

PATTERNS OF SIZE VARIATION IN THE SHEARWATER GENUS *PUFFINUS*

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SUMMARY

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Using multivariate methods, we investigated patterns of trait variation in the shearwater genus *Puffinus* in terms of specific, sexual and geographic variation. We found no significant interaction between sex and population, indicating that there is no geographical variation in the magnitude of sexual dimorphism. Species for which a significant difference was found between the sexes exhibit low levels of sexual size dimorphism, expressed only in bill-depth dimensions (male bills are deeper). Only species with widespread distributions exhibit significant geographic variation in their morphometrics.

Key words: Shearwaters, *Puffinus* spp., morphology, geographic variation, sexual size dimorphism, interspecific variation

INTRODUCTION

Varying degrees of predation, inter- and intraspecific competition, inter- and intrasexual competition and food availability may result in individual, sexual or geographic variation in size (Endler 1977, Wikelski & Trillmich 1997, Lovich *et al.* 1998). Historically many of the leading papers on avian size variation have been concerned with terrestrial birds (Hamilton 1961, Selander 1966, Grant 1968, James 1970, Johnston & Selander 1973) with little work on seabirds. The remote location of many seabird colonies, the general trend for monogamy, and the nocturnal habits of some seabird species have probably contributed to the paucity of such studies.

No previous comprehensive studies of size variation in the shearwater genus *Puffinus* (Procellariiformes) are available, yet the genus lends itself to a study of size variation in seabirds. The genus contains approximately 20 species that vary in such aspects as ecology, geographic range, size, migratory habit, and timing of breeding and the climatic zone, hemisphere and habitat in which they breed (Warham 1990, del Hoyo *et al.* 1992). Differences in such aspects are expected to contribute to size variation of a species over its geographic range.

The primary objective of this paper is to describe the major patterns of size and shape variation of *Puffinus* species over their respective ranges. This objective was achieved by addressing these questions:

- Do sympatric congeners differ in size and shape?
- Do the sexes of each *Puffinus* species differ morphometrically?
- Do *Puffinus* species exhibit interpopulation variation in their morphometrics?
- Does the degree of sexual size dimorphism exhibited by *Puffinus* species differ over the species range?

METHODS

Taxonomy

The taxonomy used in this study largely follows that proposed by Sibley & Monroe (1990). The Yelkouan *P. yelkouan* and Balearic *P. mauretanicus* Shearwaters have been variously classified at the subspecific level, most often as subspecies of the Manx Shearwater *P. puffinus* (Murphy 1952, Jouanin & Mouglin 1979, Harrison 1983). We have followed the present consensus that, based on morphologic, plumage, behavioural, geographic and genetic differences, treats each taxon as a full species (Bourne *et al.* 1988, Walker *et al.* 1990, del Hoyo *et al.* 1992, Wink *et al.* 1993, Heidrich *et al.* 1996, Heidrich *et al.* 1998, Sangster *et al.* 2002). Furthermore, we have followed the classification of Newell's Shearwater *P. newelli* as a full species (BirdLife International 2000) rather than as a subspecies of Townsend's Shearwater *P. auricularis* (Sibley & Monroe 1990). These birds differ in size, proportions, colouration, winter range and breeding season (King & Gould 1967, Jehl 1982).

Data collection

Morphometric measurements were taken from 2689 museum study skins of 18 *Puffinus* species (see Table 1 for common names) held in major museum ornithological collections (see Acknowledgments). Juvenile and immature specimens were not included in the data set. Species sample sizes varied because of specimen availability in the collections.

The traits measured were bill length (BL), bill depth at base (BDB), bill depth at nares (BDN), wing length (maximum flattened chord, WL), tarsus length (TL) and midtoe length (MT). All measurements were taken by LSB. A steel rule with an end stop was used to measure wing length to the nearest 0.5 mm, and digital Vernier

calipers were used to measure bill, tarsus and midtoe to the nearest 0.01 mm. For consistency, specimens were measured on the right-hand side of the body. For each trait, each bird was measured three times, not consecutively, and the average was used in the statistical analyses.

Populations of shearwaters generally have discrete distributions such as archipelagos with several colonies (islands) and subcolonies within islands (Rabouan *et al.* 2000). Sample sizes were too small to investigate differences between subcolonies on individual islands, and so data were pooled into populations (Appendix 1). Pooling was determined by the overall distribution of a species and concentrations of collecting localities within certain areas. Pooling specimens into *a priori* subspecies obscures patterns of geographic variation, and so individuals were analysed on a species basis (Zusi 1982, Zink & Remsen 1986).

Statistical analysis

All analyses were conducted using the SAS (version 6.12) statistical package. Preparatory methods of the study skins dictated the variables that could be measured. In some cases not all of the earlier-noted morphometrics (most often BDB) could be taken from each specimen. Multivariate analyses require a full data set for each individual, and the sample sizes were consequently greatly reduced.

Morphologic variation owing to sex and population was examined for each character by a mixed-model, two-way analysis of variance, with sex as a fixed effect and population as a random effect (MANOVAs and ANOVAs, GLM procedure). This design provided tests of three null hypotheses: i) no sexual dimorphism; ii) no effect of population location; and iii) no geographic variation in sexual dimorphism (as indicated by sex \times population interaction). To test for the effect of sex on the other morphometrics, MANCOVA and ANCOVA (GLM procedure) were then performed, with

body size (represented by TL) as a covariate. Species were deemed sexually size dimorphic if the average measurements of individual morphometrics differed between the sexes by 5% or more. *Puffinus bulleri*, *P. huttoni*, *P. mauretanicus* and *P. newelli* have very restricted breeding distributions and so were not included in the population analyses.

Canonical discriminant analyses (CANDISC procedure) were performed to compare size and shape variation among *Puffinus* species. To check these procedures, the data were on each occasion randomly split into two even subsets according to the variable being tested. One subset (training data) was used to generate the model and the other (test data) to validate it. The results from the test data are presented here.

RESULTS

Interspecific variation

Table 1 shows the sample sizes and mean morphometrics for each species included in this study, and Table 2 shows the results of the canonical discriminant analyses carried out on the species data. The differences in factor loadings indicate differences in the relative size and shape of appendages in the species. Canonical variable 1 (CAN1) is generally defined by differences in size, and canonical variable 2 (CAN2) is defined by differences in relative size and shape (Gould & Johnston 1972, Slotow & Goodfriend 1996). On the basis of size (CAN1), the genus is divided into small (*P. assimilis*, *P. gavia* and *P. lherminieri*), medium (*P. puffinus*, *P. mauretanicus*, *P. yelkouan*, *P. huttoni*, *P. newelli*, *P. nativitatis*, *P. opisthomelas* and *P. auricularis*) and large (*P. tenuirostris*, *P. pacificus*, *P. bulleri*, *P. carneipes*, *P. creatopus*, *P. griseus* and *P. gravis*) shearwaters (Fig. 1).

Comparison of sympatric species (Appendix 1) in Fig. 1 reveals that in only one instance (*P. nativitatis* and *P. newelli*) is there

TABLE 1
Sample sizes (n) and mean \pm standard deviation measurements (mm) of the 18 *Puffinus* species

Species	n	Bill length	Bill depth at base	Bill depth at nares	Wing length	Tarsus length	Midtoe length
Scientific name							
Common name							
<i>P. pacificus</i>	576	38.47 \pm 1.89	12.84 \pm 0.80	9.17 \pm 0.70	292.99 \pm 9.99	48.67 \pm 1.82	49.97 \pm 2.07
<i>P. bulleri</i>	93	41.20 \pm 1.44	13.91 \pm 0.63	10.43 \pm 0.72	286.62 \pm 9.21	51.75 \pm 1.58	52.76 \pm 1.71
<i>P. carneipes</i>	127	41.24 \pm 1.84	16.01 \pm 0.95	11.73 \pm 0.76	319.46 \pm 7.84	54.40 \pm 1.43	56.87 \pm 1.86
<i>P. creatopus</i>	116	42.22 \pm 1.53	16.39 \pm 0.99	12.30 \pm 0.68	333.40 \pm 8.17	55.45 \pm 1.32	58.82 \pm 1.63
<i>P. gravis</i>	124	45.61 \pm 1.81	15.02 \pm 1.06	11.14 \pm 0.79	322.01 \pm 14.80	59.37 \pm 1.81	62.58 \pm 1.98
<i>P. griseus</i>	247	41.43 \pm 1.71	13.27 \pm 0.92	9.74 \pm 0.69	291.10 \pm 14.30	56.57 \pm 2.04	55.46 \pm 1.90
<i>P. tenuirostris</i>	204	31.82 \pm 1.37	11.15 \pm 0.74	7.97 \pm 0.60	267.11 \pm 13.06	50.96 \pm 1.55	51.50 \pm 1.69
<i>P. nativitatis</i>	175	30.96 \pm 1.15	10.81 \pm 0.65	7.83 \pm 0.55	247.85 \pm 6.70	44.40 \pm 1.29	42.73 \pm 1.23
<i>P. puffinus</i>	82	34.88 \pm 1.41	10.39 \pm 0.70	7.91 \pm 0.63	235.88 \pm 5.34	45.14 \pm 1.17	42.75 \pm 1.45
<i>P. yelkouan</i>	50	35.46 \pm 1.56	10.46 \pm 0.82	8.00 \pm 0.75	232.10 \pm 7.44	45.61 \pm 1.57	42.95 \pm 1.59
<i>P. mauretanicus</i>	12	38.84 \pm 1.73	11.61 \pm 0.67	8.72 \pm 0.64	246.07 \pm 5.44	48.34 \pm 1.28	45.74 \pm 1.11
<i>P. auricularis</i>	17	31.21 \pm 1.15	9.99 \pm 0.34	7.46 \pm 0.28	228.02 \pm 5.72	45.19 \pm 1.08	41.96 \pm 1.10
<i>P. newelli</i>	64	33.12 \pm 1.22	10.76 \pm 0.64	7.59 \pm 0.53	233.39 \pm 9.60	46.91 \pm 1.34	43.78 \pm 1.21
<i>P. opisthomelas</i>	75	36.59 \pm 1.48	11.32 \pm 0.68	8.42 \pm 0.61	239.95 \pm 7.85	45.65 \pm 1.38	43.87 \pm 1.37
<i>P. gavia</i>	144	32.94 \pm 1.46	9.20 \pm 0.67	7.06 \pm 0.57	205.83 \pm 7.56	42.03 \pm 1.43	40.10 \pm 1.28
<i>P. huttoni</i>	59	36.18 \pm 1.33	9.87 \pm 0.56	7.37 \pm 0.46	220.39 \pm 4.65	41.97 \pm 1.27	41.15 \pm 1.38
<i>P. lherminieri</i>	333	27.00 \pm 1.75	8.61 \pm 0.73	6.50 \pm 0.60	197.10 \pm 7.77	38.30 \pm 1.79	36.18 \pm 2.05
<i>P. assimilis</i>	191	24.65 \pm 1.24	8.06 \pm 0.59	5.97 \pm 0.57	182.22 \pm 8.15	38.01 \pm 2.00	36.73 \pm 0.16

considerable overlap in size and shape. In all other cases, the size and shape of the sympatric species overlap only slightly or not at all. A more detailed analysis of sympatric species reveals that other isolating mechanisms besides size and shape variation—such as differences in the time of breeding, in the method of feeding, in feeding location or in nest type—may be used by *Puffinus* species to reduce interspecific competition (Table 3).

Sexual size dimorphism

Of seven MANOVAs for which the interaction term (sex \times population) was included and for which data were sufficient, only

TABLE 2
Results of the canonical discriminant analysis carried out on the morphometric measurements of the 18 species of the genus *Puffinus*

Factor loadings	Canonical 1	Canonical 2	Canonical 3
Bill length	0.64	-0.53	-0.53
Bill depth at base	0.54	-0.17	0.17
Bill depth at nares	0.43	-0.2	0.03
Wing length	0.77	-0.12	0.38
Tarsus length	0.73	0.39	-0.47
Midtoe length	0.77	0.32	-0.13
Eigenvectors	28.71	4.55	2.36
Variance (%)	78.3	12.4	6.4
Cumulative variance (%)	78.3	90.7	97.1

one showed a significant interaction (*P. griseus*: Wilks $\lambda = 0.12$, $F_{24,57} = 1.99$, $P = 0.02$; Table 4). A Bonferroni correction for multiple testing indicates effectively no significant interaction. This result indicates that, in *Puffinus*, sex and colony can be treated as non-interactive variables.

Significant differences were found (Table 4) between the sexes of *P. assimilis* (Wilks $\lambda = 0.84$, $F_{6,73} = 2.33$, $P = 0.04$), *P. carneipes* (Wilks $\lambda = 0.48$, $F_{6,26} = 4.63$, $P = 0.003$), *P. griseus* (Wilks $\lambda = 0.76$, $F_{6,68} = 3.59$, $P = 0.004$), *P. lherminieri* (Wilks $\lambda = 0.86$, $F_{6,94} = 2.54$, $P = 0.03$), *P. nativitatis* (Wilks $\lambda = 0.68$, $F_{6,49} = 3.92$, $P = 0.003$), *P. pacificus* (Wilks $\lambda = 0.74$, $F_{6,128} = 7.63$, $P < 0.0001$) and *P. tenuirostris* (Wilks $\lambda = 0.73$, $F_{6,72} = 4.53$, $P = 0.0006$).

Males tend to be the larger sex for most morphometrics, but this is not invariable (Table 5). In only one instance of a female being larger was the ANOVA significant (*P. yelkouan*: WL: $F_{1,16} = 9.79$, $P = 0.0065$). Sample sizes were generally small for those species in which females were found to be larger in one morphometric or more; however, this was not the case for *P. griseus* WL ($\text{♀ } n = 80$, $\text{♂ } n = 100$) and *P. assimilis* TL ($\text{♀ } n = 69$, $\text{♂ } n = 79$).

In *Puffinus* species, sexual size dimorphism as defined for this study (5% difference between the sexes) was expressed only in bill depth dimensions, with the bills in males being deeper (Table 5). The magnitude of sexual size dimorphism was low, with the greatest difference being found for *P. mauretanicus* BDN. The sample size for this species was very small ($\text{♀ } n = 6$, $\text{♂ } n = 4$), and this level of sexual size dimorphism is likely to be an overestimation for this

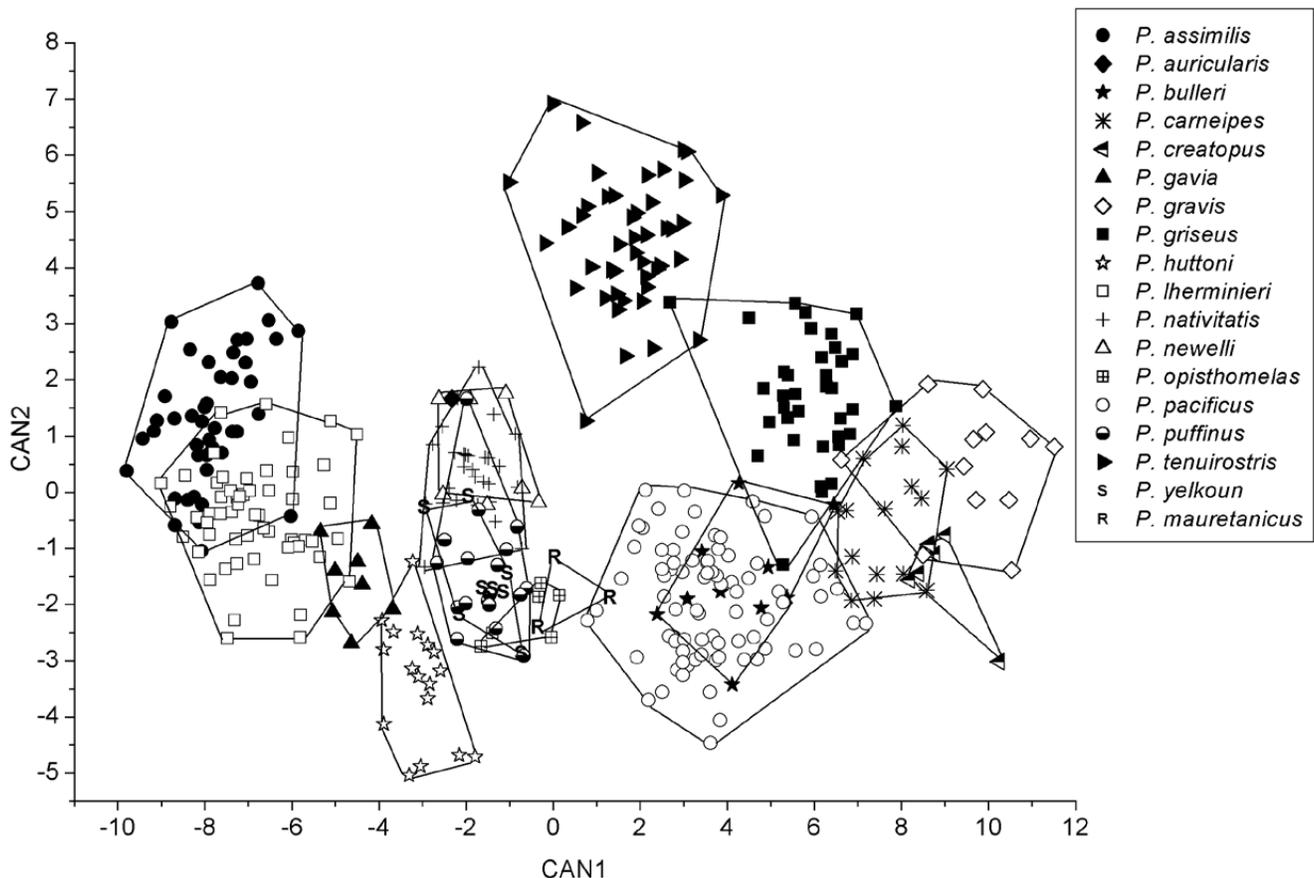


Fig. 1. Differences in size and shape of 18 *Puffinus* species as illustrated by a plot of canonical 1 (differences in size) against canonical 2 (differences in relative size and shape).

TABLE 3
Morphologic, foraging and breeding parameters of *Puffinus* species breeding at sympatric locations

Location	Coexisting species	BL	BDB	BDN	WL	TL	MT	Feeding zone ^a	Feeding method	Nest type	Egg laying dates	Source
Montague Is, Australia	<i>P. pacificus</i>	37.25	12.85	9.23	290.32	47.99	49.34	OS	SF, CD, PPL	Bu	27–29 Nov	Marchant & Higgins (1990)
	<i>P. tenuirostris</i>	32.45	12.01	—	276.00	—	52.99	OS+	PD	Bu	20 Nov – 3 Dec	Schultz & Klomp (2000a)
Lord Howe Is	<i>P. assimilis</i>	23.30	7.73	5.70	175.03	36.37	35.79	OS	SD, PPL, PD	Bu	July	Hutton (1991)
	<i>P. pacificus</i>	36.51	12.53	9.00	287.14	48.10	49.26	OS	SF, CD, PPL	Bu	December	Hutton (1991)
Kermadec Is, New Zealand	<i>P. carneipes</i>	42.32	16.62	12.17	316.86	55.34	57.21	NS, OS	SF	Bu	Mid-Dec	Hutton (1991)
	<i>P. assimilis</i>	25.12	8.20	5.87	187.73	38.99	37.33	OS	SD, PPL, PD	Bu	10 June – mid-July	Merton (1970)
Western Australia	<i>P. pacificus</i>	41.26	14.44	10.39	310.37	51.55	53.52	OS	SF, CD, PPL	Bu	12–28 Dec	Crockett (1975)
	<i>P. assimilis</i>	24.79	8.10	5.93	174.58	37.66	36.94	OS	SD, PPL, PD	Bu	21–26 June	Glauert (1946)
Hen & Chicken Is, New Zealand	<i>P. pacificus</i>	38.64	12.17	8.95	285.42	47.82	48.46	OS	SF, CD, PPL	Bu	17–22 Nov	Garkaklis <i>et al.</i> (1998)
	<i>P. carneipes</i>	41.06	15.79	11.38	320.00	53.11	55.42	NS, OS	SF	Bu	23–30 Nov	Warham (1958)
Norfolk Is	<i>P. assimilis</i>	25.54	8.56	6.27	189.13	41.09	38.60	OS	SD, PPL, PD	Bu	23 June – 24 Aug	Booth (2000b)
	<i>P. gavia</i>	34.01	9.16	6.93	208.40	43.20	40.98	NS	PPL	Bu	Late Sep – early Oct	Marchant & Higgins (1990)
Tristan da Cunha	<i>P. carneipes</i>	39.98	15.47	11.39	324.61	54.20	56.90	NS, OS	SF	Bu	Late Nov – mid-Dec	Falla (1934)
	<i>P. griseus</i>	—	—	—	—	—	—	OS	PD	Bu	?	Marchant & Higgins (1990)
Seychelles	<i>P. assimilis</i>	24.27	7.85	5.94	178.36	36.64	35.96	OS	SD, PPL, PD	Bu	From 7 July	Hermes <i>et al.</i> (1986)
	<i>P. pacificus</i>	39.89	12.98	10.06	303.51	50.06	52.49	OS	SF, CD, PPL	Bu	Dec – early Feb	Hermes <i>et al.</i> (1986)
Johnston Atoll	<i>P. assimilis</i>	25.65	8.55	6.39	184.22	39.76	38.58	OS	SD, PPL, PD	Bu	Spring	Richardson (1984)
	<i>P. gravis</i>	44.71	14.61	10.78	322.87	59.44	61.87	OS	SD, PD	Bu	November	Rowan (1952), Elliot (1957)
NW Hawaiian Is.	<i>P. lherminieri</i>	26.29	8.45	6.57	192.72	37.69	34.79	NS, OS	SD, PD	Bu, Cr	Oct – March	Feare (1981)
	<i>P. pacificus</i>	36.68	12.68	8.97	281.39	47.05	48.15	OS	SF, CD, PPL	Bu	End Oct – end Nov	Feare (1981)
Marshall Is	<i>P. nativitatis</i>	30.68	10.79	7.53	244.10	43.52	42.65	OS	PPL	Un	Late Mar – early May	Amerson & Shelton (1976)
	<i>P. pacificus</i>	38.58	12.30	8.72	288.69	47.78	49.32	OS	SF, CD, PPL	Bu	Late June – early July	King (1974)
Phoenix Is	<i>P. nativitatis</i>	30.79	10.56	7.72	246.33	44.48	42.80	OS	PPL	Un	April – June	Amerson (1971), King (1974)
	<i>P. pacificus</i>	38.86	12.73	8.91	293.99	48.75	49.78	OS	SF, CD, PPL	Bu, Cr, Un	Mid-June	Harrison (1990)
Christmas Is	<i>P. nativitatis</i>	30.38	11.33	7.94	240.92	43.37	42.13	OS	PPL	Un	April	Amerson (1969)
	<i>P. pacificus</i>	39.16	12.81	8.98	290.17	47.96	49.39	OS	SF, CD, PPL	Bu	Mid-June	King (1974)
Christmas Is	<i>P. lherminieri</i>	25.11	8.13	6.17	192.52	37.27	34.36	NS+	SD, PD	Bu	All year	King (1967, 1974)
	<i>P. nativitatis</i>	30.69	10.83	7.82	243.00	44.23	41.94	OS	PPL	Un	King (1967, 1974)	King (1967, 1974)
Christmas Is	<i>P. pacificus</i>	37.41	12.84	9.02	289.20	47.23	48.58	OS	SF, CD, PPL	Bu	Late Nov – early Dec	Garnett (1984)
	<i>P. lherminieri</i>	26.18	8.21	6.30	197.83	35.54	35.01	NS+	SD, PD	Bu	March	Schreiber & Ashmole (1970)
Christmas Is	<i>P. nativitatis</i>	30.68	11.14	8.07	246.49	43.94	42.64	OS	PPL	Un	All year, peak Oct–Jan	Schreiber & Ashmole (1970)
	<i>P. pacificus</i>	37.26	12.09	8.78	286.41	46.94	48.66	OS	SF, CD, PPL	Bu, Cr	Late June – July	Gallagher (1960)

^a Schreiber & Burger (2001).

BL = bill length; BDB = bill depth at base; BDN = bill depth at nares; WL = wing length; TL = tarsus length; MT = midtoe length; SF = surface feeder; SD = contact dipper; PPL = pursuit plunger; Bu = burrow; OS = offshore feeder; PD = pursuit diver; NS = nearshore feeder; Cr = crevice; Un = under tree or bush.

species. The observed sexual size dimorphism in the bill depth was statistically significant even after allowing for overall body size (as measured by TL) in all cases but *P. mauretanicus* BDN (Table 5).

Geographic variation

For species in which a significant difference was found between the sexes (Table 4), geographic variation of males and females was analysed separately. MANOVAs (Table 4) confirmed significant morphologic differences between populations of *P. assimilis* (♂: Wilks $\lambda = 0.02$, $F_{48,112} = 3.02$, $P < 0.0001$; ♀: Wilks $\lambda = 0.01$, $F_{54,102} = 2.48$, $P < 0.0001$), *P. griseus* (♂: Wilks $\lambda = 0.02$,

$F_{24,29} = 2.44$, $P = 0.01$), *P. lherminieri* (♂: Wilks $\lambda = 0.02$, $F_{60,173} = 3.32$, $P < 0.0001$; ♀: Wilks $\lambda = 0.01$, $F_{60,162} = 3.93$, $P < 0.0001$), *P. nativitatis* (♀: Wilks $\lambda = 0.04$, $F_{36,73} = 2.18$, $P = 0.003$) and *P. pacificus* (♂: Wilks $\lambda = 0.03$, $F_{78,238} = 2.85$, $P < 0.0001$; ♀: Wilks $\lambda = 0.03$, $F_{96,267} = 2.38$, $P < 0.0001$).

DISCUSSION

Sympatric congeners

As noted by Brooke (2004) and found in all but one case in this study, sympatric *Puffinus* congeners show little or no overlap in

TABLE 4
Results of MANOVAs and ANOVAs for geographic variation and sexual size dimorphism

Species	Test	n	MANOVA	BL	BDB	BDN	WL	TL	MT
<i>P. assimilis</i>	Interaction	120	NS	NS	NS	NS	NS	NS	NS
	Sex	80	a	NS	b	b	NS	NS	NS
	Population (m)	36	c	b	b	b	c	c	c
	Population (f)	34	c	b	a	b	c	b	c
<i>P. auricularis</i>	Sex	4	—	NS	NS	NS	NS	NS	NS
<i>P. bulleri</i>	Sex	18	NS	NS	NS	NS	NS	NS	NS
<i>P. carneipes</i>	Interaction	21	NS	NS	NS	NS	NS	NS	NS
	Sex	33	b	NS	c	c	NS	NS	a
	Population (m)	11	NS	a	a	a	NS	NS	NS
	Population (f)	10	NS	NS	NS	NS	NS	NS	NS
<i>P. creatopus</i>	Sex	13	NS	a	NS	NS	NS	NS	NS
	Population	4	—	a	NS	NS	NS	NS	NS
<i>P. gavia</i>	Sex	16	NS	NS	a	a	NS	NS	NS
	Population	6	—	NS	a	NS	a	a	a
<i>P. gravis</i>	Sex	29	NS	NS	NS	NS	NS	NS	NS
	Population	7	—	a	NS	NS	NS	NS	NS
<i>P. griseus</i>	Interaction	34	a	NS	NS	NS	a	NS	NS
	Sex	75	b	b	a	b	NS	c	a
	Population (m)	18	a	NS	NS	NS	a	NS	NS
	Population (f)	16	NS	NS	NS	NS	NS	NS	NS
<i>P. huttoni</i>	Sex	37	NS	a	a	NS	NS	NS	NS
<i>P. lherminieri</i>	Interaction	94	NS	NS	NS	NS	NS	NS	a
	Sex	101	a	a	a	a	NS	NS	NS
	Population (m)	48	c	c	c	c	c	c	c
	Population (f)	46	c	c	c	c	c	c	c
<i>P. mauretanicus</i>	Sex	4	—	NS	a	a	NS	NS	NS
<i>P. nativitatis</i>	Interaction	54	NS	NS	NS	NS	a	NS	NS
	Sex	56	b	c	c	b	NS	b	NS
	Population (m)	26	NS	NS	NS	NS	a	a	NS
	Population (f)	28	b	NS	NS	NS	b	NS	NS
<i>P. newelli</i>	Sex	9	NS	NS	NS	NS	NS	NS	NS
<i>P. opisthomelas</i>	Sex	16	NS	a	b	a	NS	NS	NS
	Population	6	—	NS	NS	NS	NS	NS	NS
<i>P. pacificus</i>	Interaction	129	NS	NS	NS	NS	NS	NS	NS
	Sex	135	c	b	c	c	NS	NS	NS
	Population (m)	61	c	c	c	c	c	c	c
	Population (f)	68	c	c	c	c	c	c	c
<i>P. puffinus</i>	Interaction	20	NS	NS	a	b	NS	NS	NS
	Population	23	NS	NS	NS	NS	NS	NS	NS
	Sex	27	NS	NS	NS	NS	b	NS	NS
<i>P. tenuirostris</i>	Sex	79	c	a	c	c	NS	NS	NS
<i>P. yelkouan</i>	Sex	18	NS	NS	NS	NS	b	NS	NS

^a $P < 0.05$. ^b $P < 0.01$. ^c $P < 0.001$

BL = bill length; BDB = bill depth at base; BDN = bill depth at nares; WL = wing length; TL = tarsus length; MT = midtoe length; (m) = male; (f) = female; — = insufficient data; NS = nonsignificant.

TABLE 5
Comparison of *Puffinus* mean female (♀) and male (♂) morphometrics and average sexual size dimorphism calculated as the difference between male and female means expressed as a percent of the male mean. Negative values indicate variables in which the female was the larger sex. Bold text indicates a significant ANCOVA ($\alpha = 0.05$). Shaded cells indicate sexual size dimorphism (i.e. >5% difference between the means of the sexes)

Species	Bill length		Bill depth at base		Bill depth at nares		Wing length		Tarsus length		Midtoe length							
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂						
<i>P. assimilis</i>	24.38	24.87	1.97	7.86	8.22	4.38	5.81	6.12	5.07	181.56	182.79	0.67	38.06	37.97	-0.24	36.40	37.02	1.67
<i>P. auricularis</i>	31.32	31.03	-0.93	9.84	10.11	2.67	7.43	7.50	0.93	229.33	225.83	-1.55	45.25	45.08	-0.38	41.85	42.08	0.55
<i>P. bulleri</i>	40.82	41.51	1.66	13.62	14.19	4.02	10.19	10.62	4.05	283.34	289.07	1.98	51.29	52.15	1.65	52.64	52.87	0.44
<i>P. carneipes</i>	40.47	41.93	3.48	15.40	16.52	6.78	11.27	12.13	7.09	319.14	319.72	0.18	54.13	54.64	0.93	56.42	57.26	1.47
<i>P. creatopus</i>	41.12	42.60	3.47	15.65	16.75	6.57	11.95	12.39	3.55	332.16	333.88	0.52	55.44	55.45	0.02	58.89	58.90	0.02
<i>P. gavia</i>	32.68	33.25	1.71	8.98	9.47	5.17	6.95	7.19	3.34	204.94	206.91	0.95	41.89	42.20	0.73	39.82	40.41	1.46
<i>P. gravis</i>	44.68	46.02	2.91	14.47	15.24	5.05	10.86	11.28	3.72	322.81	321.54	-0.39	58.77	59.65	1.48	61.77	62.96	1.89
<i>P. griseus</i>	40.64	42.02	3.28	13.08	13.44	2.68	9.52	9.89	3.74	292.51	289.98	-0.87	56.13	56.89	1.34	55.22	55.62	0.72
<i>P. huttoni</i>	35.38	36.58	3.28	9.48	10.05	5.67	7.12	7.51	5.19	219.46	220.89	0.65	41.35	42.29	2.22	40.86	41.31	1.09
<i>P. lherminieri</i>	26.63	27.33	2.56	8.43	8.80	4.20	6.32	6.67	5.25	196.11	198.04	0.97	38.07	38.52	1.17	35.85	36.46	1.67
<i>P. mauretanicus</i>	38.40	39.45	2.66	11.42	11.84	3.55	8.46	9.12	7.24	245.33	247.17	0.74	48.12	48.56	0.91	45.76	45.73	-0.07
<i>P. nativitatis</i>	30.52	31.43	2.90	10.54	11.13	5.30	7.55	8.12	7.02	246.52	249.18	1.07	43.96	44.93	2.16	42.50	42.96	1.07
<i>P. newelli</i>	32.79	33.76	2.87	10.69	10.81	1.11	7.66	7.46	-2.68	232.53	235.11	1.10	46.73	47.29	1.18	43.57	44.10	1.20
<i>P. opisthomelas</i>	35.53	37.39	4.97	10.84	11.63	6.79	8.12	8.68	6.45	241.01	239.26	-0.73	45.41	45.86	0.98	43.60	44.10	1.13
<i>P. pacificus</i>	38.09	38.84	1.93	12.61	13.09	3.67	8.98	9.36	4.06	292.36	293.60	0.42	48.54	48.81	0.55	49.88	50.07	0.38
<i>P. puffinus</i>	34.60	35.07	1.34	10.19	10.50	2.95	7.84	7.96	1.51	234.11	237.02	1.23	44.71	45.38	1.48	42.29	43.14	1.97
<i>P. tenuirostris</i>	31.45	32.19	2.30	10.85	11.46	5.32	7.74	8.19	5.49	264.69	269.43	1.76	50.88	51.04	0.31	51.20	51.79	1.14
<i>P. yelkouan</i>	35.14	35.75	1.71	10.22	10.67	4.22	7.84	8.14	3.69	234.23	230.41	-1.66	45.39	45.85	1.00	42.73	43.14	0.95

size and shape, indicative of a mechanism to reduce interspecific competition. Those sympatric species that did overlap in size and shape (*P. nativitatis* and *P. newelli*) reduce interspecific competition by segregation of nesting habitats, with *P. nativitatis* surface-nesting at low altitude on islets and atolls and *P. newelli* burrow-nesting inland at high altitude (Harrison 1990). Other means by which sympatric *Puffinus* congeners may reduce interspecific competition for resources include segregation of breeding seasons, foraging zones, prey type and prey size (Brown *et al.* 1981, Stone *et al.* 1995, Monteiro *et al.* 1996, Schultz & Klomp 2000). Like a number of seabirds, shearwaters forage opportunistically depending on the availability of prey in their preferred habitat (Harrison *et al.* 1983, Spear *et al.* 1995, Ballance *et al.* 2001). Consequently, differences in habitat are hypothesized as being more important than differences in prey selection in enabling co-existence (Ballance *et al.* 2001).

Body size can often be used to predict the outcome of interference competition (Ballance *et al.* 2001, Hamer *et al.* 2001). Historically the differences in size between sympatric congeners may have provided a means by which species have been able to co-exist. Now, however, with reduced habitat availability for many breeding seabirds, such differences in size may be resulting in increased interference competition, possibly at the expense of the smaller congener. For example, at the Poor Knights Islands, New Zealand, *P. bulleri* are displacing gadfly petrels *Pterodroma* spp. and *P. gavia* (Harper 1983). Similarly on the Azores, interference competition among petrels has resulted in the smaller species, including *P. assimilis*, being confined to cliffs (Monteiro *et al.* 1996, Ramos *et al.* 1997). Such situations may result in higher intraspecific competition for nest sites or in decreased breeding success, or both (Monteiro *et al.* 1996, Ramos *et al.* 1997).

Sexual size dimorphism

Effectively, no significant interaction was found between sex and population, indicating that no geographic variation in the magnitude of sexual size dimorphism occurs. The selective pressures being exerted on male and female *Puffinus* therefore do not differ significantly over the species' ranges.

In birds, the average size difference between the sexes is 5%–10% (Amadon 1959). Based on the results of the present study, *Puffinus* species exhibit low levels of sexual size dimorphism. Significant differences in morphometrics were found between the sexes of *P. assimilis*, *P. carneipes*, *P. griseus*, *P. lherminieri*, *P. nativitatis*, *P. pacificus* and *P. tenuirostris*. Although males were generally larger in all morphometrics, sexual size dimorphism (i.e. a 5% difference) was expressed only in the bill-depth parameters. Bills are used for feeding and aggressive encounters and are presumably much more prone to selection for dimorphism than are wings and legs, which are used for locomotion and are likely to be an optimum physical dimension in relation to body size (Agnew & Kerry 1995). Because of its dual role, the adaptive significance of sexual size dimorphism in the bill has been the topic of much debate (Hedrick & Temeles 1989, Shine 1989).

Natural selection attributable to ecologic differences between the sexes may cause sexual size dimorphism (Shine 1989, Andersson 1994). The intersexual food-competition hypothesis proposes that sexual differences in size might evolve from niche partitioning between the sexes as a mechanism to reduce intersexual competition for food (Selander 1966, 1972). Sexual differences in foraging zones, migration routes, diet composition and prey size have been

reported for seabirds (Gilardi 1992, Kato *et al.* 1996, Weimerskirch *et al.* 1997, González-Solís *et al.* 2000, Forero *et al.* 2002). These differences may occur at any stage of the breeding and non-breeding seasons.

Studies of *Puffinus* foraging and food-provisioning strategies are fairly well represented in the literature for several species (Ricklefs 1984, Montague *et al.* 1986, Langlands 1991, Hamer & Hill 1997, Hamer *et al.* 1999, Booth *et al.* 2000a, Schultz & Klomp 2000, Guicking *et al.* 2001), although few have investigated the roles of the sexes. Perrins & Brooke (1976) identified different foraging grounds used by the sexes of breeding *P. puffinus* from Skokholm and Skomer Islands during the pre-laying exodus: female *P. puffinus* foraged in the rich sardine fishery in Biscay Bay, while the males remained close to the colony. Furthermore, Gray & Hamer (2001) found that, during the breeding season, the mean foraging trip duration was significantly longer for female *P. puffinus* than for males, indicating the possible use of different foraging zones.

With regards to sympatric species, Johnson (1966) wrote that "Bill length may be only partially satisfactory in revealing differences in foraging niche ... because divergence in bill width and/or bill depth between congeners can strikingly alter bill shape and function when bill length is constant." This concept could be applied to differences in bill shape between the sexes. Bill depth is an important factor in determining the snapping power of a bill, and it has been hypothesized that males with deeper bills should have a better handling performance for powerful prey than should females (Ashmole 1968, Koffijberg & Van Eerden 1995). However, because of difficulties associated with obtaining dietary samples (particularly with respect to rates of digestion), little information exists about *Puffinus* prey size. It is therefore unknown whether sexual size dimorphism in *Puffinus* bill morphology is attributable to intersexual competition for food items of different size.

The sexual selection hypothesis proposes that, within one sex, characteristics that confer an advantage in either competition for mates (intrasexual selection) or mate choice (intersexual selection) are selected for (Darwin 1871). Evidence supporting sexual selection in *Puffinus* species would be that, in males, a deeper bill confers some advantage (reproductive or survival) over a smaller bill. Male *Puffinus* generally take the predominant role in obtaining and defending a burrow (Brooke 1990, Warham 1990). Fights may ensue over nest ownership, during which the bill is the primary weapon (Nelson 1979). If deeper bills in males convey an advantage in nest attainment or defence, we would expect that characteristic to be selected for in colonies in which high intraspecific competition for nest sites occurs. Brooke (1990) described high intraspecific competition for *P. puffinus* nest sites at Skomer Island, Wales, and found significant differences between the sexes in bill size.

Female mate choice, which may result in long-term fitness consequences, cannot be eliminated as a mechanism for the observed sexual size dimorphism in *Puffinus* species (Forero *et al.* 2001). Because members of *Puffinus* species, like other seabirds, are monogamous and exhibit high mate fidelity, mechanisms for mate choice would be difficult to detect (Warham 1990, Barbraud 2000). However, *P. tenuirostris* do exhibit significant assortative mating with respect to age and bill depth (Meathrel & Bradley 2002). Assortative mating may arise from either active mate choice by one or both of the sexes or through passive contact between phenotypes (Forero *et al.* 2001). Meathrel & Bradley (2002)

suggest that because assortative mating based on age and bill depth in *P. tenuirostris* is a predictor of breeding success, mate selection may be adaptive.

Both sexual selection and natural selection can influence the evolution of the same trait to different degrees (Shine 1989, Wittzell 1991, Fitzpatrick 1999, Forero *et al.* 2001). Furthermore, the forces maintaining sexual size dimorphism may be different from those that caused it, making ascertainment of the original causes of its evolution difficult (Perry 1996, Szekely *et al.* 2000). Nevertheless, long-term morphometric and breeding studies, and remote-tracking and feeding studies, are necessary to obtain a better understanding of the processes responsible for sexual size dimorphism in *Puffinus* bill size.

Geographic variation

Typically, 50%–90% of the body-size difference between individuals is attributable to genetic causes (Boag & van Noordwijk 1987); the remaining 10%–50% of the difference is attributable to environmental causes (Brooke 1990). Selection pressures vary according to location, because populations of a species must adapt to the local conditions, often resulting in geographic variation in characteristics (Mayr 1963, Endler 1977, Wikelski & Trillmich 1997, Lovich *et al.* 1998). It is unlikely that any single factor may be responsible for variation in size, but rather a combination. The potential for geographic variation increases with the number of islands that a species occupies (Mayr & Diamond 2001). This appears to be the case in *Puffinus* species, because significant intraspecific variation was found only in species with widespread breeding distributions (see Appendix 1). Species whose populations are distributed over a wide range are likely to be exposed to differing climatic environments.

Once fully developed, skeletal structures should be little affected by the environment, but during development, food availability or even temperature might influence expression of the genotype (Duffy 1987). The growth patterns of *Puffinus* species are similar to those of other petrels; that is, a rapid growth in tarsus, relatively slow increase in bill length and intermediate growth in wing length (Pettit *et al.* 1984, Brooke 1990, Warham 1990, Booth *et al.* 2000b, Saffer *et al.* 2000). Consequently, intraspecific differences in wing and bill morphology may be related to differences in the post-fledging environment, but differences in tarsus morphology may be attributable to such factors as the age and experience of the parents, climatic conditions, and the availability and quality of resources (Saffer *et al.* 2000).

Ecogeographic rules imply patterns of variation based on correlation with environmental and climatic conditions (Lincoln *et al.* 1998). Probably the most well-known and debated are the Bergmann and Allen Rules (McNab 1971, Geist 1987). Procellariiform seabirds travel vast distances and spend extensive periods at sea (Weimerskirch *et al.* 1988, Spear *et al.* 1995, Klomp & Schultz 2000). Many of them return to land only to breed and, unlike many land birds, are not constrained to one set of climatic parameters. Therefore, among procellariiform seabirds, patterns of geographic variation are unlikely to be a result of a thermoregulatory response, as is proposed by the Bergmann and Allen Rules. Although the Bergmann Rule has been described for *P. pacificus* (Murphy 1951), statistical methodology (particularly multivariate analysis) has advanced since that time, and the pattern therefore warrants re-examination (Bull 2002).

The magnitude of variation in morphometrics was similar between the sexes in species (*P. assimilis*, *P. lherminieri* and *P. pacificus*) for which both males and females exhibited geographic variation. Furthermore, the geographic variation was attributable to a combination of differences in all traits of both sexes. This finding may indicate that the selective forces shaping the sexes are similar over the species range. In comparison, only one sex of *P. griseus* (males) and *P. nativitatis* (females) exhibited significant geographic variation. Furthermore, that variation was a result of differences in the wing length over each species' range. Wing morphology is affected by pressures of migration, foraging, sexual selection and predation (Ainley 1980, Alatalo *et al.* 1984, Hedenström & Møller 1992, Marchetti *et al.* 1995, Møller *et al.* 1995, Copete *et al.* 1999, Voelker 2001). Differences in the wing length could reflect differences in the ecologic sex roles over the species range. Long pointed wings are more cost efficient for long-distance flights (Savile 1957), therefore differences in foraging range between the sexes may result in differences in wing morphology. In Wandering Albatrosses *Diomedea exulans* breeding in the Iles Crozet, sexual size dimorphism in wing morphology was found to have a functional role in flight performance, which in turn influences the at-sea distribution of adults and fledglings (Shaffer *et al.* 2001). Shaffer *et al.* suggested that the differences in wing loadings made it more optimal for males to forage in the windier sub-Antarctic and Antarctic regions, with adult females and juveniles being better adapted to exploit the lighter winds of the subtropical and tropical regions.

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APPENDIX 1
Breeding localities and sample sizes of 18 *Puffinus* spp. sampled

	<i>P. assimilis</i>	<i>P. auricularis</i>	<i>P. bulleri</i>	<i>P. carneipes</i>	<i>P. creatopus</i>	<i>P. gavia</i>	<i>P. gravis</i>	<i>P. griseus</i>	<i>P. huttoni</i>	<i>P. herminieri</i>	<i>P. mauretanicus</i>	<i>P. nativitatis</i>	<i>P. newelli</i>	<i>P. opisthomelas</i>	<i>P. pacificus</i>	<i>P. puffinus</i>	<i>P. tenuirostris</i>	<i>P. yelkouan</i>
Auckland Is, SPO								3										
Antipodes Is, SPO	6							2										
Austral Is, SPO	+											7			3			
Azore Is, NAO	1															2		
Bermuda										3								
Bonin Is, NPO															6			
Canary Is, NAO	5															+		
Caribbean islands										51								
Caroline Is, NPO										4					+			
Chatham Is, SPO	7							2										
Tierra del Fuego, Chile								8										
Campbell Is, SPO								9										
Cocos-Keeling Is, IO															2			
Cook Strait islands, New Zealand				+	19		+											
Corsica, MED																		1
Cape Verde Is, NAO	18									10								
Easter Is, PO												2						
Falkland Is, SAO							1	1										
Faroe Is, NAO																	3	
Fiji, SPO										+					30			
France																5		
Galapagos Is										53								
Gambier Archipelago, PO										17		+						
Greece																		5
Guadalupe Is, NPO														10				
Hauraki Gulf islands, New Zealand	10			16														
Hawaiian Archipelago, NPO												66	48		146			
Iceland																2		
Irish Sea region																43		
Italy																		8
Johnston Is, PO												6			32			
Juan Fernandez Is, SPO					18													
Kermadec Is, SPO	43														53			
Lord Howe Is, TAS	23			38											33			
Kiribati, PO										2		27			22			
Macquarie Is, SO								7										
Madeira Is, NAO	11															+		
Maldives Is, IO										5								
Malta																		2
Marcus Is, NPO												1			3			
Marquesas Is, PO										+		17			15			
Marshall Is, NPO												4			11			
Mauritius, IO										+					12			
Isla de la Mocha, SPO					7													
Isla Natividad, SPO														4				
Norfolk Is, TAS	23														+			

APPENDIX 1 (continued)

	<i>P. assimilis</i>	<i>P. auricularis</i>	<i>P. bulleri</i>	<i>P. carneipes</i>	<i>P. creatopus</i>	<i>P. gavia</i>	<i>P. gravis</i>	<i>P. griseus</i>	<i>P. huttoni</i>	<i>P. lherminieri</i>	<i>P. mauretanicus</i>	<i>P. nativitatis</i>	<i>P. newelli</i>	<i>P. opisthomelas</i>	<i>P. pacificus</i>	<i>P. puffinus</i>	<i>P. tenuirostris</i>	<i>P. yelkouan</i>
Niue, PO															4			
Northern north islands, New Zealand			20	+		43		4										
New South Wales, Australia								1							40		1	
Panama										11								
Pelew Is, PO										54								
Phoenix Is, PO										61		18			45			
Pitcairn Is, SPO												21			+			
Queensland, Australia															3			
Réunion Is, IO										6					1			
Salvage Is, NAO	4																	
Samoa, PO										11					+			
Revillagigedo Is, NPO		13													12			
Seychelles group, IO										25					23			
Snares Is, SPO								8										
Society Is, PO										2					13			
Southern south islands, New Zealand								19										
South Western Australia	4			12											3		+	
Tasmanian islands, Australia								+									3	
Tristan da Cunha group, SAO	4						13											
Turkey																		
Vanuatu, SPO										1					4			
Victoria, Australia																		18
Volcano Is, NPO															9			
Wake Is, NPO												3			8			
Mariana Is, NPO															+			
St. Paul Is, IO	+			+														
Kaikoura, New Zealand									21									
New Caledonia, SPO															+			
Solomon Is, SPO															+			
South Australia				+													+	
Chagos Archipelago, IO										+					+			
Cargados Carajos Shoals, IO															+			
Comoros Is, IO										+								
Balearic Is, MED											7							
San Benito Is, NPO														+				
Newfoundland, Canada																	+	
Massachusetts, USA																	+	
Sardinia, Italy																		1
Tonga, SPO															+			

SPO = South Pacific Ocean; NAO = North Atlantic Ocean; NPO = North Pacific Ocean; IO = Indian Ocean; MED = Mediterranean Sea; PO = Pacific Ocean; SAO = South Atlantic Ocean; TAS = Tasman Sea; + = breeds at that location, but not sampled for this study; shaded cells = species no longer breed at those localities.