. G. Murray. 1986. The evolution of normal and reverse sexual dimorphism in shorebirds and other birds. Pages. 1-86 *in* *Current Ornithology*, vol. 3 (R. F. Johnston, Ed.). New York, Plenum.
- Jones, I. L., S. Rowe, S. M. Carr, G. Fraser, and P. Taylor. 2002. Different patterns of parental effort during chick-rearing by female and male Thick-billed Murres (*Uria lomvia*) at a low-arctic colony. *Auk* 119:1064-1074.
- Jordán, R. 1971. Distribution of anchoveta (*Engraulis ringens*) in relation to the environment. *Investigación Pesquera* 35:113-126.

- Le Boeuf, B.J. 1974. Male-male competition and reproductive success in elephant seals. *American Zoologist* 14:163-176.
- Le Corre, M. 1997. Diving depths of two tropical Pelecaniformes: the Red-tailed Tropicbird and the Red-footed Booby. *Condor* 99:1004-1007.
- Lewis, S., S. Benvenuti, L. Dall'Antonia, R. Griffiths, L. Money, T. N. Sherratt, S. Wanless, and K. C. Hamer. 2002. Sex-specific foraging behavior in a monomorphic seabird. *Proceeding of the Royal Society of London B* 269:1687-1693.
- Lorentsen, S-H., and T. Anker-Nilssen. 1999. Diet of Common Murres wintering in the northern Skagerrak during 1988-1990: variation with sex, age and season. *Waterbirds* 22:80-89.
- Mills, K. 1998. Multispecies seabird feeding flocks in the Galápagos Islands. *Condor* 100:277-285.
- Mueller, H. C. 1989. Aerial agility and the evolution of reversed sexual dimorphism (RSD) in shorebirds. *Auk* 106:154-155.
- Murphy, R. C. 1936. *Oceanic Birds of South America*. American Museum of Natural History, New York.
- Nelson, J. B. 1978. *The Sulidae: Gannets and Boobies*. Oxford University Press, Oxford.
- Pietsch, T.W. 1976. Dimorphism, parasitism and sex: Reproductive strategies among deep-sea ceratoid anglerfishes. *Copeia* 1976:781-793.
- Quintana, F. 2001. Foraging behaviour and feeding locations of Rock Shags *Phalacrocorax magallanicus* from a colony in Patagonia, Argentina. *Ibis* 143:547-553.

- Ralls, K. 1976. Mammals in which females are larger than males. *Quarterly Review of Biology* 51:245-276.
- Schoener, T.W. 1967. The ecological significance of sexual size dimorphism in the lizard *Anolis conspersus*. *Science* 155:474-477.
- Schreer, J. F., and K. M. Kovacs. 1997. Allometry of diving capacity in air-breathing vertebrates. *Canadian Journal of Zoology* 75:339-358.
- Selander, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 1968:113-151.
- Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* 64:419-461.
- Slatkin, M. 1984. Ecological causes of sexual dimorphism. *Evolution* 38:622-630.
- Sokal, R., and F. Rohlf. 1995. *Biometry*. 2nd Edition. W.H. Freeman and Company, New York.
- Taylor, S. S., M. L. Leonard, D. Boness, and P. Majluf. 2001. Foraging trip duration increases for Humboldt Penguins tagged with recording devices. *Journal of Avian Biology* 32:369-372.
- Taylor, S. S., M. L. Leonard, D. J. Boness, and P. Majluf. 2002. Foraging by Humboldt Penguins (*Spheniscus humboldti*) during the chick-rearing period: general patterns, sex differences, and recommendations to reduce incidental catches in fishing nets. *Canadian Journal of Zoology* 80:700-707.
- Torres, R., and H. Drummond. 1999. Does large size make daughters of the Blue-footed Booby more expensive than sons? *Journal of Animal Ecology* 68:1133-1141.

- Velando A., and C. Alonso-Alvarez. 2003. Differential body condition regulation by males and females in response to experimental manipulations of brood size and parental effort in the Blue-footed Booby. *Journal of Animal Ecology* 72:846-856.
- Wagner, R. H., and C. Safina. 1989. Relative contribution of the sexes to chick feeding in Roseate and Common terns. *Wilson Bulletin* 101:497-500.
- Walker, B.G., and P.D. Boersma. Diving behavior of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. *Canadian Journal of Zoology* 81:1471-1483.
- Wanless, S., A. E. Burger, and M. P. Harris. 1991. Diving depths of Shags *Phalacrocorax aristotelis* breeding on the Isle of May. *Ibis* 133:37-42.
- Warner, R.R. 1984. Mating behavior and hermaphroditism in coral reef fishes. *American Scientist* 72:128-136.
- Watanuki, Y. 1992. Individual diet difference, parental care and reproductive success in Slaty-backed Gulls. *Condor* 94:159-171.
- Watanuki, Y., Y. Mori, and Y. Naito. 1992. Adélie Penguin parental activities and reproduction: effect of device size and timing of its attachment during chick rearing period. *Polar Biology* 12:539-544.
- Watanuki, Y., A. Kato, and Y. Naito. 1996. Diving performance of male and female Japanese Cormorants. *Canadian Journal of Zoology* 74:1098-1109.
- Weimerskirch, H., M. Salamolard, F. Sarrazin, and P. Jouventin. 1993. Foraging strategy of Wandering Albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110:325-342.

- Weimerskirch, H., Y. Cherel, F. Cuenot-Chaillet, and V. Ridoux. 1997. Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. *Ecology* 78:2051-2063.
- Wikelski, M., and F. Trillmich. 1997. Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. *Evolution* 51:922-936.
- Williams, T. D. 1995. *The Penguins: Spheniscidae*. Oxford University Press, Oxford.
- Wilson, R. P. 1989. Diving depths of Gentoo *Pygoscelis papua* and Adélie *P. adeliae* penguins at Esperanza Bay, Antarctica Peninsula. *Cormorant* 17:1-8.
- Wilson R. P., and M-P. T. Wilson. 1989. A peck activity record for birds fitted with devices. *Journal of Field Ornithology* 60:104-108.
- Wilson, R. P., D. Grémillet, J. Snyder, M. A. Kierspel, S. Garthe, H. Weimerskirch, C. Schafer-Neth, J. A. Scolaro, Ch-A. Bost, J. Plotz, and D. Nel. 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* 228:241-261.
- Wood, A. G., B. Naef-Daenzer, P. A. Prince, and J. P. Croxall. 2000. Quantifying habitat use in satellite-tracked seabirds: application of kernel estimation to albatross locations. *Journal of Avian Biology* 31:278-286.
- Zar, J. H. 1984. *Biostatistical Analysis*. Prentice-Hall, Inc., New Jersey.
- Zavalaga, C. B., and J. Jahncke. 1997. Maximum dive depth of the Peruvian Diving-Petrel. *Condor* 99:1002-1004.