INFLUENCE OF MIGRATORY BEHAVIOUR ON THE MORPHOLOGY AND BREEDING BIOLOGY OF *PUFFINUS* SHEARWATERS

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SUMMARY

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Ecological, life-history, breeding biology and morphologic data were collected for 18 shearwater species *Puffinus* spp., and the relationships between these parameters and migratory behaviour were investigated. Intraspecific variation in relative wing length was associated with differences in migratory behaviour of the Little Shearwater *Puffinus assimilis* populations, but not the Wedge-tailed Shearwater *P. pacificus.* This study emphasises the need for long-term studies, which are generally lacking, to be able to estimate robust breeding and demographic parameters from populations of long-lived seabird species such as those in the *Puffinus* genus.

Key words: Shearwaters, *Puffinus* spp., breeding biology, migration, morphology

INTRODUCTION

Ecomorphology proposes that the association between morphology and ecology represents the expression of the phenotype–environment interaction and that this association may be modified by variation in behaviour or performance (Ricklefs & Miles 1994). The morphology of a species is determined by various selection pressures (James 1982). For instance, the wing of a bird may be affected by migration (Norberg 1995), foraging (Hertel & Ballance 1999), sexual selection (Møller *et al.* 1995) and predation (Alatalo *et al.* 1984). With respect to migration, longer wings are more cost efficient for long-distance flight (Savile 1957). Consequently, variation in wing morphology may be a functional response to differences in migratory habit within a species (Gaston 1974).

Migration may exert sexual selection processes on quality indicators: for example, migratory birds might exhibit greater sexual size dimorphism than non-migratory ones, because they may have a shorter period during which to obtain a nest and mate (Fitzpatrick 1998). Furthermore, competition may be more intense among migratory birds because they are unfamiliar with each other, unlike non-migratory individuals (Fitzpatrick 1998). Therefore, a short period of intense competition, like that expected for migratory groups, may increase benefits from exaggerated signals of resource-holding potential, such as sexual size dimorphism (Fitzpatrick 1998). Alternatively Allee & Schmidt (1951, as well as Trivelpiece *et al.* 1983) proposed that migratory birds are morphologically more uniform the shorter the time they spend at their breeding sites—that is, the more pronounced their migratory nature.

Comparing patterns of behaviour and morphology among species, populations or sexes enables the investigation of the functional relationships between phenotypic variation and ecology. The shearwater genus *Puffinus* provides an ideal group on which to conduct such a study. The genus contains both migratory and non-migratory species; two species (Little Shearwater *Puffinus assimilis* and Wedge-tailed Shearwater *P. pacificus*), for both of which migratory and non-migratory populations have been suggested (Marchant & Higgins 1990); and species exhibiting sexual size dimorphism (Warham 1990, Bull *et al.* 2004). As such, this group is used to investigate the potential influence of migratory behaviour on morphology and life-history traits.

In terms of the ecology of this group, the pressure to complete a breeding cycle before migrating may result in greater synchronisation or contraction of breeding parameters such as prelaying exodus, laying period, incubation period, nestling period and desertion period (Warham 1990). The first objective of this paper is to summarise and review some of the main features of the breeding biology, demography and general ecology of the *Puffinus* shearwaters. This information is then used to investigate behavioural and ecological variables as a means of elucidating patterns of interactions between the phenotype and environment within the *Puffinus* genus by addressing the following questions:

- Within the genus *Puffinus,* do migratory and non-migratory species exhibit different life-history strategies?
- Are intraspecific differences in relative wing length associated with migratory habit?
- Within the genus *Puffinus,* does the magnitude of sexual size dimorphism differ between migratory and non-migratory species.

METHODS

Breeding biology

Despite *Puffinus* species being amongst the world's most numerous seabirds, data regarding life history and breeding biology are lacking for a number of the species. Ecological and demographic data were therefore derived mostly from Marchant & Higgins (1990) and references therein. In general, when data from several sources were available, the average of means was used. All analyses were conducted using the SAS statistical package (version 6.12).

The data had non-normal distributions and so Mann–Whitney *U* and Fisher exact tests were used.

For the purpose of this study, the pre-laying exodus is defined as the period after mating during which birds leave the colony before returning to lay the egg (Warham 1990).

Morphology

Morphometric measurements were taken from 2689 museum study skins of 18 *Puffinus* species held in major ornithological collections (see "Acknowledgments"); sample sizes of the species varied because of specimen availability (see Table 1). Juvenile and immature specimens were not included in the data set. The traits measured were bill length (BL), bill depth at base (BDB), bill depth at nares (BDN), wing length (WL), tarsus length (TL) and middle-toe length (MT). Wing length (flattened) was measured to the nearest 0.5 mm using a steel rule with an end stop, and bill, tarsus and middle toe were measured to the nearest 0.01 mm using digital Vernier callipers. For consistency, specimens were measured on the right-hand side. For each trait, each bird was measured three times, not consecutively; the average was used in the statistical analyses. Measurement error was evaluated previously (Bull 2002) and found to contribute little variation to the data (0.67% ± 0.30%).

Canonical discriminant analyses (CDA: CANDISC procedure) were performed to compare intraspecific size and shape variation between *P. assimilis* and *P. pacificus* populations. To check these procedures, the data were randomly split on each occasion 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. Results from the test data are presented here.

Sexual dimorphism

Canonical discriminant analyses were performed on morphometrics (BL, BDB, BDN, WL, TL and MT) of each species. Canonical variable 1 (CAN1) is generally defined by differences in size, and canonical variable 2 (CAN2) by differences in relative size and shape (Gould & Johnston 1972, Slotow & Goodfriend 1996). Therefore, CAN1 is used as a representative measure of size in this study.

Bull *et al.* (2005) found that sexual size dimorphism (calculated as the percentage difference between male and female measurements) is exhibited only in bill depth measurements (BDB and BDN) in *Puffinus* species. Sexual size dimorphism was plotted against CAN1 to determine if the magnitude of sexual size dimorphism (relative to a measure of body size) differs between migratory and non-migratory *Puffinus* species.

RESULTS

Details of ecological and life-history data for all *Puffinus* species are presented in Table 1. The species exhibit the general life-history and breeding characteristics of Procellariiformes: delayed onset of reproduction, high adult survival, and protracted development periods.

Breeding biology

Differences in the mean length of the pre-laying exodus in migratory (mean: 18.5 ± 5.44 days, n = 8) and non-migratory (mean = 18 ± 13.5 days, n = 3) species were not statistically significant (Mann–Whitney *U*-test: Z = –0.31; *P* = 0.76). Migratory species had shorter laying periods (mean = 20.38 ± 12.59 days, n = 10) than non-migratory species did (mean = 47.50 days ± 17.68 days, n = 8), but this difference was not significant (Mann–Whitney *U*-test: Z = 1.59, *P* = 0.11).

Migratory species were found to have significantly longer (Mann–Whitney *U*-test: Z = –2.09, *P* = 0.04) mean incubation shifts (mean = 9.46 ± 4.05 days, n = 5) during the egg period than non-migratory species did (mean = 3.33 ± 1.26, n = 3). Mean chick-rearing periods were also longer in migratory (mean = 91.09 ± 12.90 days, n = 9) than non-migratory species (mean = 11.71 ± 81.49 days, n = 7), but not significantly so (Mann–Whitney *U*-test: Z = –1.33; *P* = 0.19).

Although a greater proportion of migratory species (83%) have a pre-fledging desertion period than non-migratory species do (33%, Table 1), the difference was not statistically significant (Fisher exact test: *P* = 0.23; n = 9).

Morphology

Puffinus assimilis and *P. pacificus* both have migratory and non-migratory populations (Marchant & Higgins 1990), thus providing a test for the hypothesis that WL is associated with migratory habit. Canonical discriminant analyses of these species' populations found that the CAN1 of both *P. assimilis* and *P. pacificus* had a high positive loading for WL. Higher CAN1 values are indicative of longer wings (Table 2). The Chatham Island and Tristan da Cunha populations of *P. assimilis* are both described as migratory, and these populations are the ones that had the highest CAN1 values (Table 3). Mean WL was greater in migratory populations (mean = 185.15 ± 0.81 mm; range: 184.22–185.71 mm; n = 3) than in non-migratory populations (mean = 178.94 ± 7.47 mm; range: 167.25–190.61 mm; n = 10), and a significant difference was found in the relation between WL and TL in those two groups (Mann–Whitney *U*-test: Z = –2.22; *P* = 0.03).

Australian and Hawaiian *P. pacificus* are migratory (Marchant & Higgins 1990), but the CAN1 values for these populations were not amongst the highest for this species (Table 4). Mean WLs, although slightly longer in non-migratory (mean = 292.50 mm ± 8.91 mm; range: 279.00–310.37 mm; n = 20) than in migratory populations (mean = 291.11 ± 4.25 mm; range: 285.42–294.71 mm; n = 4), were not statistically significant (Mann–Whitney *U*-test: Z = –1.08; *P* = 0.28).

Despite differences between the sexes in the mean BDB and BDN being greater in migratory species (BDB: mean = 4.69% ± 1.42%; range: 2.68%–6.78%; n = 10; BDN: mean = 4.21% ± 1.47%; range: 1.51%–7.09%; n = 10) than in non-migratory species (BDB: mean = 4.15% ± 1.74%; range: 1.11%–6.79%; n = 8; BDN: mean = 4.08% ± 3.44%; range: –2.68 to 7.24; n = 8), these differences were not statistically significant (Mann–Whitney *U*-tests: BDB, Z = –0.58, *P* = 0.56; BDN, Z = 0.31, *P* = 0.76). Therefore, there appears to be no correlation between migratory habit and level of sexual size dimorphism in *Puffinus* species (Fig. 1).

DISCUSSION

Data limitations

As is the case with most seabirds, data regarding life history and breeding biology are lacking for a number of *Puffinus* species, despite their global abundance. Unfortunately, this lack of general information restricts the robustness of the results presented here. Nevertheless, this paper provides an example of how variation in behaviour or performance has the potential to influence the morphology and ecology of seabirds.

TABLE 1
Demographic, breeding and ecological data for 18 *Puffinus* species

Scientific name (species code)	Common name	n	Adult mass (kg)	CAN1	Movement	Pre-laying exodus (d)	Laying period (d)	Incubation period (d)	First shift (d)	Mean shift (d)	Nestling period (d)	Feeding interval (d)	Desertion period (d)	First breed (y)	Foraging range	Annual adult survival (%)	References[a]
P. pacificus (pa)	Wedge-tailed Shearwater	576	0.30–0.57	3.48	Mig	6–21	33	52			105	~1		4	OS		1, 2, 3, 4, 5
P. bulleri (bu)	Buller's Shearwater	93	0.41	3.82	Mig	30	4	51		5	100				OS		4, 5, 6
P. carneipes (ca)	Flesh-footed Shearwater	127	0.58–0.75	7.44	Mig	20	14	54			92	2			OS		5, 7, 8
P. creatopus (cr)	Pink-footed Shearwater	116		8.30	Mig					14					IS		5, 9, 10
P. gravis (gv)	Great Shearwater	124	0.72–0.95	9.33	Mig	14	14	55			105				OS		5, 11, 12
P. griseus (gr)	Sooty Shearwater	247	0.63–0.95	5.60	Mig	14	12	52.7	9.5	9.4	97	4	12	6	OS	93.1	4, 5, 13, 14
P. tenuirostris (te)	Short-tailed Shearwater	204	0.47–0.64	1.53	Mig	21	14	53	12.6	13	94	2.87	14	7	OS	93.5	4, 5, 15, 16
P. nativitatis (na)	Christmas Shearwater	175	0.32–0.34	–1.86	Sed	14	>60	53		4.5	96	1.4		6.7	OS		2, 5, 17
P. puffinus (pu)	Manx Shearwater	82	0.35–0.58	–2.20	Mig	14–21	37	51.3	6.3	5.9	71	1.23	8.5	6	OS	90.5	5, 18, 19
P. yelkouan (ye)	Yelkouan Shearwater	50	0.34–0.42	–2.38	Mig			52			72				IS		5, 20
P. mauretanicus (ma)	Balearic Shearwater	12		0.31	Disp			50			72				IS		5, 21
P. auricularis (au)	Townsend's Shearwater	17	0.34	–3.75	Disp			62			92.4			4–7	OS		5, 22
P. newelli (ne)	Newell's Shearwater	64	0.39	–1.59	Disp			62			93			4–7	OS	90	2, 5, 23
P. opisthomelas (op)	Black-vented Shearwater	75	0.41	–1.74	Disp			50			69				IS		5, 24
P. gavia (ga)	Fluttering Shearwater	144	0.23–0.42	–4.64	Sed	7									IS		5, 25
P. huttoni (hu)	Hutton's Shearwater	59	0.37	–3.94	Mig	18	35	50.3			83.8	1.4		4–6	OS	93.1	4, 5, 26, 27, 28
P. lherminieri (lh)	Audubon's Shearwater	333	0.15–0.23	–7.15	Sed			49–51			75	1.3		8	IS	95	5, 29, 30, 31
P. assimilis (as)	Little Shearwater	191	0.18–0.26	–8.88	Sed	33	35	54			73	1.05	9.5		OS		4, 5, 32, 33

[a] 1 = Shallenberger (1973); 2 = Harrison (1990); 3 = Crockett (1975); 4 = Marchant & Higgins (1990); 5 = Schreiber & Burger (2001); 6 = Harper (1983); 7 = Warham (1958); 8 = Hutton (1991); 9 = Guicking *et al.* (2001); 10 = Harrison (1983); 11 = Rowan (1952); 12 = Elliott (1957); 13 = Warham *et al.* (1982); 14 = Richdale (1963); 15 = Skira (1991); 16 = Bradley *et al.* (1991); 17 = Amerson & Shelton (1976); 18 = Brooke (1990); 19 = Harris (1966); 20 = Bourne *et al.* (1988); 21 = de Juana (1984); 22 = Jehl (1982); 23 = Spear *et al.* (1995); 24 = Everett (1988); 25 = Falla (1934); 26 = Cuthbert (1999); 27 = Sherley (1992); 28 = Harrow (1976); 29 = Harris (1969); 30 = Snow (1965); 31 = Wingate (in Palmer 1962); 32 = Warham (1990); 33 = Booth *et al.* (2000).

CAN1 = canonical variable 1; Mig = migrant; Sed = sedentary; Disp = dispersive; OS = offshore feeder; IS = inshore feeder.

Breeding biology

No significant differences were found in the mean length of the pre-laying exodus, laying period and nestling period between migratory and non-migratory *Puffinus* species. However, migratory species had significantly longer incubation shifts than non-migratory species did. This may indicate that, in general, the migratory habit in *Puffinus* does not serve to contract or synchronise those breeding parameters more than in non-migratory species. However, the sparse data set prevents any robust conclusions being drawn until further estimates of these breeding parameters can be collected.

The prevalence of a desertion period was associated with migratory behaviour; however, no significant difference was observed between the length of desertion periods of migratory and non-migratory *Puffinus* species. The need for adults to leave to undertake migrations has been proposed as a reason for the desertion, but Warham (1990) found no direct evidence that birds that leave their chicks immediately begin their migratory movements. Alternatively, because of the costs incurred through reproduction, adults are at a low weight at the end of the breeding season, and so they may desert their chicks to regain body condition locally before migrating (Lill & Baldwin 1983).

TABLE 2

Results of canonical discriminant analyses (CAN1, CAN2, CAN3) on morphometric data of Little Shearwater *Puffinus assimilis* and Wedge-tailed Shearwater *P. pacificus* populations across their respective breeding ranges

	P. assimilis			*P. pacificus*		
Factor loadings	CAN1	CAN2	CAN3	CAN1	CAN2	CAN3
Bill length	0.41	–0.34	0.73	0.59	–0.28	0.16
Bill depth at base	0.12	0.45	0.28	0.45	0.53	–0.03
Bill depth at nares	0.14	0.38	0.12	0.38	0.65	0.33
Wing length	0.49	0.32	–0.37	0.72	0.17	–0.39
Tarsus length	0.36	0.63	0.11	0.64	0.07	0.60
Midtoe length	0.25	0.63	0.42	0.71	–0.01	0.31
Eigenvectors	8.81	3.34	1.23	3.94	1.44	0.74
Variance (%)	60.1	22.9	8.4	58.1	21.3	10.9
Cumulative variance (%)	60.1	83.0	91.4	58.1	79.4	90.3

Migration

It is generally accepted that seabirds undertake lengthy migrations because ocean resources are seasonal (Elphick 1995), but Croxall & Davis (1999) alluded to the paradox of various penguin species at similar latitudes and in broadly equivalent biotopes exhibiting different migratory habits. This same paradox was also found for *Puffinus* species: *P. pacificus,* the Christmas Shearwater *P. nativitatis* and Newell's Shearwater *P. newelli* all breed sympatrically in the Hawaiian islands, yet *P. pacificus* is the only species to migrate. Furthermore, *P. pacificus* and *P. nativitatis* belong to the same feeding guild (foraging over tuna schools), an inclusion that results in similar opportunistic feeding strategies and diets (Harrison *et al.* 1983). Therefore it seems unlikely that *P. pacificus* migrate as a result of the seasonal abundance of a prey item; rather, it may migrate to avoid direct competition with *P. nativitatis.* Although these two species belong to the same feeding guild, their chick feeding periods overlap only slightly: *P. nativitatis* chicks are fed from June to mid-September, and *P. pacificus* chicks are fed from mid-August to November (Harrison 1990).

Although WL was shown to be associated with the possible migratory behaviour in *P. assimilis,* this was not the case for *P. pacificus.* As has been pointed out by other authors, when studying wing shape variation, the relative importance of many flight-dependent activities needs to be considered (Norberg 1981, Mulvihill & Chandler 1990).

For instance, the intraspecific effects of migration on WL are perhaps not expected to be great in seabirds, because many forage a considerable distance from their colony during the breeding season (Klomp & Schultz 2000, Guicking *et al.* 2001). Similarly, a number of the non-migratory *Puffinus* species (e.g. Townsend's Shearwater *P. auricularis,* Audubon's Shearwater *P. lherminieri, P. newelli*

TABLE 3

Average canonical variables for colonies of the Little Shearwater *Puffinus assimilis* constructed from morphometric data

Population	Latitude	Longitude	n	Movements	CAN1	CAN2
Tristan da Cunha	–37.08	–12.28	3	Mig	3.26	1.40
Chatham Islands	–43.92	–176.50	6	Mig	2.19	1.47
Kermadec Islands	–29.27	–177.92	41	Sed	1.81	0.78
Cape Verde Island	16.00	–24.00	18	Sed	1.47	–1.37
Hauraki Gulf Islands	–36.63	175.07	10	Sed	1.39	3.97
Madeira Island	32.73	–17.00	8	Sed	0.13	–1.86
Norfolk Island	–28.97	168.05	18	Sed	–0.99	–1.10
Canary Islands	28.00	–15.50	5	Sed	–1.45	–2.34
Salvage Island	30.08	–15.92	4	Sed	–2.06	–0.63
SW Australian Islands	–34.50	120.00	4	Sed	–2.30	0.78
Lord Howe Islands	–31.55	159.10	23	Sed	–4.99	0.84

CAN1 = canonical variable 1; CAN2 = canonical variable 2; Mig = migrant; Sed = sedentary.

and *P. nativitatis*) have been observed feeding in association with dolphin and tuna schools (Au & Pitman 1986, Brooke 2004)—a foraging method that requires the ability for quick flight and possibly, therefore, longer wings. To date, most studies testing the hypothesis that WL is associated with migratory habit have been conducted using land birds (Gaston 1974, Mulvihill & Chandler 1990, Marchetti *et al.* 1995, Fitzpatrick 1998), but wing morphology in shearwaters (and other petrels) has likely adapted generally to long-distance and possibly fast flight. Nevertheless, why would certain populations of a species migrate and others not?

Interestingly, the two populations of *P. pacificus* recorded as migratory are at the subtropical periphery of the species' range (Australia and Hawaii); the migratory populations of *P. assimilis* are at only the southern extent of the species' range (Tristan da Cunha, Chatham and Antipodes Islands) (Marchant & Higgins 1990). *Puffinus assimilis* are winter breeders, and so it is unlikely that these populations migrate to avoid unfavourable weather conditions. Rather, the avoidance of competition for food is the likely cause of this migratory behaviour. The populations of *P. assimilis* and *P. pacificus* that do migrate both occupy breeding grounds for significant populations of other petrels. Therefore, moving away from the breeding colony outside of the breeding season might provide better foraging opportunities.

Sexual size dimorphism in bill depth dimensions was not associated with migratory or non-migratory behaviour in *Puffinus* species. If migration promoted sexual dimorphism in *Puffinus* species through

TABLE 4
Average canonical variables for colonies of the Wedge-tailed Shearwater *Puffinus pacificus* constructed from morphometric data. Abbreviations as for Table 1

Population	Latitude	Longitude	n	Movements	CAN1	CAN2
Kermadec Islands	–29.27	–177.92	48	Sed	4.36	0.66
Niue Island	–19.03	–169.90	4	Sed	1.72	0.72
Hawaiian Archipelago	20.50	–156.00	132	Mig	0.12	–1.01
SW Australian islands	–34.50	120.00	3	Mig	–0.13	–1.76
Marquesas Islands	–9.50	–140.00	15	Sed	–0.38	2.73
New South Wales	–33.00	146.00	33	Mig	–0.57	1.55
Wake Island	19.30	166.58	8	Sed	–0.60	0.72
San Benedicto Island	14.00	–110.79	10	Sed	–0.62	0.01
Johnston Island	16.75	–169.53	31	Sed	–0.64	–1.86
Coco-Keeling Island	–12.00	96.82	2	Sed	–0.87	0.39
Lord Howe Islands	–31.55	159.10	29	Sed	–1.16	0.21
Mauritius	–20.30	57.57	10	Sed	–1.30	2.71
Phoenix Island	–3.50	–172.00	46	Sed	–1.33	0.71
Line Island	0.00	–157.00	22	Sed	–1.71	–0.23
Seychelles	–4.57	55.67	21	Sed	–1.82	0.60

CAN1 = canonical variable 1; CAN2 = canonical variable 2; Mig = migrant; Sed = sedentary.

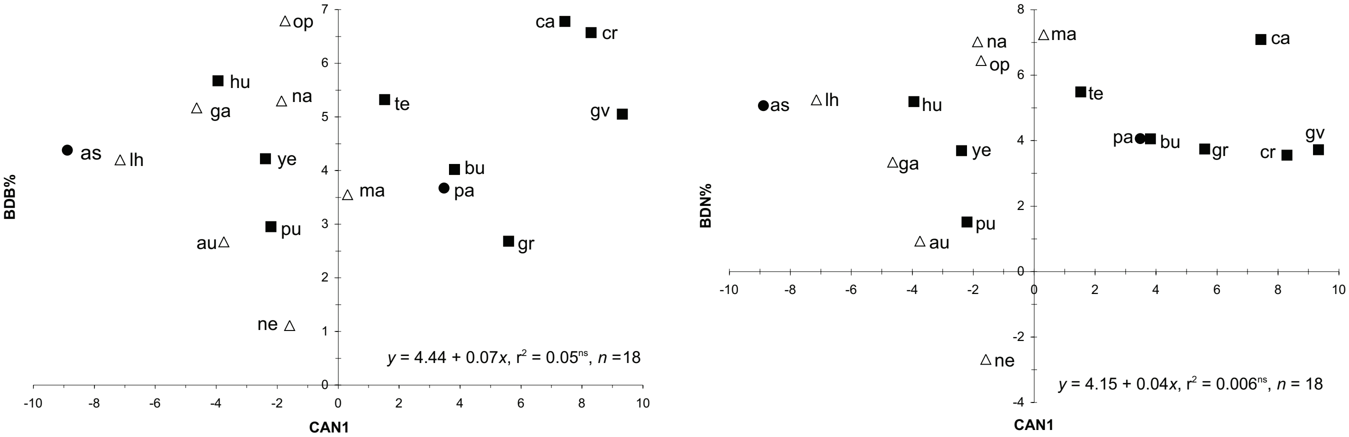

Fig. 1. Levels of sexual size dimorphism exhibited by Puffinus species in (a) bill depth at the base, and (b) bill depth at the nares, both plotted in relation to body size (CAN1). ■ = migratory species; △ = non-migratory species; ● = species having both migratory and non-migratory populations; CAN1 = canonical variable 1; BDB% = percentage difference between male and female bill depth at base; BDN% = percentage difference between male and female bill depth at nares (negative values indicate female being the larger sex); see Table 1 for species codes.

intense competition and sexual selection, the dimorphism would be expected in species such as *P. bulleri* and *P. tenuirostris* which are both highly migratory and have highly synchronised laying (Harper 1983, Skira 1991). However, these two species exhibit levels of sexual size dimorphism similar to non-migratory species with extended laying (Bull *et al.* 2005). Therefore, a mechanism other than migratory behaviour is responsible for the sexual size dimorphism in bill depth dimensions of *Puffinus* species.

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