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Parental investment, adult sex ratios, and sexual selection in a socially monogamous seabird

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Abstract Although most birds are monogamous, theory predicts that greater female parental investment and female-biased adult sex ratios will lower the polygyny threshold. This should result in polygynous mating, unless obligate biparental care or the spatial and temporal distribution of fertilizable females constrains a male's ability to take advantage of a lowered polygyny threshold. Here we present data on the extent of male sexually dimorphic plumage, adult sex ratios and breeding season synchrony in three populations of a socially monogamous seabird, the brown booby *Sula leucogaster*. For one of these populations, San Pedro Mártir Island, we also present data on differences in male and female parental investment, mortality and probability of pairing. The extent of plumage dimorphism varied among populations. Sex ratios were female biased in all populations. On San Pedro Mártir Island, parental investment was female biased, females failed more often than males to find a mate, but there was no polygyny. We suggest that on San Pedro Mártir: (1) a period of obligate biparental care coupled with a relatively synchronous breeding season constrained the ability of males to take advantage of a high environmental polygamy potential and (2) the resulting socially monogamous mating system, in combination with the female-biased adult sex ratio, caused females to be limited by the availability of males despite their greater parental investment.

Key words *Sula leucogaster* · Polygyny · Parental investment · Sexual dimorphism · Sex ratios · Brown booby · Breeding synchrony · Gulf of California

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Introduction

Two fundamental questions in behavioural ecology are the reasons variance in reproductive success is typically higher in males than in females, and the conditions under which males will provide parental care. Trivers (1972) predicted that the sex with greater parental investment, typically females, would limit the reproductive success of the other sex and have lower variance in reproductive success. This is because, if individuals of the limiting sex are able to survive and garner sufficient resources to produce offspring, they should have little trouble finding a mate willing to provide less than half the parental investment for a 50% share of the resulting reproductive success. For the sex with lower parental investment, typically males, variance in reproductive success is generally higher because individuals must not only survive and garner sufficient resources for gamete production, they must also attract a mate willing to provide more than half the parental investment. Consequently, more low-quality individuals of the limited sex fail to attract a mate, while some high-quality individuals may attract more than one mate.

In the limited sex, the effect of greater variance in reproductive success is expected to heighten intrasexual competition for mates. This, in turn, leads to the development of secondary sexual characteristics and life history strategies that result in higher mortality. Emlen and Oring (1977) showed that variance in the reproductive success of the limited sex is influenced by the operational sex ratio (the ratio of fertilizable females to sexually active males). The operational sex ratio is a function of differential mortality by sex, the spatial distribution of mates, and the synchrony of the breeding season. Theory predicts that female-biased parental investment will be associated with increased variance in male reproductive success, which, in turn, will heighten male intrasexual conflict for access to female mates and result in increased male mortality.

Initial asymmetries in gamete investment and certainty of parentage predispose males to provide less parental

care than females (Trivers 1972). However, if some male parental care is necessary for offspring survival, or if the spatial and temporal distributions of fertilizable females are such that males can only pair with one female per season, then males are expected to provide parental care (Emlen and Oring 1977; Maynard Smith 1977).

The brown booby (*Sula leucogaster*) is a colonial, ground-nesting seabird found throughout the tropics (Nelson 1978). It has sexually monochromatic plumage in most of its range, except in the eastern tropical Pacific where all populations exhibit sexually dichromatic plumage (Nelson 1978; Howell and Webb 1995). In a study on San Pedro Mártir Island, we have found that the extent of plumage dimorphism was under current sexual selection and was positively correlated with number of offspring fledged (Tershy 1998). Despite apparent sexual selection for plumage dimorphism, extra-pair copulations and extra-pair fertilizations were rare (Tershy 1998). In this paper, we compare the extent of plumage dimorphism, adult sex ratios, and breeding season synchrony from three different populations of brown boobies in the eastern tropical Pacific. We then use data from a detailed field study on San Pedro Mártir Island to examine sexual differences in parental investment, mortality, and the probability of mating.

These data address three questions: (1) Does a period of obligate biparental care constrain the ability of males to take advantage of female-biased parental care and a high environmental polygamy potential caused by a female-biased adult sex ratio? (2) Can a socially monogamous mating system, when combined with low levels of extra-pair paternity, create a situation where females, despite their higher parental investment, may not be the limiting sex? (3) Can the extent of plumage dimorphism in different populations be explained by differences in the synchrony of the breeding season?

Methods

Study site

The primary study site was San Pedro Mártir Island, Gulf of California, México (28°23' N, 112°20' W). San Pedro Mártir is a 1.9-km² rocky desert island with a mixed colony of >20,000 pairs each of brown boobies and blue-footed boobies (*S. nebouxii*) (Tershy et al. 1992; Tershy 1998). We conducted field work on the island during 14 months in the 1990–1993 breeding seasons (25 March–1 August 1990; 13 February–30 June 1991; 20 January–15 May 1992; 1–15 March, 29 May–7 June, 23–25 June 1993). Data on plumage dimorphism, sex ratios, and breeding season synchrony were collected from two additional populations breeding on Cocos Island, Costa Rica (5°33' N, 87°03' W) 2,600 km south-east of San Pedro Mártir Island and Clipperton Atoll (10°18' N, 101°131' W) 1,800 km south of San Pedro Mártir Island.

We selected four adjoining study plots which, depending on the year, contained 110–206 brown booby nests. The study plots were contiguous, but separated by distinct topographic features (plot 1=1300 m², 2=1350 m², 3=4225 m² and 4=1000 m²). We subdivided the plots into a 5×5 m grid, and made a detailed 250:1 scale map of the study area in which the locations of nests were recorded. Distances between nest sites were measured from this

map with dial calipers and converted to metres. Throughout the 1991–1992 breeding season, each nest was checked once a week from courtship through fledging or failure for nest activity and content. In 1993, nests were checked weekly from courtship through laying and during periodic visits throughout the remainder of the breeding season.

In the study plots, brown boobies quickly habituated to our presence and birds with eggs or chicks could usually be picked up off the nest, banded and measured, then replaced. Brown boobies continued behaviours such as courting and copulating while we walked through the colony and could be observed, without a blind, from ≥10 m without any apparent impact on their behaviour. There was no indication that our research activities had any impact on the numbers of brown boobies nesting in the study plots (Tershy 1998).

Plumage measurements

Brown booby populations show varying degrees of sexually dimorphic plumage, with males having a lightly coloured region of contour feathers from the base of the culmen extending caudally. We quantified the extent of male coloration (plumage score) by holding males flat on a grey table and gently straightening the neck so that the distance from the insertion of the humerus to the base of the culmen was 18 cm. We measured the distance from the base of the culmen to the posterior end of white plumage on the dorsal and ventral surfaces of the head and neck. These two measurements were summed to derive the plumage score used in analysis. The repeatability of plumage score measurements was 93% (Tershy 1998).

To examine differences in the extent of plumage dimorphism in different populations, we compared plumage measurements from live birds on San Pedro Mártir Island to those of skins at the Smithsonian Institution and the California Academy of Sciences collected on Clipperton Island and Cocos Island, Costa Rica. We were unable to straighten the neck to a constant length when taking plumage measurements on museum skins, and unable to measure museum skins of birds collected on San Pedro Mártir Island. In addition, while we were able to measure known breeding adults on San Pedro Mártir, the breeding status of adults measured from study skins was unknown. However, because the plumage scores of live birds from San Pedro Mártir Island were intermediate between those of study skins collected from the other two populations (see Results), there does not appear to be a systematic bias from either source that was strong enough to overwhelm natural differences between these populations.

Parental investment

Incubation and chick guarding

To measure incubation and chick-guarding effort, we walked a fixed route through the study plots once each day at 2-h (1990) or 1-h (1991–1992) intervals during all daylight hours. For each nest, we recorded which adult was incubating eggs or guarding the chick.

Nest building, preening, chick feeding and adult fights

One to three times a week we conducted intensive focal observations on three to eight haphazardly selected nests from our study plots from dawn to dusk throughout the breeding season. We conducted instantaneous scan samples at 5-min intervals and recorded the behaviour of adult females and males on the nest as nest maintenance, chick preening, or other. We used event sampling to record all fights between adults, and all chick feeds by adult females and males. In 1990 and 1991 we determined the weight of these feeds (see Chick provisioning, below).

Predator and nesting territory defence

Throughout the study period, we opportunistically recorded attempts of natural predators, common ravens (*Corvus corax*), to predate brown booby nests. For each incident, we recorded the sex of the defending adult booby and whether the attempt was successful. In addition, blue-footed boobies will attempt to usurp brown booby nest sites during the breeding season. For each take-over attempt opportunistically observed, we recorded which member of the brown booby pair defended the nest and whether the attempt was successful.

From 1990 to 1992, we visited each nest once a week during the ~40-day incubation period and ~90-day chick-raising period. On each visit we recorded the sex of the adult guarding the nest, and whether it stayed on the nest when we approached and had to be gently pushed to the side to examine the nest contents (defended), or fled the nest when we approached (failed to defend).

Chick provisioning

Following Guerra and Drummond (1995), we weighed chicks in three to eight haphazardly selected nests (see above) periodically throughout the day and then exactly 4 min after being fed by an adult throughout the breeding season. Through our periodic weighings, all chicks were weighed at least 2 h prior to being fed. We subtracted the most recent pre-feeding weight from the post-feeding weight to determine the amount of food transferred during each feeding bout. Chicks were weighed on an electronic balance with a precision of ± 2.5 g. The balance was calibrated between weighings.

We recorded the date, time, location, and individuals involved in all fights, copulations, and chick feeds seen in ad lib observations. For chick feeds we recorded the age class of the chicks on a seven-point categorical scale based on plumage development. These ad lib observations complimented the dawn-to-dusk focal observations by providing an alternative measure of chick provisioning with a larger sample size.

To determine whether chicks were fed at night, we weighed a total of 63 chicks at dusk and before sunrise the following day throughout 1990 and 1991. Eleven (17.5%) chicks gained weight during the night. Because there was no systematic tendency for females or males to feed chicks more at dawn or at dusk, data on the ratio of male to female chick feeds collected during the day are likely to be representative of the ratio of male to female chick feeds during the night. Only 17.5% of chicks were fed at night, but more than 97% of chicks were fed during the day. Thus, nighttime feeds are likely to be a less important form of parental investment. Consequently, we only used daytime feeds to quantify chick feeding effort.

Adult sex ratios

We measured the sex ratio of all birds with adult plumage on or near the study sites on San Pedro Mártir Island. The plumages of adult males, adult females, and sub-adult birds are easily discriminated. Therefore we were able to visually determine the sex of perched and flying brown boobies. On San Pedro Mártir Island we used two methods to record adult sex ratios each week in the 1991 and 1992 field seasons. First, we walked a fixed route through all four study plots ≤ 2 h after sunrise and counted the number of adult males and females seen. Second, we counted adult males and females flying just offshore of the island. We used 10 \times 50 binoculars mounted on a tripod and during a 5-min watch counted all birds that could be sexed which flew within our field of view. We divided the day into 4-h periods starting at 0600 hours and during each period we made a minimum of four counts, each consisting of a minimum of 50 individuals of each sex. All counts for all periods of the day were totalled and the number of adult males and females constituted our second estimate of adult sex ratio.

In a previous study, we recorded the sex ratios of brown boobies from the San Pedro Mártir population during seabird censuses

conducted from a small boat between April 1985 and April 1986 (see Tershy et al. 1993 for a detailed description of methods). For sex ratios of brown boobies in the Clipperton Atoll populations, we used data obtained from at-sea censuses by R.L. Pitman and L.T. Ballance. Their counts were conducted in 1989, 1990 and 1992 between sunrise and sunset using 20 \times 120 binoculars mounted on a gimbaled tripod. For Cocos Island population sex ratios, we used data from at-sea censuses by A. Acevedo-Gutierrez. He counted all adults that could be sexed during 10-min watches evenly distributed between sunrise and sunset on weekly small-boat surveys in 1993.

Return rate, mortality and probability of mating

We banded birds to identify individuals. Boobies incubating eggs or guarding chicks were captured on their nests by hand, and banded with unique combinations of three-coloured plastic bands and one USFWS numbered metal band.

Throughout the field season we continuously searched for colour-banded birds to determine mortality, return rate and the probability of an individual mating. Every year from 1991 to 1994 we also made intensive searches of our study plots and much of the rest of the island for colour-banded boobies. We recorded the location and behaviour of colour-banded boobies and any birds with which they were interacting. Our most intensive effort outside our study plots was a band 100–300 m from the edges of our study plots where we checked each nest in the region one to four times for colour-banded adults. Most nesting boobies that left our study plots would have nested in this band because the mean distance moved between subsequent nest sites was less than 10 m, and fewer than 2% of individuals moved more than 50 m (Tershy 1998).

Differences between male and female band loss could bias our analyses of return rate and mortality. To calculate band loss, all colour-banded birds with missing bands were captured, their band combination was determined by reference to the numbered band or by a combination of the remaining colour bands and morphometric measurements. Missing bands were then replaced.

Results

Results are reported as means \pm SD unless otherwise noted.

Plumage variation

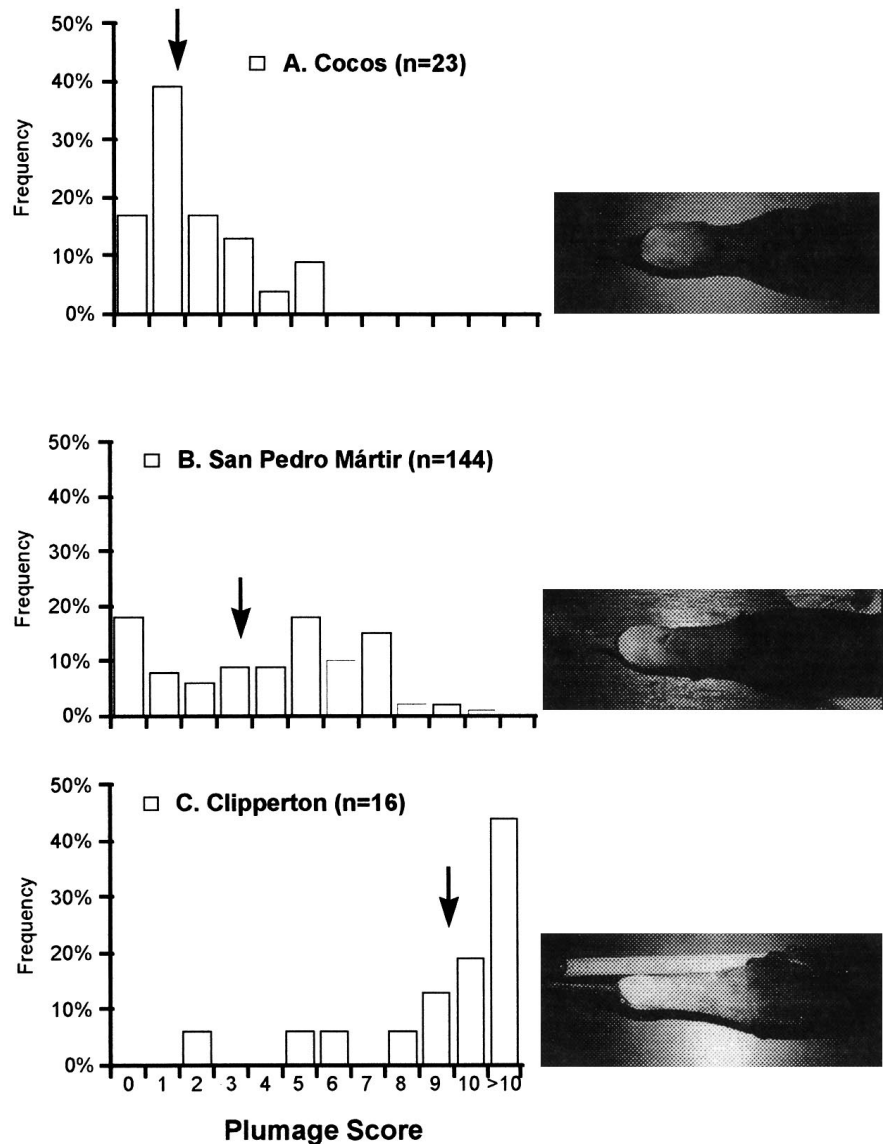
Within the eastern tropical Pacific, sexually dimorphic plumage in brown boobies varies both between individuals within a population and between populations. The mean plumage score (linear extent of white plumage in centimetres on the dorsal and ventral surface of the head and neck) of males in the study population on San Pedro Mártir Island was 3.8 ± 2.64 ($n=164$), which is intermediate between values at Clipperton Island (1800 km south), where birds were highly dimorphic (9.5 ± 3.73 , $n=16$) and Cocos Island, Costa Rica (2600 km south-east), where birds were slightly less dimorphic (1.4 ± 1.39 , $n=23$) (Fig. 1, non-parametric Kruskal-Wallis multiple comparison, $H=43.19$, $P<0.001$ for all comparisons).

Parental investment

Incubation and brooding

Female and male investment in incubation and brooding were essentially equal. Females were present on 49.5%

Fig. 1A–C Frequency distribution of plumage scores for male brown boobies from three different populations in the eastern tropical Pacific. *Arrows* show the mean value for each population and photographs are of a bird from that population with a plumage score closest to its mean



of incubation and brooding scans while males were present on 50.5% (combining data from 32 all-day continuous nest surveys of 20–57 nests during 1990–1992). Incubation lasted about 42 days and chicks fledged about 90 days after hatching (Nelson 1978; B.R. Tershy unpublished data).

Because unattended eggs and small chicks were quickly preyed on by yellow-footed gulls (*Larus livens*) or common ravens (Tershy et al. 1992), there was a period of obligate egg and chick guarding. We assumed that the duration of this obligate guarding period lasted until chicks were left alone on the nest and not taken by predators. Chicks at this time were 5–6 weeks old and weighed ≥ 600 g. Including the 42-day incubation period, the duration of obligate egg and chick guarding on San Pedro Mártir Island was 75–85 days, representing 57–64% of the period from egg laying to fledging.

Nest building and preening

Once a full clutch is laid, any additional nest construction or nest maintenance can be considered a form of parental investment. Females were engaged in such actions roughly twice as often as males (females=32 scan samples, males=17 scan samples, $\chi^2=4.71$, $P=0.030$, data from 1990–1992 combined). In contrast, females preened chicks only about half as often as males (females=47 scan samples, males=84 scan samples, $\chi^2=10.54$, $P=0.001$). Despite these significant differences, nest maintenance and chick preening made up only a small part of adults' total time and energy budgets because they each accounted for less than 2.5% of the 5,946 scan samples.

Predator and nesting territory defence

Both sexes contributed equally to nest and territory defence. On seventeen occasions, common ravens were ob-

Table 1 Chick provisioning by male and female brown boobies

Comparison (1990 and 1991) ^a	Female	Male	Percent male	χ^2	<i>P</i>
Number of chick feeds from ad libitum sampling	360 feeds	124 feeds	25.6	115	0.0001
Number of chick feeds during all-day focal nest watches ^b	121 feeds	60 feeds	33.2	20	0.001
Weight of food delivered during all-day focal nest watches ^b	6,185.5 g	2,465.5 g	28.5	160	0.0001

^a See Methods for detailed explanation

^b Data from 109 focal nest watch days at 76 different nests

served trying to force an adult brown booby off its nest to prey on the eggs or small chicks. The number of attempts and successful attempts was evenly distributed between male and female boobies (females=6 unsuccessful:2 successful; males=6:3). Because the sample size for natural predation attempts on nests was low, we recorded the response of incubating or brooding adults to our approach during weekly nest checks. Twenty-six (15.7%) of 166 females either walked or flew away from the nest at our approach, thus “failing” to defend their young on one or more visits. Similarly, 30 (18.1%) of 166 males “failed” to defend their young on one or more visits. These figures are not significantly different ($\chi^2_c=0.19$, $P=0.66$).

After eggs were laid, females and males contributed equally to defence against blue-footed boobies when the latter tried to usurp nest sites. In 1991 and 1992 we recorded 88 interspecific fights at brown booby nest sites, 38 involving males and 50 involving females ($\chi^2=1.64$, $P=0.20$). When blue-footed boobies successfully usurped nest sites, they tossed out any eggs or chicks, so it is not possible to separate predator and territory defence.

Chick provisioning

The durations of female and male foraging trips were not significantly different (Tershy 1998), but females delivered heavier food loads to chicks than did males (females: 57.2 ± 43.54 g, $n=121$, males: 45.2 ± 39.04 g, $n=60$; $Z=1.86$, $P=0.03$). Females also fed chicks more often than males did (Table 1). Consequently, females delivered more food to chicks than did males in a comparison of both the total weight of food delivered to all chicks (Table 1), and in a paired comparison of each nest on each nest watch day (Fig. 2; 1990 and 1991 combined, $n=76$ pairs and 109 nest days, $df=108$; females: 56.8 ± 52.85 g food delivered/day, males: 22.2 ± 38.26 g; Wilcoxon signed rank test $Z=4.98$, $P<0.001$). Males failed to feed chicks on over 56.6% of the all-day focal nest watches, whereas females failed to feed chicks on only 14.5%.

Adult sex ratios

On San Pedro Mártir Island, 38.6–46.4% of breeding and non-breeding adult brown boobies counted were males

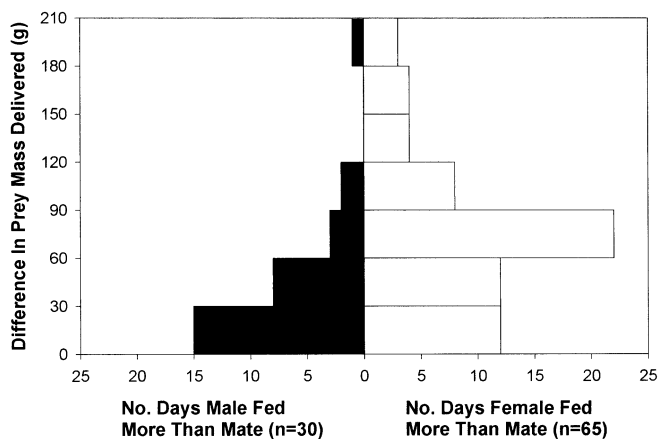


Fig. 2 Number of dawn-to-dusk focal nest watches when the male or female at the nest fed more food to the chick (by weight) than their mate (x-axis). Data are also divided into seven categories of difference in prey weight fed to chicks by the two parents (y-axis)

depending on the year and the method used (Table 2). In all cases the sex ratios were significantly female biased (Table 2). On both Clipperton Atoll and Cocos Island sex ratios were significantly female biased (Table 2), with males constituting 43.6% and 38.4% of brown boobies counted offshore of each island, respectively.

Return rate, mortality, and probability of breeding

Female brown boobies had a higher annual return rate than males. Of the 78 females colour-banded in 1990, 45 (57.7%) were sighted on the colony in 1994, but of the 131 males colour-banded in 1990, only 51 (42.3%) were sighted ($\chi^2_c=6.194$, $P=0.0128$). Of all birds colour-banded in 1990–1993, 74 (58.3%) of 127 females, but only 69 (41.3%) of 167 males were sighted in 1994 ($\chi^2_c=7.63$, $P=0.006$).

Different female and male return rates could be due to differences in (1) mortality, (2) band loss, (3) site fidelity or (4) the probability of skipping one or more years of colony attendance.

The available evidence supports greater male mortality as the cause of lower male return rates. The sex ratio of adults found dead in or around our study sites, 13 males to 5 females, was consistent with this hypothesis. This ratio was significantly different from the ex-

Table 2 Sex ratio counts of eastern Pacific brown boobies

Population and sample ^a	Number of males	Number of females	Percent males	Z _{ct} ^b	P
San Pedro Mártir Island					
Mean of weekly colony counts 1991	197	274	41.8	3.13	<0.0001
Mean of weekly colony counts 1992	351	413	44.9	3.84	<0.0001
Sum of weekly counts of birds flying offshore 1991	2,426	2,808	46.4	7.21	<0.0001
Sum of weekly counts of birds flying offshore 1992	3,526	4,269	45.2	11.41	<0.0001
At-sea counts 1985/1986	812	1,294	38.56	14.85	<0.0001
Clipperton Atoll					
At-sea counts 1989, 1990, 1992 ^c	246	318	43.6	4.01	<0.0001
Cocos Island					
At-sea counts 1993 ^d	3,003	4,827	38.4	27.0	<0.0001

^a See Methods for detailed description

^b Two-tailed normal approximation of the binomial sign test

^c Unpublished data courtesy of R.L. Pitman and L.T. Ballance, SWFC/NMFS, La Jolla, Calif

^d Unpublished data courtesy of A. Acevedo, Texas A&M University, Galveston, Tex

pected value of 8.02:9.98 based on the average sex ratio for San Pedro Mártir ($\chi^2=5.58$, $P=0.018$).

Band loss cannot explain differences in female and male return rates. There was no difference between male and female brown boobies in the probability of losing colour bands (B.R. Tershy and D. Breese, unpublished data). All banded birds that lost \leq three bands were successfully recaptured, identified (based on remaining bands and morphometric measurements), and rebanded. The probability of a brown booby losing its metal band and all three colour bands was $<0.01\%$ (B.R. Tershy and D. Breese, unpublished data).

Differences in within-colony nest site fidelity also cannot explain differential return rates. Females moved to new nest sites on 113 of 228 (49.5%) nesting attempts, and males moved to new nest sites on 101 of 285 (40.3%) nesting attempts ($\chi^2_c=4.066$, $P=0.001$). The mean distance moved between nests sites in the study plots was higher for females (10.4 \pm 13.81 m) than males (9.2 \pm 21.80 m) (Mann-Whitney U -test $Z_{ct}=2.05$, $P=0.001$). Males were recorded in new nests off the study plots in 6 of 285 (2.1%) new nesting attempts, while females were recorded in new nests off the study plots in 5 of 228 (2.2%) new nesting attempts ($\chi^2_c=0.72$, $P=0.789$). We have no evidence of emigration to other breeding colonies.

Differences in female and male return rates cannot be explained by breeding individuals skipping a year of colony attendance. The probability of males and females skipping one or more years of colony attendance was not different [7 of 127 (5.5%) banded females, and 6 of 167 (3.6%) banded males; $\chi^2_c=0.26$, $P=0.613$].

For birds that had bred in previous years and subsequently returned to the colony, females were less likely than males to breed. This pattern was consistent whether (1) comparing the percentage of years when individuals were present on the colony, but failed to breed (females: 32.1% of subsequent years without breeding, $n=115$; males: 18.8%, $n=118$; Mann-Whitney U -test $Z_{ct}=3.16$,

$P<0.001$), (2) comparing the total number of seasons present on the colony when not breeding [females did not breed in 88 of 285 (30.9%) seasons on the colony, males in 47 of 284 (16.5%) seasons on the colony; $\chi^2_c=15.53$, $P<0.001$] or (3) comparing the number of individuals that failed to breed at least once during the study period [1990–1993; females: 60 (53.6%) of 115 failed to breed at least once; males: 43 (36.5%) of 118; $\chi^2_c=6.14$, $P=0.013$].

Intrasexual competition for mates appeared to be at least as great between females as males. Females were rarely courted by two males at the same time (9 of 53, 17.0% of females were recorded courting \geq twice), but single males frequently courted two females simultaneously (50 of 115, 44.0%; $\chi^2_c=10.05$, $P=0.002$). Similarly, only one female was observed copulating with two males, but nine males were observed copulating with \geq two females ($\chi^2=6.5$, $P=0.011$ when compared to an expected ratio of 1:1). Many of the males that courted more than one female eventually bred with one of the females as their primary mate. These males also maintained a social bond with another “secondary” female that they courted less often and with whom they did not nest. These secondary females sometimes copulated with mated males, but did not lay eggs, even when they had a separate nest site. Fights between primary and secondary females occurred during the pre-laying period. Some fights lasted more than 7 min, longer than fights we observed between males. The number of female-female and male-male fights observed was no different than expected based on the colony sex ratio (data from 1991 and 1992 combined; females: 48 fights, males: 51 fights; $\chi^2=0.75$, $P=0.387$).

Breeding season synchrony

On San Pedro Mártir, the first and last eggs laid on the study plots were 28, 50 and 56 days apart in 1990–1992,

respectively. On Cocos Island, brown booby chicks of different age classes were censused from November 1993 through May 1994 (A. Acevedo, unpublished data). Chicks ≤ 1 month old were recorded from November through March, but 94% were recorded during December, January and February, suggesting that the majority of egg laying takes place within 90 days. On Clipperton Atoll, however, breeding occurs throughout the year. In all months for which there are records (March, May, August, September and November), birds were reported in all stages of breeding from courting through post-fledging care (Snodgrass and Heller 1902; Dodson and Fitzgerald 1980). Thus, breeding was asynchronous on Clipperton Atoll and relatively synchronous on San Pedro Mártir and Cocos Islands.

Discussion

Parental investment

Owens and Bennett's (1994) review of parental investment in birds identified defence and feeding of chicks as the two most costly forms of parental care – as measured by adult mortality. In brown boobies on San Pedro Mártir Island, chick and nest site defences were shared equally by males and females. Incubation and brooding, which were shared equally by males and females, are probably not risky or energetically expensive forms of parental investment because (1) there are no predators of adults on the nesting grounds (Nelson 1978; Tershy 1998) and (2) adults are unlikely to seriously deplete energy reserves during 5–7 h nest attendance stints (Tershy 1998). Chick feeding, however, was strongly female biased. Females and males spent the same amount of time away from the nest, but females were responsible for over 70% of food delivered to chicks during the day (Fig. 1, Table 1). Some nighttime chick feeds occurred, but we have no reason to believe they were male biased, because there was no tendency for males to feed chicks later in the day than females.

Foraging flight has been found to be roughly twice as energetically expensive as incubation and brooding in other sulids [2.4 and 1.95 times incubation or brooding in northern gannets (*S. bassana*) and red-footed boobies (*S. sula*), respectively; Birt-Friesen et al. 1989; Ballance 1995]. The cost in brown boobies is probably somewhere between these species because brown boobies are intermediate between these two species in wing loading (Nelson 1978; Ballance 1995), and use flapping flight more than red-footed boobies do (B.R. Tershy, personal observation). Male and female brown boobies appeared to spend the same amount of time foraging. However, females fed chicks larger prey loads than did males, and fed chicks more often (Table 1, Fig. 2). Thus, females invested a greater proportion of the energetic costs of foraging for chicks than did males.

Sex ratios

The sex ratio of brown boobies censused on San Pedro Mártir Island (Table 2) was female biased using three different methods (colony counts, small boat censuses, and shore counts of birds at sea) in all 3 years. A similar sex ratio bias was also present in separate populations on Cocos Island and Clipperton Atoll. These observations suggest that female-biased adult sex ratios were not simply due to temporary fluctuations in environmental conditions, but persist long enough to exert selective pressure.

Our data indicate that the female-biased adult sex ratio was caused by greater male mortality. There was a lower return rate of colour-banded males than colour-banded females, and a significantly greater number of males than females are known to have died. Sexual differences in nest site fidelity are unlikely to explain the lower male return rate because males changed nest sites less frequently and moved shorter distances between nest sites than females (Tershy 1998). Sexual differences in band loss do not explain lower male return rates as there was no difference in colour-band loss between males and females, band loss was low, and we determined the identity of all birds that lost ≤ 3 bands.

An alternative hypothesis for the female-biased adult sex ratio is a skewed primary sex ratio. We did not record hatching or fledging sex ratios. However, it is unlikely that primary sex ratios in brown boobies are female biased for several reasons: (1) most studies of birds (Clutton-Brock 1986; Breitwisch 1989) including studies of one species in the same order as brown boobies (Graves et al. 1993) have found no bias in hatching sex ratios, (2) Torres and Drummond (1999) found a male-biased sex ratio at both hatching and fledging in blue-footed boobies, a congener of brown boobies, on Isla Isabel (off the Pacific coast of Mexico) and (3) Fisher's (1930) equilibrium sex ratio theory predicts that any deviation in the primary sex ratio should result in the production of the cheaper sex – in this case male brown boobies because they are 10% smaller than females (Nelson 1978; Tershy 1998).

On San Pedro Mártir, the ultimate cause of greater male mortality is likely mating effort rather than parental effort, since female's parental investment was higher. Females provided over 70% of the food delivered to chicks (Table 1). Thus, variance in a female's abilities to provision young is likely to be an important determinant of male reproductive success. Theoretically, a number of factors could lead to a female-biased sex ratio: male-male competition for nest sites, competition for access to high-quality females, competition for extra-pair copulations or earlier age of first reproduction in males. However, nest sites did not appear to be limited (personal observations), extra-pair copulations and fertilizations were rare (Tershy 1998), and males appear to breed later than females on San Pedro Martir (B.R. Tershy, unpublished observations).

One way males may compete for access to high-quality females is with sexually dimorphic plumage, spe-

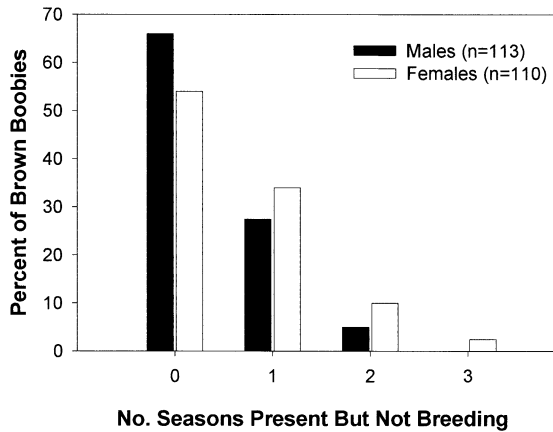


Fig. 3 Percent of brown boobies that bred once and then failed to breed in the subsequent 0–3 years they were present on the colony

cifically the extent of white plumage on the head and neck. This trait is positively correlated with success at fledging chicks on San Pedro Mártir Island and appears to be under current sexual selection (Tershy 1998). The expression of sexually dimorphic traits can have predation, aerodynamic, energetic and immune system costs (Andersson 1994; Møller et al. 1996), of which only the latter two are expected to limit the expression of plumage dimorphism in brown boobies.

A more likely explanation for a skewed sex ratio is that males suffer greater mortality than females because they breed more regularly (Fig. 3). This would cause their average annual combined parental and mating effort to be greater than that of females.

Which sex is limiting?

When we compared adult birds that had bred in a previous year, females failed to breed more often than males (Fig. 3). This difference may be due to the female-biased sex ratio creating a shortage of potential male mates. Females may also have failed to breed more often than males because they were not in adequate physiological condition to initiate investment in egg production and chick provisioning (Sotherland and Rahn 1987).

Females were significantly more likely than males to court and copulate with only one partner. Unmated adult females, including females that had bred in previous years, often maintained a pair-like relationship with a mated male that included copulation and nest building. However, these secondary females did not lay eggs. Females and males had equal numbers of intrasexual fights. Although we were not able to determine the cause of these fights, most female-female fights were likely over access to mates while most male-male fights were likely over access to both mates and nest sites. In combination, these data suggest that both females and males competed for access to mates, but that female reproductive success was more often limited by access to monogamous mates than was male reproductive success.

Why are males on San Pedro Mártir Island monogamous?

Our data suggest that (1) parental investment (chick feeding) was female-biased (Table 1, Fig. 2), (2) this female-biased sex ratio was due to greater mortality of adult males (Table 2), (3) female competition for mates was equal or greater than male competition for mates and (4) mating success was greater for males than for females (Fig. 3). Theory predicts that these conditions should result in an increase in polygynous mating. Indeed, when adult sex ratios have been naturally (Kempnaers 1994) or experimentally (Greenlaw and Post 1985) biased toward females in passerines, polygynous mating increased. However, brown boobies on San Pedro Mártir Island were not socially polygynous.

We suggest that simultaneous pair bonds were not possible because males needed to spend ~50% of daylight hours on the nest during the first ~80 days of the breeding season (when eggs and chicks need protection from raven and gull predation). This precluded the possibility for a male to have time to breed with two females simultaneously.

Males are important for guarding the chicks against predators, at least during the initial portion of the nestling phase. However, once chicks are old enough to be left alone, males could (theoretically) abandon females and their offspring and seek additional partners. There are two potential costs, however, to males of abandoning their mates to engage in sequential socially polygyny: (1) chick mortality may be high in the absence of paternal care and (2) in long-lived birds such as the brown booby, fledging success is often lower with new mates (Choudhury 1995). Neither of these costs appeared high on San Pedro Mártir. First, males only provided 29% of chick food by weight. One female's mate died 87 days after laying (42 days of incubation, 45-day-old chick), yet she successfully raised the chick to above-average weight at fledging. Second, about half of all males did not retain the same mate 2 years in a row due to divorce or the failure of their mate from the previous year to return to the colony (Tershy 1998).

A reason males may not abandon females approximately 80 days after laying is that the egg-laying season on San Pedro Mártir was less than 60 days. Thus, the breeding season is sufficiently synchronous that a male cannot start a second brood after his first brood has reached 80 days. If males cannot increase their fitness by desertion, they may benefit by continued investment in their current offspring (Emlen and Oring 1977). Such investment is expected, even when not necessary for chick survival, as long as it increases male reproductive success through increased chick survival or quality, more than abandonment would by increasing the male's current or future mating opportunities. Thus, as predicted by Emlen and Oring (1977), the combination of a need for biparental care plus the temporal constraint on the availability of females resulted in the absence of the potential for polygyny on San Pedro Mártir Island.

Limited data from Cocos Island suggest that most egg laying takes place over approximately 90 days (A. Ace-

vedo, personal communication). Consequently, for all but the earliest-breeding males, the egg-laying period is also too synchronous for sequential social polygyny. If nests started at the end of the breeding season have lower fledging success, even the earliest-breeding males may not benefit by abandoning females with chicks that no longer need brooding. For females, the threat of male abandonment could even select against even earlier egg-laying dates. We therefore predict that brown booby males at Cocos Island are forced to be monogamous.

On Clipperton Atoll, in contrast, breeding occurs year round. The adult sex ratio, as on Cocos and San Pedro Mártir Islands, is female biased. Thus, some males should be able to abandon females approximately 80 days after laying, find a new mate, and start a second nest in the same year. If this sequential polygyny occurs on Clipperton Atoll it would increase the variance in male reproductive success over that found on San Pedro Mártir Island. The possibility of sequential polygyny could create a male-biased operational sex ratio, despite the female-biased adult sex ratio. Increased variance in male reproductive success and a female-biased operational sex ratio would intensify male-male competition for mates (Emlen and Oring 1977). Male brown boobies in these populations likely use sexually dimorphic plumage in competition for access to females (Tershy 1998). If, as we hypothesize, breeding synchrony on San Pedro Mártir and Cocos Islands prohibits sequential polygyny, then the lack of breeding synchrony on Clipperton Atoll may permit sequential polygyny. We therefore predict that sequential polygyny will occur on Clipperton Atoll. This would be consistent with the finding of greater sexual dimorphism on Clipperton Atoll (Fig. 1), and warrants further investigation.

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