# SEXUAL SIZE DIMORPHISM AND ASSORTATIVE MATING IN THE BROWN NODDY[1]

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*Abstract.* We report the results of a biometric study of adult Brown Noddies (*Anous stolidus*) nesting within the Culebra National Wildlife Refuge, Puerto Rico in 1985–1988. The body mass of adults varied significantly between years, but linear measurements did not. Males were significantly larger than females in all body measurements. This difference also was reflected within pairs. A discriminant function using head-bill and wing length successfully predicted the sex of 90% of birds. Measurements of male and female partners indicated that they were not paired at random with respect to body mass and showed positive assortative mating for this character. The causes and consequences of this relationship are discussed.

*Key words: Morphometrics; sexual dimorphism; assortative mating; Brown Noddy;* Anous stolidus; *tropical; Culebra.*

## INTRODUCTION

The study of biometrics has proved to be useful in a range of applications in seabird biology. For example, geographical variation in body size is commonly used to study taxonomic relationships (e.g., Barth 1967, Monaghan et al. 1983, Barrett et al. 1985). Ashmole (1968) and Pennycuick et al. (1984) showed that body-size differences within assemblages of seabird species have important effects of scale on feeding ecology. Pennycuick (1987) showed that the relative size of body parts affects flight characteristics and the economics of foraging. Many species of otherwise monomorphic seabirds show some degree of sexual size dimorphism and field measurements are often used to determine the sex of individuals (e.g., Shugart 1977, Ryder 1978, Fox et al. 1981, Coulson et al. 1983, Hanners and Patton 1985).

As part of a long-term study of the reproductive biology of Brown Noddies (*Anous stolidus*) breeding near Culebra, Puerto Rico, we have had the opportunity to measure adults during banding exercises; here we present biometric data on this species. We report on: (1) annual variation in body size over the 4 years of study, (2) sexual size dimorphism, and (3) the degree to which males and females mated assortatively with respect to the examined body measurements.

## METHODS

The study was carried out at two colonies of Brown Noddies on islands (Cayo Noroeste and Cayo Yerba) within the Culebra National Wildlife Refuge, Culebra, Puerto Rico (18°20′N, 65°18′W). Brown Noddies on these islands nest on the ledges of low cliffs or in shrubbery. A total of 149 incubating adults (139 from Cayo Noroeste; 10 from Cayo Yerba) were captured during May–June over the 4 years of study, either by hand, with a nest trap or with a noose (Chardine and Morris 1987). We banded each adult with a USFWS stainless steel band and a unique combination of three PVC (Darvic) color bands. We measured: (1) body mass of adults with a hand-held 300-g Pesola balance, (2) head-bill length (distance between the bill tip and the back of the skull) with calipers, (3) bill depth at the gonys with calipers, (4) culmen length with calipers, (5) wing length (distance between the carpal joint of the bent wing and the tip of the longest, straightened primary) with steel rule, and (6) foot length (distance from back of "ankle" joint to end of claw on middle toe) with steel rule. All measurements made with calipers were taken to the nearest 0.1 mm, while those with the steel rule were taken to the nearest millimeter. Body mass was measured to the nearest gram. Measurements 3 to 6 were not taken in some years. Brown Noddies were molting their inner primaries during the months of the study and all

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longer primaries were present and usually unworn. Wing lengths of birds with worn primaries were discarded.

Of the 149 birds captured in the 4 years, 59 were sexed (32 males and 27 females) by extensive observations of courtship feeding (males feed females) from a blind located about 10 m from the colony or by deduction from the known sex of partners, assuming heterosexual pairing. The sex of one female was confirmed by necropsy. The sample included 13 pairs in which both the male and female were measured in the same year. Copulation was observed extremely rarely and could not be used as an aid to sexing individuals.

Stepwise discriminant function analysis (BMDP: P7M, Dixon et al. 1985) was performed on head-bill length, wing length, and body mass (cube root) of known males ($n = 26$) and females ($n = 23$) that were measured for all characters. Culmen length, bill depth, and foot length were measured infrequently and were not included in the analysis. We used a jackknife validation method, wherein each bird was sexed using a function based on the total sample less the bird in question, to obtain an unbiased estimate of the success rate of the function (see Dixon et al. 1985).

## RESULTS

### BODY MEASUREMENTS

Measurements for Brown Noddies caught in each year of study are shown in Table 1. Very little yearly variation in linear measurements (head-bill length, bill depth, culmen length, wing length, and foot length) was evident and no annual trends were significant (ANOVA, $P$'s > 0.05). In contrast, mean body mass varied considerably with body mass being higher in 1986 and 1988 than in the other 2 years. Interyear variation in body mass was significant ($F = 4.77$; df = 3, 142; $P < 0.005$).

### SEXUAL SIZE DIMORPHISM

The frequency distributions of body measurements for all birds that were captured, and for known males and females are in Figure 1. The underlying frequency distributions for known males and females showed some overlap but clearly indicated that for all characters, most males were larger than females. Indeed, for all characters measured, males were significantly larger than females (Table 2, $t$-tests, $P$'s < 0.001).

Size differences between male and female Brown Noddies also were reflected within breeding pairs. In the pairs where both mates of known sex were measured in the same year ($n = 13$), the mean difference (female from male) in body measurements within pairs was positive for all characters, and most differences were significant (Table 3, paired $t$-tests, $P$'s < 0.05). In almost all pairs the male was larger than the female.

Was the magnitude of the difference in size between paired males and females more or less than would be expected based on overall size differences between the sexes? To test this, the 13 measured male and female partners were randomly re-assorted in a pairing simulation. The number of random pairs in which the male was larger than the female (for a particular character) did not differ significantly from that reported in Table 3 (Fisher's tests, all $P$'s > 0.05). Furthermore, the mean differences in size between males and females paired at random were identical or very similar to those reported in Table 3.

Stepwise discriminant function analysis was performed on head-bill length, wing length, and body mass (cube root) of known males and females that were measured for all characters (total $n = 49$ comprising 26 males and 23 females). Only head-bill length (first) and wing length (second) were chosen in the stepwise analysis; body mass did not add significantly to the discriminating power of the function. The resulting function was:

$$0.536(\text{head-bill length}) + 0.133(\text{wing length}) = 81.920,$$

and correctly classified 90% (44 of 49) of known sex birds ($F = 27.5$; df = 2, 46; $P < 0.001$). Birds that scored higher than 81.920 when their measurements (in mm) were applied to the equation were classed as males and those that scored less were classed as females. The classification success rates of functions using head-bill length or wing length on their own were 84% and 71%, respectively.

The classification success rates of these functions are artificially high because they are assessed on the same sample of birds used to calculate the function. The jackknife validation procedure available in BMDP predicts the sex of each bird in the sample using a classification function derived from all the data, except those of the bird being classified. In this way a more realistic success rate can be estimated. The jackknife classification success rate of the function

TABLE 1.  Body measurements of Culebran Brown Noddies according to year of capture.

|  |  | 1985 | 1986 | 1987 | 1988 | F[b] | df |
|---|---|---|---|---|---|---|---|
| Head-bill length (mm) | $\bar{x}$ | 85.6 | 85.1 | 85.5 | 85.4 | 0.40 | 3, 145 |
|  | SD | 1.8 | 2.2 | 1.6 | 2.0 | ns |  |
|  | n | 51 | 30 | 15 | 53 |  |  |
| Bill depth (mm) | $\bar{x}$ | 8.3 | 8.2 | —[a] | 8.3 | 0.11 | 2, 108 |
|  | SD | 0.5 | 0.5 | — | 0.4 | ns |  |
|  | n | 29 | 30 |  | 52 |  |  |
| Culmen length (mm) | $\bar{x}$ | — | — | — | 42.3 | — |  |
|  | SD |  |  |  | 1.4 |  |  |
|  | n |  |  |  | 56 |  |  |
| Wing length (mm) | $\bar{x}$ | 272 | 270 | — | 271 | 1.04 | 2, 126 |
|  | SD | 5.9 | 6.1 |  | 5.2 | ns |  |
|  | n | 50 | 29 |  | 50 |  |  |
| Foot length (mm) | $\bar{x}$ | — | 67 | — | 67 | 0.20 | 1, 81 |
|  | SD |  | 1.9 |  | 2.1 | ns |  |
|  | n |  | 30 |  | 53 |  |  |
| Body mass (g) | $\bar{x}$ | 173 | 182 | 171 | 178 | 4.77 | 3, 142 |
|  | SD | 11.2 | 15.4 | 7.3 | 11.2 | $P < 0.005$ |  |
|  | n | 51 | 30 | 12 | 53 |  |  |

[a] Indicates measurement was not taken in that year.
[b] Tests differences between years.

using head-bill length and wing length was 88% (43 of 49 birds correctly classified) and was thus only two percentage points below the biased estimate of success rate for this function.

ASSORTATIVE MATING

We had the opportunity to study assortative mating for morphometric characters in those pairs in which both birds were measured in the same year. A total of 34 pairs was used in the analysis including the 13 pairs containing birds of known sex and an additional 21 pairs sexed using the discriminant function given above. Measurements of paired males and females are plotted in Figure 2 and indicate the degree to which assortative mating was observed for each continuous character. No significant correlation was found between partners in linear measurements (head-bill length, bill depth, wing length). In contrast, a significant positive relationship was found in the body mass of paired males and females ($r = 0.51$, $n = 34$, $P < 0.01$), indicating assortative mating for this character.

DISCUSSION

Over the 4 years of study the linear body dimensions of Brown Noddies caught in each year did not change significantly. In contrast, body mass varied significantly from year to year. Taken together, these observations suggest annual variation in the body condition of noddies at the

Culebran colonies. Aspects of the breeding biology, behavior, and morphometrics of seabirds can be important indicators of marine food supplies (Cairns 1987), and we suggest that the trend observed in Brown Noddies indicates annual fluctuations in food availability on noddy feeding grounds.

Male Brown Noddies captured at the colonies were, on average, significantly larger than females in all body measurements. This difference has been reported in other studies of larids (e.g., Ashmole 1968, Ingolfsson 1969, Shugart 1977, Ryder 1978, Fox et al. 1981, Pierotti 1981, Coulson et al. 1983, Hanners and Patton 1985, Coulter 1986) although the degree of sexual size dimorphism varies considerably between species. Gulls appear to be the most dimorphic of larids. For example, Fox et al. (1981) reported data showing that male Herring Gulls (*Larus argentatus*) averaged 5–22% larger (percent difference = $[\bar{x}_{male} - \bar{x}_{female}/\text{pooled } \bar{x}] \times 100$) than females depending on the character considered. Terns appear to be the least dimorphic; Coulter (1986) found that male Common Terns (*Sterna hirundo*) were either similar in size or up to only 5% larger than females depending on the measurement. The degree of sexual dimorphism in Culebran Brown Noddies was intermediate between these two species with male body measurements varying from 2–7% larger than those of females (this study).
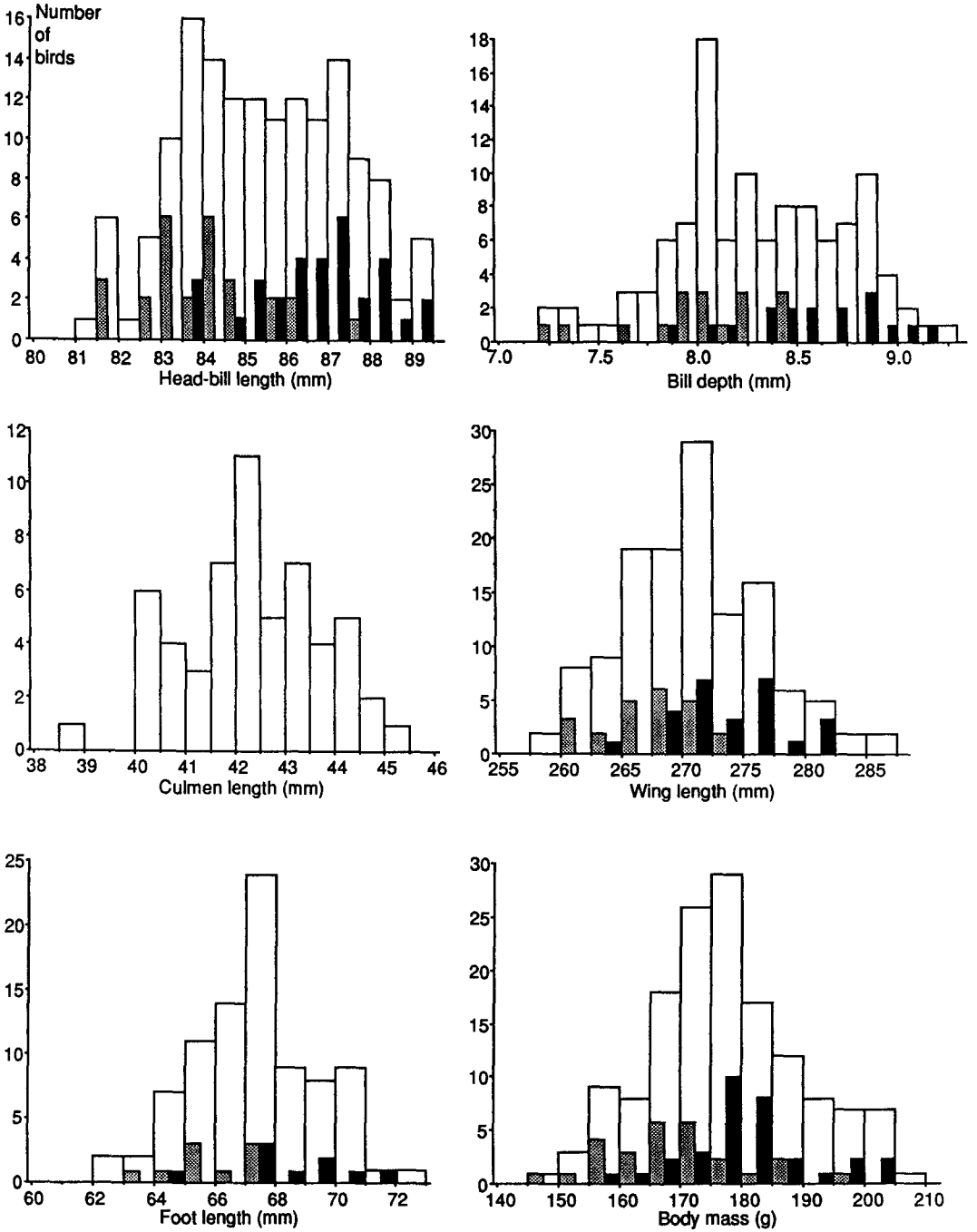
FIGURE 1.   The frequency distributions of body measurements of adult Brown Noddies caught in Culebra National Wildlife Refuge in 1985–1988. Clear bars are all birds ($n = 149$), black bars are known males ($n = 32$), and grey bars are known females ($n = 27$). Sample sizes for some measurements are smaller due to missing data.

TABLE 2. Body measurements of Culebran Brown Noddies according to sex.

| Character[a] | | *n* | *x̄* | SD | *t*[b] | *P* |
|---|---|---|---|---|---|---|
| Head-bill length (mm) | Male | 32 | 86.6 | 1.4 | 6.89 | <0.001 |
| | Female | 27 | 84.1 | 1.4 | | |
| Bill depth (mm) | Male | 18 | 8.6 | 0.4 | 4.81 | <0.001 |
| | Female | 17 | 8.0 | 0.4 | | |
| Wing length (mm) | Male | 26 | 273 | 4.2 | 5.17 | <0.001 |
| | Female | 23 | 268 | 3.7 | | |
| Foot length (mm) | Male | 9 | 68 | 2.1 | 3.06 | <0.01 |
| | Female | 9 | 65 | 1.4 | | |
| Body mass (g) | Male | 32 | 180 | 10.3 | 4.07 | <0.001 |
| | Female | 27 | 168 | 11.4 | | |

[a] Not sufficient sample of known-sex birds to compare culmen length.
[b] Unpaired *t*-test.

Culebran Brown Noddies could be sexed in 90% of cases using head-bill and wing length in a discriminant function analysis (DFA). Validation methods suggested that a more realistic estimate of the success rate of the function was 88%. Thus, using the function on other Brown Noddies from the two study locations, we would expect to make an error in the sex of the bird slightly more than one in 10 times. If the discriminant function derived from Culebran noddies were used on noddies from elsewhere, we would expect size differences to produce success rates lower than this. Thus, although we have shown that Brown Noddies can be sexed with relatively high success using DFA, we recommend that workers interested in using this technique derive functions on locally caught samples of birds.

The success rate achieved for noddies here is intermediate between that reported in many gull species (usually well over 90%: e.g., Fox et al. 1981, Coulson et al. 1983, Hanners and Patton 1985) and the success rate observed in the Common Tern (80%: Coulter 1986). Although the results of DFA are sensitive to sample size and other statistical attributes (Morrison 1984), we

suggest that much of the variation in success rates between species is most likely the result of variation in relative degree of sexual size dimorphism.

The stepwise DFA used to determine the classification function chose head-bill length first, followed by wing length, indicating that head-bill length was the better discriminator of sex. The value of the head-bill measurement in determining sex in larids has been reported previously (Coulson et al. 1983). These authors suggested that head-bill length alone was a useful method of sexing some larids. Used alone, head-bill length successfully sexed 84% of Culebran noddies in the sample. With the expected reduction in success rate when used with a sample from another location, this is probably an unacceptably high error rate and we recommend the use of both head-bill length and wing length in Brown Noddies.

In almost all Brown Noddy pairs observed in this study, the male was the larger of the two birds. Size differences within a pair were no larger or smaller than those found in a random pairing simulation and thus were a result of overall size differences between males and females. Coulter

TABLE 3. Magnitude of the difference between male and female Culebran Brown Noddy measurements within the same pair.

| Character[a] | Mean difference[b] | SD | *t*[c] | Total *n* | Male larger *n* | *P* |
|---|---|---|---|---|---|---|
| Head-bill length (mm) | 2.4 | 2.8 | 3.17 | 13 | 10 | <0.01 |
| Bill depth (mm) | 0.5 | 0.6 | 1.97 | 6 | 5 | ns |
| Wing length (mm) | 6.2 | 6.9 | 3.11 | 12 | 10 | <0.05 |
| Body mass (g) | 13.8 | 11.3 | 4.38 | 13 | 12 | <0.001 |

[a] Sample of known-sex birds not sufficient to compare culmen or foot length.
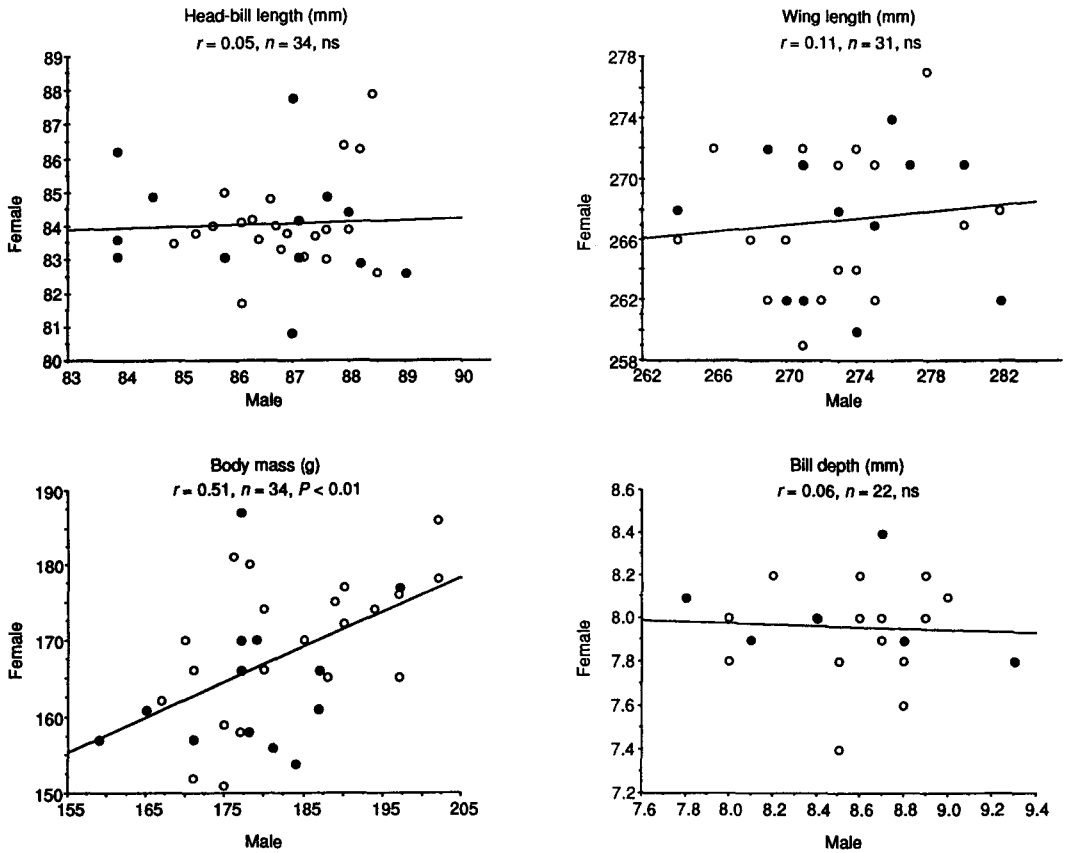[b] Female from male.
[c] Paired *t*-test.

FIGURE 2.    Relationships between measurements of males and females in 34 pairs of Culebran Brown Noddies captured in the 4 years of study. Measurements of partners were taken in the same year. Thirteen pairs were sexed by observation (filled circles) and the balance (open circles) by the discriminant function using head-bill length and wing length given in the text. Sample sizes for some measurements were smaller due to missing data. Lines of best fit were determined by least squares regression. Correlation coefficients are shown.

(1986) found similar results in Common Terns. Tinbergen (1960, p. 104) noted that despite some overlap in the size of male and female Herring Gulls, within pairs, males were always larger than females. At least in the Brown Noddy and Herring Gull, relative size of certain body parts within a pair may be a reliable indicator of sex in most cases, without the need for discriminant function analysis.

Culebran Brown Noddies showed positive assortative mating according to body mass, but no significant trends for linear body measurements. This suggests that the body condition of male and female partners was positively related. These results contrast with those of Coulter (1986) who found positive assortative mating for bill length but not body mass (or other measurements) in Common Terns. We consider several hypotheses

for this trend in the Brown Noddy. The correlation of male and female body mass within a pair could be a consequence of long- or short-term seasonal changes in body mass. Most (90%) paired males and females in the analysis were caught within 5 days of one another and the observed trend could result if the changes in body mass affected all birds regardless of sex. The correlation could also result from short-term changes in body mass caused, for example, by good or poor feeding days. Another explanation involves the foraging ability of males. Male Brown Noddies feed their mates frequently before egg laying (Morris and Chardine, unpubl.) and the ability of a male to forage may affect the body mass of his mate as well as his own, thus resulting in a positive association of body mass and condition within partners. Finally, if the age of noddy part-

ners is correlated (see Reid 1988) and foraging ability varies with age, these two effects would tend to produce a correlation in body mass and condition within pairs. As yet we have no data with which to test these hypotheses.

Depending upon the degree to which body mass in Brown Noddies is heritable, the assortative mating patterns reported here could affect the genetic variability of this character in the population (Partridge 1983). However, body mass is probably less heritable than a character such as head-bill or bill length because of the much greater environmental influence on variability in the former character. Thus, the likelihood of a significant genetic effect as a result of the assortative mating pattern for body mass reported here is probably less than that suggested by Coulter (1986) for assortative mating according to bill length in Common Terns.

## ACKNOWLEDGMENTS

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