

# SEXUAL SIZE DIMORPHISM AND ASSORTATIVE MATING IN THE SHORT-TAILED SHEARWATER *PUFFINUS TENUIROSTRIS*

LUKE D. EINODER,<sup>1,2</sup> BRAD PAGE<sup>1</sup> & SIMON D. GOLDSWORTHY<sup>1,2</sup>

<sup>1</sup>South Australian Research and Development Institute (Aquatic Sciences), PO Box 120, Henley Beach, 5022, South Australia  
(lukeeinoder@hotmail.com)

<sup>2</sup>School of Earth and Environmental Sciences, Adelaide University, Adelaide, 5000, South Australia

Received 6 January 2008, accepted 25 September 2008

## SUMMARY

EINODER, L.D., PAGE, B. & GOLDSWORTHY, S.D. 2008. Sexual size dimorphism and assortative mating in the Short-tailed Shearwater *Puffinus tenuirostris*. *Marine Ornithology* 36: 167–173.

To improve methods for sexing live birds in field studies, we assessed sexual size dimorphism in the Short-tailed Shearwater *Puffinus tenuirostris* and produced a sex-discriminating function. Despite a degree of overlap in body size, males were significantly larger than females. A stepwise discriminant function analysis of five morphometric characters indicated that bill depth and head length were the most dimorphic characters, and the resultant sex model correctly discriminated 92.0% of known males (23 of 25), and 92.3% of known females (24 of 26). The model was validated by applying it to an additional group of birds whose sex was assumed, based on their pairing with known-sex individuals. Of the assumed females, 93% were correctly classified ( $n = 15$ ), as were 96% of males ( $n = 15$ ). Application of the sex model to another breeding colony reduced its performance to 70%–82% accuracy because of the existence of significant geographic variation in body size in this species. For individuals in which certainty was low (i.e. when small males are confused with large females), sexing could be improved by measuring the body size of the breeding partner. This improvement was a result of significant positive assortative mating with respect to bill depth and a body size index. This sex model provides a quick and easy means of sexing in instances in which molecular methods and other techniques are not feasible.

Key words: Assortative mating, bill depth, intercolony variation, sexing, sexual size dimorphism

## INTRODUCTION

The magnitude of sexual size dimorphism (SSD) varies between seabird species and between traits within each species. Male-biased SSD is most common among the world's seabirds, but female-biased SSD exists in the Fregatidae, Hydrobatidae and Sulidae (Serrano-Meneses & Székely 2006). In some species, male-biased SSD is very pronounced, with females being only 80% the size of males [e.g. Northern Giant Petrel *Macronectes halli* (González-Solis 2004)]. In these cases, birds can be sexed visually, because the larger body size and disproportionately broader bills of males are clearly recognisable (González-Solis 2004). However, in many other seabird species, SSD is less pronounced, and size differences can be identified only by applying morphological traits to a sex model (e.g. Hamer & Furness 1991, Granadeiro 1993). The application of such a model first requires an investigation into the direction and extent of dimorphism that exists in a species, and identification of the skeletal trait that shows the greatest degree of dimorphism. The general trend among the Procellariiformes (albatross, petrels and shearwaters) that breed at mid to higher latitudes of the southern hemisphere is that males are heavier and larger than females (Fairbairn & Shine 1993). This male-biased SSD has been identified for the Short-tailed Shearwater *Puffinus tenuirostris* (Bull *et al.* 2005), with significant size differences suggesting that sex discrimination based on body size may be applicable.

Discriminant functions analysis (DFA) combines the discriminatory power of several morphometric variables into one formula that

best discriminates between the sexes (Weidinger & van Franeker 1998). This method determines which morphometric traits are the most variable in terms of sex, and produces a model into which the measurements of birds of unknown sex can be entered to assign a likelihood of male or female sex. Discriminant functions analysis has proven useful for identifying dimorphism in a range of Procellariiformes, such as the fulmarine petrels *Fulmarus* spp. (van Franeker & Ter Braak 1993), Cape Petrel *Daption capense* (Weidinger & van Franeker 1998), Cory's Shearwater *Calonectris diomedea* (Granadeiro 1993, Lo Valvo 2001), Pink-footed Shearwater *P. creatopus* (Guicking *et al.* 2004) and Balearic Shearwater *P. mauretanicus* (Genovart *et al.* 2003). The present study aimed

- to identify the degree of SSD in the Short-tailed Shearwater and to determine in which traits it is expressed.
- to develop a discriminant function based on the traits that show SSD.
- to identify the extent of assortative mating with respect to body size.
- to assess the degree of confidence in sex discrimination by the model.
- to determine the intercolony applicability of the model.

The overall aim was to provide an accurate means of determining sex in field studies in which other means of establishing sex are either not present or not available.

## STUDY AREA AND METHODS

### Study area

This study was conducted at breeding colonies on Althorpe Island (35°37'S, 136°86'E) and Evans Island (32°22'S, 133°28'E) in South Australia. Althorpe Island was visited on five occasions during the 2004/05 austral summer breeding season (17–23 October 2004, 15–21 December 2004, 21 January–11 February 2005, 18–25 March 2005, 4–8 April 2005), and Evans Island on four occasions (28 October–2 November 2004, 27 November–12 December 2004, 24 January–8 February 2005, 29 March–1 April 2005) in conjunction with other research. All measurements were taken by the same researcher (LE) to avoid inter-sampler error.

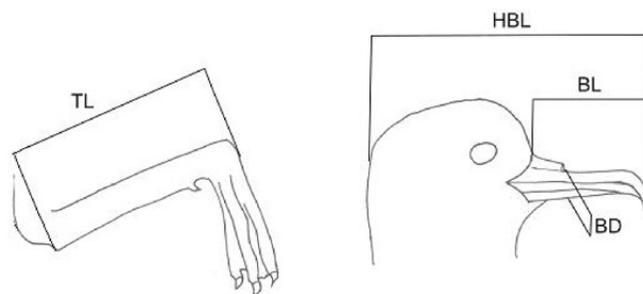
### Sexing and measurements

Breeding adults of known sex were used to develop the model. Females were positively identified by the presence of an egg *in utero* prior to laying, and most of the males were sexed by observing copulation behaviour during the mating period. However, if a bird was present in the burrow with an egg-bearing female in the brief one-to-two-day period before laying, then that bird was also considered to be a male. Where a breeding partner joined one of these known-sex individuals later in the breeding season, the joining bird was assumed to be the opposite sex. These choices were based on the assumption that breeding pairs contain one male and one female, because mating trios have not been documented in this species. Adults were deemed to belong to a breeding pair if they were observed on multiple occasions at the base of the same numbered burrow, either incubating the egg or provisioning food to the chick. These birds formed an additional group of assumed-sex individuals (Evans Island:  $n = 15$ ; Althorpe Island:  $n = 20$ ). Molecular sexing was not employed, because the accuracy of the above methods was deemed adequate for this study.

Each adult was leg-banded and body mass (BM) was determined using a spring balance (1000 g  $\pm$  5 g). Four skeletal traits were measured using digital Vernier callipers ( $\pm$  0.01 mm) to determine body size (Fig. 1): head+bill length (HBL) from supra-occipital to front edge of bill; bill length (BL) from the edge of forehead feathers to the most distal part of the hook; bill depth (BD) from concave dorsal surface just in front of tubes to base of bill; and tarsus length (TL) from distal end of tarsometatarsus to back of heel with leg bent (Reynolds *et al.* 2008).

### Assessing SSD

Univariate analysis using the SPSS software package (ver. 13: SPSS, Chicago, IL, USA) was used to determine if overall external morphometrics varied with sex or colony. After checking all raw data for normality and homogeneity of variances, the differences



**Fig. 1.** Morphometric measurements: head + bill length (HBL), bill length (BL), bill depth (BD), and tarsus length (TL).

between group means were assessed using the appropriate tests. Means and their associated standard deviation and significance level were calculated.

To measure the extent and direction of SSD in each trait, average values were  $\log_{10}$  transformed, and SSD was calculated (Abouheif & Fairbairn 1997) as

$$\log_{10}(\text{male body size}) - \log_{10}(\text{female body size}). \quad [1]$$

Ratios are commonly used to express SSD in animals, but most are considered to produce skewed data and thus to have undesirable statistical properties (Smith 1999). The difference between male and female size was therefore expressed as a logarithm (following Smith 1999). Where males were larger than females, the resulting Pearson correlation coefficient value was positive; where females were larger, the value was negative (as in Serrano-Meneses & Székely 2006). The Student *t*-test was also applied to each character for known breeding pairs to determine the extent of SSD.

### Developing a sex model and body size index

Using SPSS, a cross-validated DFA was used to explore the nature of any SSD that occurred and to produce a body size index. No significant differences between group covariance matrices occurred in the data, and all the assumptions of DFA were met (Pearson & Hartley 1976, Klecka 1980). The Evans Island sample was used to develop the sex model: each significant character was entered into a stepwise DFA (see Bosch 1996, Weidinger & van Franeker 1998, Mawhinney & Diamond 1999 for a similar procedure). The resulting discriminant function could then be used as a predictive tool to determine the sex of an individual based on the discriminant score gained. Whilst providing a sex model, the discriminant score was also used as an index of body size to further explore SSD. The value used to divide the frequency distribution of discriminant scores into sexes was the midpoint between the mean scores for males and females of known sex (Van Franeker & Ter Braack 1993, Weidinger & van Franeker 1998).

Performance of the sex model was validated by reapplying it to the original known sex group [“jack-knife method” (e.g. Amat *et al.* 1985)], and by applying it to the assumed sex group described earlier. The classification success of the sex model can be inferred from the number of misallocations of known or assumed-sex birds. Misallocations occurred when males were particularly small or females particularly large. The intercolony application of the model was assessed by applying it to a known and assumed-sex group from Althorpe Island. This step required the recalculation of the dividing point from the frequency distribution of discriminant scores of the new population (as recommended by Weidinger & van Franeker 1998).

### Assessing assortative mating

Assortative mating in regard to body size parameters was tested by estimating the slope of the relationship between the  $\log_{10}$ -transformed male size and the  $\log_{10}$ -transformed female size using major axis (MA) regression (Sokal & Rohlf 1995), which minimises the sum of the squared distances of residuals. This type of regression, unlike least-squares regression (model I), does not assume that  $x$  and  $y$  were measured without error (McArdle 1988, Sokal & Rohlf 1995) and is performed when both variables are measured on the same scales and with the same units (Quinn & Keough 2002). We performed MA regressions with software for

model II MA regression (available at Legendre 2000). Parametric 95% confidence intervals [lower confidence interval (CI) to upper CI] were computed for the slope of the line by bootstrapping the variables, and a permutation test was used to determine the significance of the MA. The closer the slope is to a 1:1 relationship between the sexes, the greater evidence of assortative mating for that character (as in Fairbairn & Preziosi 1994).

## RESULTS

### Sexual size dimorphism

For known-sex groups from both Evans and Althorpe islands, all five body-size variables had equality of group covariance matrices, and all but BM were normally distributed. For the Evans Island population, intersexual differences in BL, BD and HBL were highly significant ( $P < 0.0005$ ), and differences in TL were significant ( $P < 0.05$ ). The positive SSD values gained for all of these characters reveal male-biased SSD, with the greatest degree of SSD occurring in BD (Table 1). On Althorpe Island, male-biased SSD appeared less marked, with the only significant size difference between the sexes occurring in BD—males having the deeper bill. However, this result may be attributable to the smaller sample size at that colony: BL, HBL and TL were not significantly different in that group, although they trended toward being larger in males, gaining positive SSD values

(Table 1). Whilst BM is commonly dimorphic in seabirds (Serrano-Meneses & Székely 2006), it did not differ significantly between the sexes in the present study (Table 1). This result is not surprising, because BM varies widely across the population at any one time because of the body condition of individuals and the potential errors gained when food is present in their stomachs. Also adults of this species, like many Procellariiformes, commonly undergo large mass changes through the breeding season (Meathrel *et al.* 1993).

### Discriminant model

By running a stepwise DFA using all characters for birds of known sex from Evans Island (26 females, 25 males), BD and HBL were identified as the largest contributors to the separation of the sexes. This was evident because they gained the largest canonical discriminant function coefficients (HBL = 0.75, BD = 0.73, BL = 0.54, TL = 0.25). The assumptions of DFA were met because no significant differences between group covariance matrices or deviations from multivariate normality were found (Box  $M = 5.40$ , approximate  $F = 0.84$ ,  $P = 0.54$ ). The discriminant function ( $D$ ) was:

$$D = -56.325 + 1.964 * BD + 0.493 * HBL \quad [2]$$

Jack-knifing produced a 92% classification rate and thus did not improve the performance of the model. That finding indicates that the

TABLE 1

Variation in body size of male and female Short-tailed Shearwaters *Puffinus tenuirostris* breeding at Evans and Althorpe islands

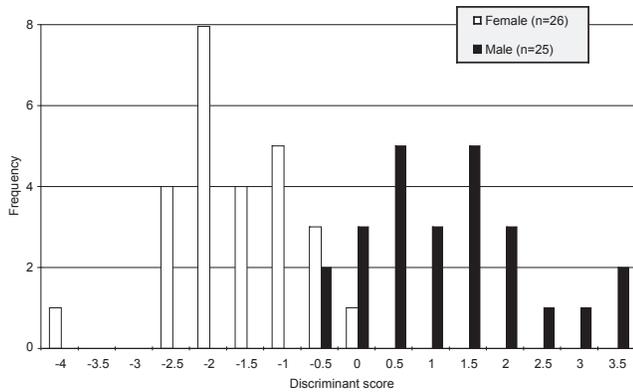
Colony	Group	Character	Sex	Mean	SD	Range	$F$	$P^a$	SSD <sup>b</sup>
Evans	Known sex 26 F, 25 M	Body mass (g)	F	729	18	580–885	2.53	*0.12	0.025
			M	774	23	610–930			
	Bill length (mm)	F	31.84	0.21	29.9–33.9	15.22	0.0003	0.015	
		M	32.97	0.20	31.17–34.79				
	Bill depth (mm)	F	7.43	0.06	6.79–8.05	58.53	<0.0001	0.040	
		M	8.14	0.07	7.33–8.90				
	Head + bill length (mm)	F	81.75	0.26	78.82–83.79	63.03	<0.0001	0.016	
		M	84.85	0.29	81.87–87.76				
	Tarsus length (mm)	F	59.40	0.26	56.55–61.40	4.65	0.04	0.007	
		M	60.28	0.32	57.35–63.42				
BSIndex (d score)	F	-1.43	0.89	-3.91 to 0.01	109.00	<0.0001			
	M	1.50	1.10	-0.11 to 3.69					
Althorpe	Known sex 10 F, 10 M	Body mass (g)	F	651	11	600–700	0.16	*0.69	-0.004
			M	645	10	590–695			
	Bill length (mm)	F	31.89	0.26	30.35–32.88	1.58	0.23	0.008	
		M	32.50	0.41	30.93–35.18				
	Bill depth (mm)	F	8.08	0.11	7.64–8.78	6.51	0.02	0.018	
		M	8.41	0.07	8.09–8.77				
	Head + bill length (mm)	F	84.22	0.54	81.27–87.23	0.18	0.68	0.005	
		M	84.54	0.53	81.88–87.77				
	Tarsus length (mm)	F	59.92	0.33	57.9–61.18	0.69	0.42	0.003	
		M	60.41	0.49	57.29–62.54				
BSIndex (d score)	F	0.81	1.05	-1.25 to 2.25	5.60	0.03			
	M	2.16	1.37	0.49–4.43					

<sup>a</sup> Univariate analysis of variance and  $U$ -test (\*).

<sup>b</sup> Log-transformed values, where a positive value indicates that males are larger than females, and a negative value indicates the reverse. SD = standard deviation; SSD = sexual size dimorphism; F = female; M = male.

classification success of the discriminant function was accurate, with an Eigen value of 2.234 (Wilks  $\lambda = 0.309$ ,  $P < 0.0001$ ). The model correctly regrouped 92.3% of females and 92.0% of males from the Evans Island known-sex group. Misclassification of some individuals indicates a degree of overlap in the discriminant scores between the sexes (Fig. 2) resulting from a slight overlap in body size. When  $D$  is greater than zero, the individual is a male (mean score: 1.49), and when smaller, a female (mean score: -1.34; Fig. 2). In known breeding pairs, where one individual was of known sex and the partner of assumed sex, males had a significantly larger body size index than did the female partners in all cases ( $t = -12.20$ ,  $N = 52$ ,  $P < 0.001$ ; Table 2). Within pairs, males also had a significantly larger BD, BL and HBL (paired  $t$ -test:  $P < 0.05$ ; Table 2). The most dimorphic character, BD, had an average difference of  $0.68 \pm 0.47$  mm between partners (Table 2). However, in four cases, the female bore a slightly deeper bill than did the male (0.01–0.2 mm).

The probabilities of group membership for each individual involved in the derivation of  $D$  were 46% for females and 44% for males, with a certainty of 0.99. By fitting these probabilities to the discriminant scores of each individual, critical scores for varying levels of probability were deduced from the nonlinear regression produced (Fig. 3). That regression provided an estimation of the reliability of allocating individuals to the correct sex using the model [Table 3 (as



**Fig. 2.** Histogram of the canonical discriminant scores of breeding adults of known sex from Evans Island based on a discriminant functions analysis of four skeletal characters, with cut-point of 0. Bill depth (BD) and head + bill length (HBL) are the two characters that explain most of the spread across the  $x$ -axis and can be explained by the classification function (sex model)  $D = -56.325 + 1.964 * BD + 0.493 * HBL$ . Open columns = females; solid columns = males.

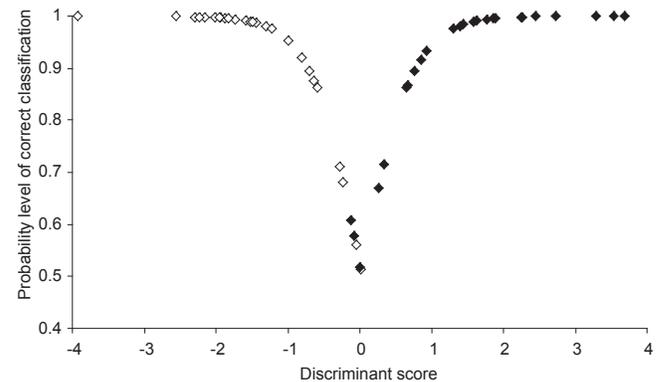
in Phillips & Furness 1997, Renner & Davis 1999)]. To assess the discriminatory power of the model derived from the known-sex group, that model was then tested on the assumed-sex group from Evans Island ( $n = 15$ ). This procedure confirmed the value of the model, because it correctly assigned 93% of females and 96% of males.

**Assortative mating of BD and body size**

The BD of males and females in known breeding pairs were highly correlated (Fig. 4;  $R^2 = 0.38$ ,  $n = 48$  pairs,  $P < 0.005$ ), as was the body size index (Table 2;  $R^2 = 0.43$ ,  $n = 52$  pairs,  $P < 0.005$ ). The slope of the MA regression for BD reveals that mating is assortative based on this character, as it was close to 1:1 (lower 95% CI to upper 95% CI: 0.53 to 1.14; Table 2; Fig. 4). This finding indicates that deep-billed males were often paired with deep-billed females, and narrow-billed males were paired with shallow-billed females. Whilst no association was found for BL, HBL or TL (Table 2), the body size index, which represents a combination of multiple characters, revealed that mating is also assortative based on body size.

**Geographic variation in body size**

Univariate analysis revealed significant differences in female BD and in HBL between colonies (Table 4), with birds on Althorpe Island being larger than those on Evans Island (Table 1). For males, BD was the only significantly different character (Table 4), with Althorpe Island birds being larger (Table 1). However, the reverse occurred for BM, with Evans Island males and females being



**Fig. 3.** Probability of correct classification as a function of discriminant scores, showing the posterior probability of belonging to the predicted group, based on the sex model. Open circles = probability of being female. Closed circles = probability of being male.

**TABLE 2**  
Assessing the magnitude of sexual size dimorphism (SSD) and the existence of assortative mating with respect to morphometric measurements and an index of body size within breeding pairs of known sex

Character <sup>a</sup>	Size difference (mm)		Total n	Male larger n	Paired $t$ -tests		MA regression <sup>b</sup>				
	Mean	SD			$t$	$P$	Slope	95% CI		$r$	$P$
								Lower	Upper		
Bill depth	0.68	0.47	52	48	10.52	<0.001	0.79	0.53	1.14	0.62	<0.005
Bill length	1.06	1.34	51	39	5.70	<0.001	0.22	-1.22	3.91	0.06	0.66
Head+bill length	1.73	2.58	48	35	4.69	<0.001	0.32	-0.15	0.94	0.27	0.07
Tarsus length	0.53	1.94	48	31	1.93	0.06	-1.01	-1.36	-0.76	0.63	0.47
BSIndex (d score)	1.77	1.05	48	52	-12.20	<0.001	0.80	0.59	1.07	0.74	<0.005

<sup>a</sup> Sample sizes of some characters were smaller because of missing data.

<sup>b</sup>  $\log_{10}$  (female size) against  $\log_{10}$  (male size) for bill depth, and bill, tarsus and head+bill length within pairs. SD = standard deviation; MA = major axis; CI = confidence interval.

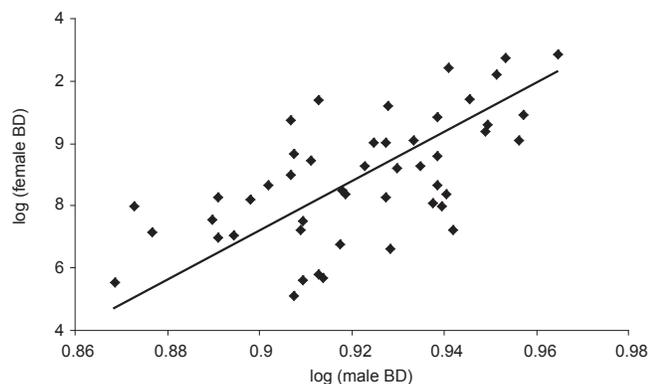
significantly heavier than their respective sexes on Althorpe Island (Tables 1 and 4). This result is most likely attributable to the time delay between colony visits, and highlights the extensive seasonal variation in weight (e.g. Lill & Baldwin 1983, Weimerskirch & Chérel 1998). Because of intercolony variation in body size, the performance of the discriminant model decreased when applied to Althorpe Island, with a greater rate of misclassification. From the known-sex group, 70% of females were correctly classified (7 of 10), with the same success rate for males (7 of 10). The model was then applied to an additional 40 birds of assumed sex, with improved success, because 90% of assumed females (18 of 20) and 75% of assumed males (15 of 20) were sexed correctly.

## DISCUSSION

The findings of male-biased SSD concur with those of previous studies for this species (Meathrel *et al.* 1993, Bull *et al.* 2005). The extent of SSD in the Short-tailed Shearwater is similar to that of other *Puffinus* species, because the sexing model has comparable discriminatory power [e.g. 92% for Cory's Shearwater (Lo Valvo 2001), 90% for Balearic Shearwater (Genovart *et al.* 2003) and 98.8% for the Pink-footed Shearwater (Guicking *et al.* 2004)]. The most dimorphic trait was BD, which is the case across the entire *Puffinus* genus (Bull *et al.* 2005). However, HBL had not been included in previous studies, and it showed significant dimorphism contributing largely to the body size index.

**TABLE 3**  
Critical discriminant scores for the probability of a bird being male or female

<i>P</i>	Female	Male
0.999	-2.30	2.43
0.995	-1.80	1.83
0.990	-1.53	1.16
0.950	-0.96	1.08
0.90	-0.72	0.78
0.80	-0.49	0.52
0.70	-0.26	0.33
0.60	-0.12	0.20
0.50	0.00	0.00



**Fig. 4.** Assortative mating by bill depth (BD) in Short-tailed Shearwaters *Puffinus tenuirostris*. Major axis regression showing  $\log_{10}$  female body size on  $\log_{10}$  male body size. The slope of the regression is 0.79, with a lower-to-upper confidence interval of 0.53 to 1.14.

The present discriminant model may be useful for field studies, because it can be applied at any time during the breeding season, and sex can be derived instantly and relatively easily. Despite the increased accuracy of molecular sexing, the need to perform lab-based analysis means that the technique is often impractical for seabird research on remote offshore islands or in instances in which sex must be determined quickly. In addition, molecular sexing is much more expensive. Other more traditional methods, such as the presence of an egg or the cloacal examination (Serventy 1956, Warham *et al.* 1977), are of limited value, because they are apparent only during certain stages of the breeding season. Whilst vocalisations are sexually dimorphic in some shearwater species, this method has been validated in only a few instances (e.g. Bretagnolle & Lequette 1990, Bretagnolle & Thibault 1995).

Assortative mating with respect to BD has been documented previously for the Short-tailed Shearwater (Meathrel & Bradley 2002). Whilst we provide further evidence of this size relationship, we also present a body size index, which reveals significant assortative mating. Assortative mating in bill dimensions also occurs in the Common Tern *Sterna hirundo* (Coulter 1986), Herring Gull *Larus argentatus* and Lesser Black-backed Gull *L. fuscus* (Harris & Hope-Jones 1969). Brown Noddys *Anous stolidus* mate assortatively based on body mass (Chardine & Morris 1989). The processes responsible for assortative mating between breeding partners are currently unclear. It has been suggested that assortative mating could occur through random mating alone (Coulter 1986, Chardine & Morris 1989), but this suggestion would apply only when the extent of SSD is large. More likely, this relationship is the result of selective mate choice for body size or parental quality. There are many possible advantages that females attain from mating with large males, and vice versa (see review by Blanckenhorn 2005). For example, BD contributes to the snapping power of a bill, and so males, and larger-billed females, should be able to handle larger prey than smaller birds should (see Ashmole 1968, Koffijberg & Van Eerden 1995). Meathrel & Bradley (2002) found that BD correlated with breeding success in Short-tailed Shearwaters, suggesting that mate selection may be adaptive. Indeed, the functional hypotheses

**TABLE 4**  
Intercolony comparison of morphometric characters between adult of known sex, showing the extent of size difference between males from both colonies and females from both colonies

Sex	Character	<i>F</i>	<i>df</i>	<i>P</i>	Colony where larger
Females <sup>a</sup>	Body mass (g)	7.11	34	0.01	Evans
	Tarsus length (mm)	3.82	34	0.06	Althorpe
	Bill length (mm)	0.02	34	0.90	Althorpe
	Head length (mm)	21.42	34	<0.001	Althorpe
	Bill depth (mm)	31.41	34	<0.001	Althorpe
Males <sup>b</sup>	Body mass (g)	12.71	32	<0.001	Evans
	Tarsus length (mm)	0.52	32	0.48	Evans
	Bill length (mm)	1.32	32	0.26	Evans
	Head length (mm)	0.18	32	0.67	Althorpe
	Bill depth (mm)	4.69	32	0.04	Althorpe

<sup>a</sup> Evans Island: n=26; Althorpe Island: n=10.

<sup>b</sup> Evans Island: n=25; Althorpe Island: n=10.

proposed to explain assortative mating are similar to those proposed for SSD in seabirds: those being sexual selection, fecundity selection or differential niche-utilisation (see review by Bull *et al.* 2005 and Serrano-Meneses & Székely 2006). However, the adaptive significance of existing male-biased SSD in shearwaters is still unclear (Fairbairn & Shine 1993). Further research investigating the influence of body size on breeding success, foraging success and prey harvest (e.g. Barbraud *et al.* 1999, González-Solis 2004) are necessary to identify the processes responsible for SSD and assortative mating in this species.

The usefulness of a sexing model derived from a single colony across a species range depends on the degree of variation in the extent of SSD (Schreiber & Schreiber 1988, Evans *et al.* 1993, van Franeker & ter Braak 1993). Where seabirds are of comparable body size, a reasonable accuracy may be obtained [e.g. Cory's Shearwater (Granadeiro 1993), Cape Petrel (Weidinger & van Franeker 1998), Herring Gull (Coulson *et al.* 1980)]. However, significant spatial variation in body size will reduce the accuracy of a sexing model derived from a single colony. In these instances, the development of a broader generalised discriminant function based on combined data from geographically separate populations can provide a more robust sexing tool [e.g. Cape Petrel (Weidinger & van Franeker 1998), fulmarine petrels (van Franeker & Ter Braak 1993)]. Given the existence of significant intercolony variation in Short-tailed Shearwater body size, it would be beneficial, when applying the current sex model, to compare the dimensions of an individual with the range reported herein. Also, when sexing a large number of birds, a new cut-point could be derived from the frequency distribution of the discriminant scores gained as a crude means of modifying the current model (as in van Franeker & Ter Braak 1993, Weidinger & van Franeker 1998).

## CONCLUSIONS

The present study has provided a relatively efficient sexing model that requires two simple measurements to provide a body size index and a likelihood of either male or female sex. Whilst 60%–70% of birds could be sexed with a certainty of 95%, within-pair comparisons of discriminant scores greatly improved sex determination of the remainder (because of significant assortative mating). Despite reduced success when applied to another colony, the current sex model provides a degree of certainty that is still comparable to that reported for many other seabird species. Thus, the current model represents a useful tool for sex determination in instances in which molecular sexing and other methods are not available.

## ACKNOWLEDGEMENTS

We thank those who assisted in the collection of data whilst in the field, including J. Thiessen, S. Pennington, D. Fraser, J. Pipitone and C. Murdoch. To J. Lawley for a guided tour of Althorpe Island and for his interest and enthusiasm in the research project. Thanks also to the regional Department of Environment and Heritage staff of Ceduna and Innes National Park for assistance in transport when in the field.

## REFERENCES

- ABOUHEIF, E. & FAIRBAIRN, D.J. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *American Naturalist* 149: 540–562.
- AINLEY, D.G., LERESCHE, R.E. & SLADEN, W.J.L. 1983. Breeding biology of the Adélie Penguin. Berkeley, CA: University of California Press. 240 pp.
- AMAT, J.A., VINUELA, J. & FERRER, M. 1985. Sexing Chinstrap Penguins (*Pygoscelis antarctica*) by morphological measurements. *Colonial Waterbirds* 16: 213–215.
- ASHMOLE, N.P. 1968. Body size, prey size and ecological segregation in five sympatric tropical terns (Aves: *Laridae*). *Systematic Zoology* 17: 292–304.
- BARBRAUD, C., WEIMERSKIRCH, H., ROBERTSON, G.G. & JOUVENTIN, P. 1999. Size-related life history traits: insights from a study of snow petrels (*Pagodroma nivea*). *Journal of Animal Ecology* 68: 1179–1192.
- BLANCKENHORN, W.U. 2005. Behavioural causes and consequences of sexual size dimorphism. *Ethology* 111: 977–1016.
- BOSCH, M. 1996. Sexual size determination of sex in Yellow-legged Gulls. *Journal of Field Ornithology* 67: 534–541.
- BRETAGNOLLE, V. & LEQUETTE, B. 1990. Structural variation in the call of the Cory's Shearwater (*Calonectris diomedea*) Aves, Procellariidae. *Ethology* 85: 313–323.
- BRETAGNOLLE, V. & THIBAUT, J. 1995. Methods for sexing fledglings in Cory's Shearwaters and comments on sex-ratio variation. *Auk* 112: 785–790.
- BULL, L.S., BELL, B.D. & PLEDGER, S. 2005. Patterns of size variation in the shearwater genus *Puffinus*. *Marine Ornithology* 33: 27–39.
- CHARDINE, J.W. & MORRIS, R.D. 1989. Sexual size dimorphism and assortative mating in the Brown Noddy. *Condor* 91: 868–874.
- COULSON, J.C., DUNCAN, N., THOMAS, C.S. & MONAGHAN, P. 1980. An age-related difference in the bill depth of Herring Gulls (*Larus Argentatus*). *Ibis* 123: 499–502.
- COULTER, M.C. 1986. Assortative mating and sexual dimorphism in the Common Tern. *Wilson Bulletin* 98: 93–100.
- EVANS, D.R., EHOOPES, M. & GRIFFIN, C.R. 1993. Discriminating the sex of laughing gulls by linear measurements. *Journal of Field Ornithology* 64: 472–476.
- FAIRBAIRN, J. & SHINE, R. 1993. Patterns of sexual size dimorphism in seabirds of the southern hemisphere. *Oikos* 68: 139–145.
- FAIRBAIRN, J. & PREZIOSI, R.F. 1994. Sexual selection and the evolution of allometry for sexual size dimorphism in the water strider, *Aquarius remiges*. *American Naturalist* 144: 101–118.
- GENOVART, M., MCMINN, M. & BOWLER, D. 2003. A discriminant function for predicting sex in the Balearic Shearwater. *Waterbirds* 26: 72–76.
- GONZÁLEZ-SOLIS, J. 2004. Sexual size dimorphism in giant petrels: ecological correlates and scaling. *Oikos* 105: 247–254.
- GRANADEIRO, J.P. 1993. Variation in measurements of Cory's Shearwater between populations and sexing by discriminant analysis. *Ring and Migration* 14: 103–112.
- GUICKING, D.W., FIEDLER, W., LEUTHER, C., SCHLATTER, R. & BECKER, P.H. 2004. Morphometrics of the Pink-footed Shearwater (*Puffinus creatopus*): influence of sex and breeding site. *Journal of Ornithology* 145: 64–68.
- HAMER, K.C. & FURNESS, R.W. 1991. Age-specific breeding performance and reproductive effort in Great Skuas (*Catharacta skua*). *Journal of Animal Ecology* 60: 693–704.
- HARRIS, M.P. & HOPE-JONES, P. 1969. Sexual differences in measurements of Herring and Lesser Black-backed gulls. *British Birds* 62: 129–133.

- KLECKA, W.R. 1980. Discriminant analysis. Beverly Hills, CA: Sage Publications. 71 pp.
- KOFFIJBERG, K. & VAN EERDEN, M.R. 1995. Sexual dimorphism in the Cormorant *Phalacrocorax carbo sinensis*: possible implications for differences in structural size. *Ardea* 83: 37–46.
- LEGENDRE, P. 2000 [updated 2008]. Program for Model II regression with permutation tests [Web page with downloadable files]. Montreal, QC: Université de Montréal. [Available at: [www.bio.umontreal.ca/Casgrain/en/labo/model-ii.html](http://www.bio.umontreal.ca/Casgrain/en/labo/model-ii.html)]; cited 12 April 2007]
- LILL, A. & BALDWIN, J. 1983. Weight changes and the mode of depot fat accumulation in migratory Short-tailed Shearwaters. *Australian Journal of Zoology* 31: 891–902.
- LO VALVO, M. 2001. Sexing adult Cory's Shearwaters by discriminant analysis of body measurements on Linosa Island (Sicilian Channel), Italy. *Waterbirds* 24: 169–174.
- MAWHINNEY, K. & DIAMOND, T. 1999. Sex determination of Great Black-backed Gulls using morphometric characters. *Journal of Field Ornithology* 70: 206–210.
- MCARDLE, B.H. 1988. The structural relationship: regressions in biology. *Canadian Journal of Zoology* 66: 2329–2339.
- MEATHREL, C.E., BRADLEY, J.S., WOOLLER, R.D. & SKIRA, I.J. 1993. The effect of parental condition on egg-size and reproductive success in Short-tailed Shearwaters (*Puffinus tenuirostris*). *Oecologia* 93: 162–164.
- MEATHREL, C.E. & BRADLEY, J.S. 2002. The prediction of individual reproductive success in the Short-tailed Shearwater *Puffinus tenuirostris*. In: (Schodde, R.). (Eds). Abstracts of the 23rd International Ornithological Congress; 11–17 August 2002; Beijing, PR China. *Acta Zoologica Sinica* 52: 82–89.
- PEARSON, E.S. & HARTLEY, H.O. 1976. Biometrika tables for statisticians. Vol. 2. Cambridge, UK: Biometrika Trust.
- PHILLIPS, R.A. & FURNESS, R.W. 1997. Predicting the sex of Parasitic Jaegers by discriminant analysis. *Colonial Waterbirds* 20: 14–23.
- QUINN, G.P. & KEOUGH, M.J. 2002. Experimental design and data analysis for biologists. Cambridge, UK: Cambridge University Press. 537 pp.
- RENNER, M. & DAVIS, L.S. 1999. Sexing Little Penguins (*Eudyptula minor*) from Cook Strait New Zealand using discriminant functions analysis. *Emu* 99: 74–79.
- REYNOLDS, S.J., MARTIN, G.R., WALLACE, L.L., WEARN, C.P. & HUGHES, B.J. 2008. Sexing sooty terns on Ascension Island from morphometric measurements. *Journal of Zoology* 274: 2–8.
- SCHREIBER, E.A. & SCHREIBER, R.W. 1988. Great Frigatebird size dimorphism on two central Pacific atolls. *Condor* 90: 90–99.
- SERRANO-MENESES, M.A. & SZÉKELY, T. 2006. Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. *Oikos* 113: 385–394.
- SERVENTY, D.L. 1956. A method of sexing petrels in field observations. *Emu* 56: 213–214.
- SMITH, R.J. 1999. Statistics of sexual size dimorphism. *Journal of Human Evolution* 36: 423–459.
- SOKAL, R.R. & ROHLF, F.J. 1995. Biometry. 3rd ed. New York, NY: W.H. Freeman. 199 pp.
- VAN FRANEKER, J.A. & TER BRAAK, C.J.F. 1993. A generalised discriminant for sexing Fulmarine Petrels from external measurements. *Auk* 110: 495–502.
- WARHAM, J., KEELEY, B.R. & WILSON, G.J. 1977. Breeding of the mottled petrel. *Auk* 94: 1017.
- WEIDINGER, K. & VAN FRANEKER, J.A. 1998. Applicability of external measurements to sexing of the Cape petrel (*Daption capense*) at within-pair, within-population and between-population scales. *Journal of Zoology, London* 245: 473–482.
- WEIMERSKIRCH, H. & CHEREL, Y. 1998. Feeding ecology of Short-tailed Shearwaters: breeding in Tasmania and foraging in the Antarctic? *Marine Ecology-Progress Series* 167: 261–274.

