

Sexual size dimorphism, within-pair comparisons and assortative mating in the short-tailed shearwater (*Puffinus tenuirostris*)

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Abstract – Biometric studies of short-tailed shearwaters (*Puffinus tenuirostris*) indicate differences in body mass and linear measurements between sexes. Here the degree of sexual size dimorphism in 390 short-tailed shearwater adults is assessed and a sex-discriminating function is produced to improve methods for sexing live birds in the field. Analysis of body mass and linear measurements showed males to be significantly heavier and larger than female birds in all variables. The largest degree of sexual size dimorphism was in bill depth (7.5%) followed by body mass (5.1%). Bill depth plus total head length were the most accurate variables in a discriminant function model. Together, these 2 variables predicted sex with 84% accuracy. Bill depth alone predicted sex with 82% accuracy. However, application of a sex-discriminating model developed from another colony, did not correctly classify the sex of adult birds as accurately. This can be explained by the existence of significant geographical variation in body size within the species and reinforces the need for colony-specific sex discriminant models. Comparisons within-pairs revealed that bill depth is a more reliable indicator of sex, without the need for a discriminant function analysis. Contrary to previous studies, measurements of male and female partners showed no evidence of assortative mating in any character assessed. If short-tailed shearwaters mate assortatively then it may be based on traits other than structural size.

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INTRODUCTION

Individuals of known sex are vital in many ecological and behavioural studies due to the importance of identifying the roles of each sex in various aspects of breeding biology. However, sex can often be difficult to determine in seabirds (Procellariiformes) because many exhibit monomorphic morphology or plumage characters (Warham 1990). Although males are usually larger than females in many procellariids, there can be a considerable overlap

between the sexes in their size ranges (Marchant & Higgins 1990; Warham 1990). Monotypic birds like shearwaters and petrels are sexed from a variety of methods, such as dissection, observing copulation, cloacal examination at the time of egg-laying (Serventy 1956; Boersma & Davies 1987), sexual voice dimorphism, particularly in the *Puffinus* group (Brooke 1978; Bourgeois *et al.* 2007) and more recently, by molecular methods using polymerase chain reaction (PCR) amplification (Kahn *et al.* 1998). Alternative *in situ* methods are desirable, especially outside the breeding season, when knowledge of a bird's sex is required.

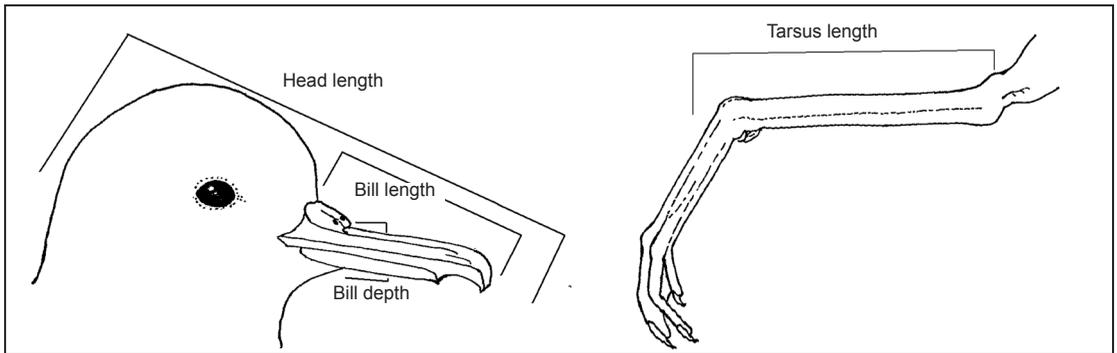


Fig. 1. Location of morphometric measurements taken on short-tailed shearwaters: head length, bill length, bill depth and tarsus. Wing length not shown. Line drawings courtesy of Vicki McCartney.

In situations outside the breeding season where invasive techniques or molecular methods are not possible or undesirable, sex can sometimes be determined from external morphometric measurements. A discriminant function analysis (DFA) combines a number of morphometric measurements and allows relatively accurate predictions of an individual's gender, even when there is considerable overlap in size ranges. These morphometric measurements can be a valuable tool for sexing birds, especially outside the breeding season, as other sexing methods can be applied only during the breeding season (e.g. vocalisations, cloacal examination, and copulation behaviour). Predictive functions from body measurements have been used successfully to discriminate gender in a variety of monomorphic seabirds, including brown noddies (*Anous stolidus*) (Chardine & Morris 1989), razorbills (*Alca torda*) (Wagner 1999), penguins (Amat *et al.* 1993; Renner *et al.* 1998) and gulls (Fox *et al.* 1981; Coulson *et al.* 1983; Hanners & Patton 1985; Evans *et al.* 1993; Torlaschi *et al.* 2000).

The application of a DFA to sex adult birds using external body measurements can be particularly useful because of the relatively non-invasive, cost effective and efficient nature of the technique. The predictive function derived from the DFA is species-specific, but caution must be observed when generalising over the entire geographical range of a species owing to morphometric differences between colonies (Guicking *et al.* 2004; Einoder *et al.* 2008). Thus, it has been suggested that a DFA should only be used in those studies of the local population from which it was derived (Evans *et al.* 1995).

Analyses can also be confounded if individuals mate assortatively by size (Coulter 1986; Fletcher & Hamer 2003). For example, in species where the sexes overlap in size but males are on average larger than females, assortative mating would lead to an increased likelihood of males in small pairs being sexed as females and females in large pairs being

sexed as males. Problems in identifying sex may be greatly reduced by using within-pair comparisons of relative size. Such within-pair comparisons result in improved sex determination in south polar skuas (*Catharacta maccormicki*) (Ainley *et al.* 1985) and cape petrels (*Daption capense*) (Weidinger & Franeker 1998). However, the usefulness of this approach has not been widely evaluated (Fletcher & Hamer 2003).

Short-tailed shearwaters (*Puffinus tenuirostris*) have no plumage differences between males and females although published measurements suggest there may be some morphological dimorphism (Marchant & Higgins 1990; Meathrel *et al.* 1993; Einoder *et al.* 2008). The life cycle and basic biology of short-tailed shearwaters have been described by Serventy (1967) and Serventy & Curry (1984), but few studies examined differences in body size of male and female birds. The objective in this study was to find an *in situ* method of identifying the sex of adult short-tailed shearwaters in the field that could be used outside the egg-laying period. This method provides rapid results and it is cost effective compared to molecular sexing. In this study, data are evaluated on sexual size dimorphism in body mass and 5 linear morphological measurements from randomly sampled males and females, and for known pairs. I also present an equation which can be used to sex live birds, and assess the usefulness of a DFA derived from another colony to sex birds in a different colony. Finally, I use the measurements collected on the large number of pairs in this study to test whether mate choice in short-tailed shearwaters is size-related.

METHODS

Adult short-tailed shearwaters were captured during the breeding seasons of 2006/07, 2007/08 and 2008/09 within a large colony on Great Dog I, Furneaux Group, Tasmania, Australia (40°15'07"S,

Table 1. Body measurements (mean \pm SD) of male (A) and female (B) short-tailed shearwaters according to year of capture on Great Dog I, Tasmania. Superscript letters denote significantly different means using Fisher's LSD *post hoc* testing.

A. Males	2006/07 (n = 90)	2007/08 (n = 90)	2008/09 (n = 13)	$F_{2,190}$	P
Head length (mm)	83.7 (\pm 1.9)	83.1 (\pm 2.1)	84.0 (\pm 1.4)	2.43	0.09
Bill length (mm)	32.7 (\pm 1.4)	32.5 (\pm 1.2)	33.0 (\pm 1.3)	1.21	0.30
Bill depth (mm)	8.9 (\pm 0.3)	8.90 (\pm 0.4)	9.1 (\pm 0.4)	1.64	0.19
Wing length (mm)	272.5 (\pm 5.7)	273.1 (\pm 6.7)	273.2 (\pm 6.3)	0.27	0.76
Tarsus length (mm)	58.8 (\pm 1.3) ^a	59.4 (\pm 1.6) ^b	60.1 (\pm 1.5) ^b	5.86	0.003
Body mass (g)	642.0 (\pm 50.9) ^a	618.8 (\pm 47.7) ^b	660.0 (\pm 60.4) ^a	6.95	0.001
B. Females	2006/07 (n = 88)	2007/08 (n = 87)	2008/09 (n = 22)	$F_{2,194}$	P
Head length (mm)	81.3 (\pm 1.7)	81.5 (\pm 2.0)	80.5 (\pm 2.4)	2.51	0.08
Bill length (mm)	31.5 (\pm 1.1)	31.7 (\pm 1.1)	31.4 (\pm 1.5)	0.87	0.42
Bill depth (mm)	8.3 (\pm 0.3)	8.2 (\pm 0.4)	8.3 (\pm 0.4)	0.30	0.74
Wing length (mm)	269.2 (\pm 6.2)	269.5 (\pm 5.6)	272.2 (\pm 5.6)	2.30	0.10
Tarsus length (mm)	58.2 (\pm 1.7)	58.3 (\pm 1.3)	58.3 (\pm 1.5)	0.21	0.81
Body mass (g)	583.4 (\pm 58.7)	612.3 (\pm 75.3)	615.4 (\pm 53.4)	9.19*	0.01

*Kruskal-Wallis (χ^2), d.f. = 2

148°15'08"E). Body mass (g), plus 5 external body measurements (after Baldwin *et al.* 1931) were taken by one person (MJC) in all 3 breeding seasons (Fig. 1). Adults were weighed using Pesola 1000 g (\pm 10 g) scales and measured using Mitutoyo Vernier callipers (Mitutoyo Corporation, Kanagawa, Japan) accurate to \pm 0.02 mm and rounded to the nearest 0.1 mm (i.e., rounded up for measurements 0.06 and 0.08 and rounded down for 0.02 and 0.04). Wing length was measured using a standard butt-ended wing ruler (to the nearest 1.0 mm). The 5 morphological measurements taken for adults were: (1) head length from the tip of the maxillary unguis (upper nail of the bill) to the rear of the skull, (2) bill length from the maxillary unguis to the posterior extremity of the nares (nasal tubes), (3) vertical bill depth at the proximal base of the nares, (4) length of the tarsometatarsus (hereafter tarsus), and (5) wing length from the carpal joint to the end of the 10th primary feather. All birds were banded with an individually identifying Australian Bird and Bat Banding Scheme (ABBBS) stainless steel band. When birds were being handled during egg-laying they were sexed by cloacal examination (Serventy 1956; Boersma & Davies 1987). Birds with an obviously distended, oedematous cloaca (i.e., evidence of an oviduct stretched by laying an egg) were presumed to be female. Birds that were partnered with females were presumed to be male, as no same-sex pairs of breeding short-tailed

shearwaters have been recorded. Only those pairs which laid an egg were included in this study.

Statistical analysis

Statistical analysis was performed using SPSS (version 17.0: SPSS, Chicago, IL, USA). All variables were tested for their normality and homogeneity of variances before using appropriate tests. Principal Components Analysis (PCA) was used to characterise variability in body dimensions within the total sample. The 1st principal component (PC1) comprised head length, bill length, bill depth, wing length and tarsus length and is used as a single composite measure of body size. Differences between the sexes for each measurement were tested with a *t*-test. The sequential Bonferroni adjustment was used as multiple measures of the same individual were used ($P = 0.008$) (Sokal & Rohlf 1995). For all other tests the significance was set to $P < 0.05$.

Sexual dimorphism (*SD*) was calculated as a percentage between the sexes in each measurement as:

$$SD = \frac{(\bar{x}_m - \bar{x}_f)}{\bar{x}_m} \times 100$$

Where \bar{x}_m and \bar{x}_f were the mean values in males and females, respectively.

A DFA based on external morphometrics was performed after Dytham (2003). Body mass was not

Table 2. Descriptive statistics of the measurements of 390 adult sexed short-tailed shearwaters (\pm SD). Percentage of sexual dimorphism and level of significance between males and females according to the *t*-test in each variable is also shown.

	Males (<i>n</i> = 193)	Females (<i>n</i> = 197)	$t_{2,388}$	<i>P</i>	% dimorphism
Head length (mm)	83.4 (\pm 2.0)	81.3 (\pm 1.9)	10.50	<0.001	2.5
Bill length (mm)	32.7 (\pm 1.3)	31.6 (\pm 1.2)	8.24	<0.001	3.1
Bill depth (mm)	8.9 (\pm 0.4)	8.3 (\pm 0.4)	16.82	<0.001	7.5
Wing length (mm)	272.8 (\pm 6.3)	269.7 (\pm 5.9)	5.11	<0.001	1.1
Tarsus length (mm)	59.2 (\pm 1.5)	58.3 (\pm 1.6)	5.73	<0.001	1.5
Body mass (g)	632.4 (\pm 51.6)	599.8 (\pm 67.4)	5.16*	<0.001	5.1
PC1 scores	0.60 (\pm 0.80)	-0.59 (\pm 0.80)	14.57	<0.001	n.a.

*Mann-Whitney *U*-test

Table 3. Accuracy of the discriminant function derived from measures of 390 short-tailed shearwaters. Frequencies (%) of classified birds with the original function and with the cross validation shown.

	Sex	Predicted sex	
		Male	Female
Original	Male	157 (81.3)	36 (18.7)
	Female	27 (13.7)	170 (86.3)
Cross validation	Male	156 (80.8)	37 (19.2)
	Female	28 (14.2)	169 (85.8)

included in the analysis because this can vary greatly according to the time since last food ingestion and stage of breeding. The reliability of the discriminant function was estimated by checking the predicted sex against the actual sex determined in the field. To test the reliability of the prediction a jack-knife procedure (cross validation) was performed, where each individual was classified using a function derived from the total sample minus the individual being classified.

Because a number of known pairs were sexed and measured, the degree to which males and females mated assortatively with respect to their body measurements were examined. To test for assortative mating, Pearson correlation coefficients (*r*) were calculated between pairs in all linear morphometric measurements, body mass and PC1 scores.

RESULTS

Morphometrics

In total, 390 adults were measured over the 3 years of the study: 178 in 2006/07, 177 in 2007/08 and 35 in 2008/09 (Table 1). Female body mass varied between years (Kruskal-Wallis $\chi^2 = 9.19$, *d.f.* = 2, *P* = 0.01) but these differences were not significant after Bonferroni adjustment. There were also differences in male body mass ($F_{2,190} = 6.95$, *P* = 0.001) and tarsus length ($F_{2,190} = 5.85$, *P* = 0.003) between years. *Post hoc* least significant difference (LSD) testing

(Fisher's LSD test) revealed that males in 2007/08 were significantly lighter than those in 2006/07 (mean difference: 23.2 g, *P* < 0.01) and 2008/09 (mean difference: 41.2 g, *P* < 0.01). Tarsus length of male adults were marginally longer in 2006/07 than those measured in 2007/08 (mean difference: 0.6 mm, *P* = 0.01) and 2008/09 (mean difference: 1.3 mm, *P* < 0.01). No other significant differences were found between sexes over the sampled years (Table 1).

Sexual dimorphism

All measurements except body mass met the assumptions of a 2-sample *t*-test according to the results of Levene's test for equality of variances. Thus, body mass was tested using a Mann-Whitney *U*-test which showed that males were significantly heavier than females (Table 2). For all other variables, males were larger than females in linear measurements, and PC1 scores (Table 2). The largest proportional differences were in bill depth (7.5%), body mass (5.1%) and bill length (3.1%). The degree of sexual size dimorphism was least in wing length (1.1%). All differences were highly significant (*P* < 0.001) between the sexes and remained significant after Bonferroni adjustment.

Discriminant function

The discriminant analysis was applied to 5 morphometric characters of 390 adult short-tailed

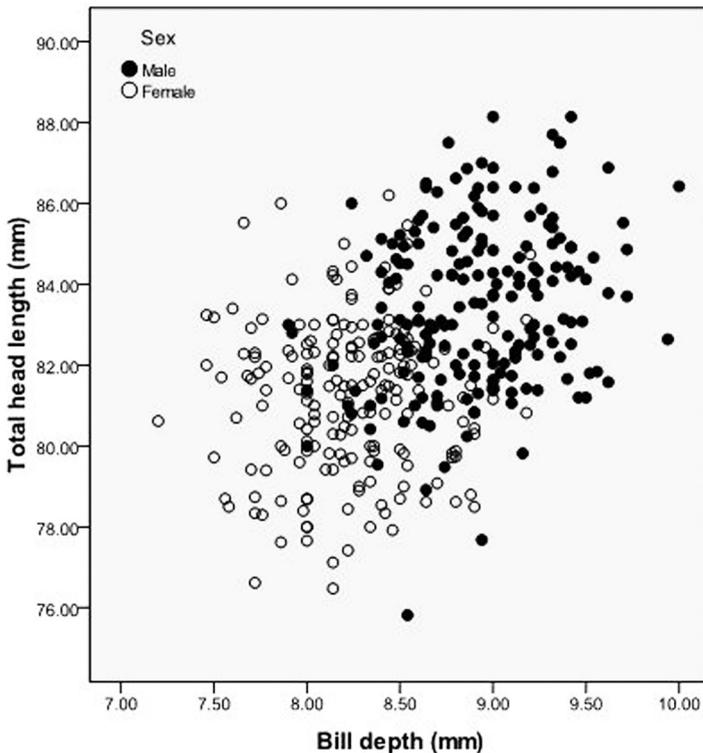


Fig. 2. Segregation of male and female short-tailed shearwaters corresponding to the most accurate variables used in the discriminant function model that included bill depth and total head length.

shearwaters (193 males and 197 females). Bill depth and head length were the most accurate variables for use in a discriminant function model, predicting sex with 83.8% accuracy (Table 3). The assumptions of the DFA were met as no significant differences between group covariance matrices or deviations from multivariate normality were found (Box $M = 1.44$, approximate $F = 0.48$, $P = 0.70$). Cross-validation classified adults marginally lower with 83.3% accuracy (Wilks' $\lambda = 0.553$, $\chi^2 = 243.52$, $P < 0.001$). The discriminant function (D) obtained was:

$$D = 0.21 (\text{head length}) + 2.138 (\text{bill depth}) - 35.616$$

When $D > 0$, the individual is classified as a male (mean 0.94 ± 1.03) and when < 0 , a female (mean -0.92 ± 0.97). Misclassification of some adults indicates a degree of overlap in the discriminant scores between the sexes resulting from a slight overlap in body size (Fig. 2). When only 1 variable, bill depth or total head length, was taken into account in the discriminant function, accuracy decreased to 82.1% and 69.7%, respectively.

To test the accuracy of a discriminant model developed by Einoder *et al.* (2008), I applied their model to the 390 known sexed birds used in this study. Of the 390 adults, only 72.5% were accurately allocated the correct sex using the Einoder *et al.* (2008)

model. This finding indicates some geographical size differences within the species.

Within-pairs, males were significantly heavier and larger than females in all linear variables tested but not based on their PC1 scores (paired t -test; Table 4). These differences were still highly significant after Bonferroni adjustment. The most dimorphic character, bill depth, had an average difference of $0.7 (\pm 0.5)$ mm between partners. In 92.4 % of cases, males had a deeper bill than their female partners.

Tests for assortative mating

In pairs where both birds were measured, there was an opportunity to study assortative mating in their morphometric characters. A total of 171 pairs were used in the analysis. No significant correlation was found between partners in morphometric measurements (Table 5). Body mass and their PC1 scores were not significantly correlated within-pairs (Table 5).

DISCUSSION

Over the 3 years of this study the linear body measurements of short-tailed shearwaters caught each year did not change significantly with the exception of male tarsus length. Body mass, which was measured at the same time each year, also

Table 4. Magnitude of difference between male and female short-tailed shearwater measurements within the same pair. Total pairs $n = 171$.

Character	Mean difference (\pm SD)	% male larger (n)	Paired t	P
Head length (mm)	2.0 (\pm 2.8)	79.5 (136)	9.4	<0.001
Bill length (mm)	1.0 (\pm 1.6)	72.5 (124)	8.1	<0.001
Bill depth (mm)	0.7 (\pm 0.5)	92.4 (158)	17.2	<0.001
Wing length (mm)	3.3 (\pm 9.1)	67.8 (116)	4.7	<0.001
Tarsus length (mm)	0.9 (\pm 2.3)	64.9 (111)	4.9	<0.001
Body mass (g)	25.9 (\pm 88.1)	64.3 (110)	3.8	<0.001
PC1	<0.00 (\pm 1.4)	53.2 (91)	<0.01	>0.05

Table 5. Correlation analyses of morphometrics of short-tailed shearwater pairs breeding on Great Dog I, Furneaux Group, Tasmania. Total pairs $n = 171$.

	Head length	Bill length	Bill depth	Wing length	Tarsus length	Body mass	PC1
r	-0.069	0.106	0.090	-0.097	0.002	-0.016	0.016
P	0.37	0.17	0.24	0.20	0.98	0.83	0.83

varied in males between years. Female body mass did fluctuate between years but was not found to be significant. These observations suggest annual variation in the body condition of male shearwaters at the Furneaux Group colonies. Aspects of the breeding biology, behaviour and adult body condition of seabirds can be an important indicator of marine food supply and the observed mass variation may indicate annual fluctuations in food availability on distant shearwater feeding grounds during the breeding season (Weimerskirch & Chérel 1998; Chérel *et al.* 2005).

Male short-tailed shearwaters captured on Great Dog I were, on average, significantly larger than females in all linear body measurements, body mass and their PC1 scores. These findings support previous studies of this species across their geographical range (Meathrel *et al.* 1993; Bull *et al.* 2005; Bradley & Meathrel 2006; Einoder *et al.* 2008). The differences between the sexes observed in this study have been reported in other studies of procellariids, such as Manx shearwater (*P. puffinus*) (Brooke 1990), Hutton's shearwater (*P. huttoni*) (Cuthbert & Davis 2002), Balearic shearwater (*P. mauretanicus*) (Genovart *et al.* 2003), pink-footed shearwater (*P. creatopus*) (Guicking *et al.* 2004), Cory's shearwater (*Calonectris diomedea*) (Lo Valvo 2001), Antarctic petrel (*Thalassoica antarctica*) (Lorentsen & Rov 1994), and Gould's petrel (*Pterodroma leucoptera*) (O'Dwyer *et al.* 2006) although the degree of sexual dimorphism varies considerably between these species. The degree of sexual size dimorphism presented in this study was between 1 - 7.5%, and a similar range was found

for Balearic shearwaters (0.3 - 8.3%; Genovart *et al.* 2003). However, this range is small given the degree of sexual dimorphism between northern giant petrels (*Marconectes halli*), with males being 20 - 25% heavier and from 5 - 16% larger than females in linear measurements (González-Solís 2004).

Short-tailed shearwaters could be sexed in 84% of cases using bill depth and total head length in a DFA. Validation methods suggested a more realistic estimate of the success rate for the function of 83%. Thus, using the DFA on other shearwaters from this study colony it would be expected that there would be an error in sexing of less than 2 in 10 times. This contradicts the findings of Meathrel *et al.* (1993) where it is suggested that sex for this species cannot be predicted based on structural size. My results show short-tailed shearwaters can be sexed with relatively high success using a DFA. However, the DFA produced can only be applied to the population used in this study. This suggests some geographical variation within the species and reinforces the need for researchers to obtain sex models from locally caught birds (Weidinger & van Franeker 1998; Guicking *et al.* 2004). Geographic variation may reflect some kind of ecomorphological adaptation to different environmental conditions (Spear & Ainley 1998; Guicking *et al.* 2004).

The success rate of the DFA model achieved in this study for short-tailed shearwaters is intermediate between that reported for many shearwater species (>90%; Lo Valvo 2001; Genovart *et al.* 2003; Guicking *et al.* 2004; Thalmann *et al.* 2007) and the success rate for petrels (59-86%, Weidinger

& van Franeker 1998; 73%, O'Dwyer *et al.* 2006). At a short-tailed shearwater colony in South Australia, 1500 km to the west of Great Dog I, Einoder *et al.* (2008) were able to predict sex 92% of the time, despite a low sample size ($n = 61$). Application of this sex model to another colony close by reduced its accuracy to 70–80% (Einoder *et al.* 2008). Although the results of a DFA are sensitive to sample size and other statistical attributes (Morrison 1984), much of the variation in success rate is most likely the result of variation in the relative degree of sexual size dimorphism (Chardine & Morris 1989).

The stepwise DFA used to determine the classification function chose bill depth, followed by total head length, indicating bill depth was the better discriminator of sex. The value of bill depth in determining sex in procellariids has been reported previously (Lo Valvo 2001; Genovart *et al.* 2003; Einoder *et al.* 2008). Used alone, bill depth successfully sexed 82% of short-tailed shearwaters in the sample. However, given the reduction of success rate it is recommended that both bill depth and total head length is used when sexing live short-tailed shearwaters in the Furneaux Group colonies. Sexual differences in procellariid bill morphology has been suggested to reflect sexual differences in foraging behaviour (González-Solis *et al.* 2000; González-Solis 2004). Furthermore, it is not known whether a sex difference in foraging behaviour exists in short-tailed shearwaters.

In almost all short-tailed shearwater pairs observed in this study, the male was larger. Similar results have been obtained by Meathrel *et al.* (1993) and Einoder *et al.* (2008) for short-tailed shearwaters. Differences in relative size of certain body parts, such as bill depth, within a pair may be a more reliable indicator of sex. Predicting sex within-pairs was achieved with a higher accuracy rate than the DFA when bill depth of both birds were analysed. Within-pair comparisons have substantially improved the accuracy of determining sex in seabirds with monomorphic plumage such as cape petrels (Weidinger & van Franeker 1998), common terns (*Sterna hirundo*), Arctic terns (*S. paradisaea*) (Fletcher & Hamer 2003), and brown noddies (Chardine & Morris 1989).

Short-tailed shearwaters from my study colony showed no assortative mating in either body mass or linear body measurements. These results contrast with those of Bradley & Meathrel (2006) and Einoder *et al.* (2008) who found positive assortative mating for bill depth, tarsus length and their body size index. Despite the fact that assortative mating has been shown to occur in brown noddies (Chardine & Morris 1989), Arctic terns (Fletcher & Hamer 2003) and other species, it seems that short-tailed shearwaters may mate randomly based on morphological traits. A lack

of assortative mating in short-tailed shearwaters based on size alone is perhaps not surprising given the structural similarity between males and females (the most dimorphic feature, bill depth, was only 7.5% larger in males). If assortative mating occurs in short-tailed shearwaters it may be based on traits other than structural size. For example, it has been suggested that assortative mating in short-tailed shearwaters may occur based on the number of years since they first bred (Wooller *et al.* 1990; Bradley *et al.* 1995), which has been found for northern giant petrels (González-Solis 2004) and some tern species (Nisbert *et al.* 1984; Bridge & Nisbert 2004).

In summary, sexual size dimorphism does occur in the short-tailed shearwater. The most dimorphic feature of the species is bill depth, and when combined with total head length, sex can be predicted with an 84% accuracy using a DFA model. Where measurements have been taken of both members of a pair accuracy increases to 92% based on a comparison of bill depth. When applying a discriminant function to other colonies of short-tailed shearwaters, it is recommended that investigators use measurements of their specific population due to geographic variation within the species. Size differences are also reflected within-pairs. In those pairs in which it may be difficult allocating gender, within-pair comparison of bill depth will assist in predicting sex. Assortative mating was not observed in this species despite the findings of Bradley & Meathrel (2006) and Einoder *et al.* (2008). Finally, it is recommended that a single observer should perform all morphological measurements to eliminate inter-observer differences as the degree of dimorphism in short-tailed shearwaters is small.

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