

Morphometrics and the breeding biology of the Tahiti Petrel *Pseudobulweria rostrata*

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The genus *Pseudobulweria* includes four extant species, three being classified as critically endangered, while the fourth (Tahiti Petrel *P. rostrata*) is near threatened. Information on the breeding biology of any species of the genus is scarce, even for the Tahiti Petrel. We monitored two Tahiti Petrel nests in New Caledonia and provide the first data on the breeding biology for the genus. Incubation lasts about 55 days, and young fledge at 110 days. Breeding in the southern lagoon of New Caledonia extends from September to April. Very strong interspecific competition for nest cavities occurs with Wedge-tailed Shearwaters *Puffinus pacificus*. We also document geographical variation in both biometry and breeding phenology over the Pacific breeding range.

Despite its vernacular name, the Tahiti Petrel *Pseudobulweria rostrata* is widespread in the southern Pacific Ocean, breeding in the Society, Gambiers and Marquesas Islands, in Vanuatu, Fiji, New Caledonia, and possibly also in the Cook and Austral Islands and American Samoa (Holyoak & Thibault 1984, Pratt *et al.* 1987, Thibault & Bretagnolle 1999, Watling 2001, Brooke 2004, J.-C. Thibault unpubl. data). The first specimen, described in 1848 by Peale, was collected on Tahiti, but the taxon was later divided into two subspecies, *rostrata* (Polynesia) and *trouesarti* (New Caledonia: Brazil 1917), on the basis of a heavier bill for the New Caledonian birds (De Naurois & Erard 1979). Imber (1985) recommended that it be moved from *Pterodroma* to *Pseudobulweria*, a suggestion later confirmed on genetic grounds (Bretagnolle *et al.* 1998). The Tahiti Petrel is the largest species of the genus, which includes four other species: *rupinarum* is extinct from St Helena Island, Fiji Petrel *P. macgillivrayi* is restricted to Gau Island, Fiji (Watling & Lewanavanua 1985), Beck's Petrel *P. becki* is known only from two specimens collected near the Solomon Islands (Murphy & Pennoyer 1952) and considered by some authors to be conspecific with *P. rostrata*, and Mascarene Petrel *P. aterrima* is an elusive species nesting only on Réunion Island, Indian Ocean (Attié *et al.* 1997). The last three species are classified as critically endangered (BirdLife

International 2000), whereas *rostrata* is near threatened, with a tentative estimate of 10 000 pairs (Brooke 2004). Information on the breeding biology of any species of the genus is almost non-existent, and the scanty data available for *rostrata* were summarized by Brooke (2004). Although Tahiti Petrels breed on more or less inaccessible cliffs in most breeding sites, some pairs breed on small islets of easy access in New Caledonia, thus providing an opportunity for their study. In this paper, we provide the first breeding biology data from New Caledonia for the Tahiti Petrel, and review reproductive and biometric data with regard to sexual dimorphism and geographical variation.

METHODS

Study area and methods

In New Caledonia, Tahiti Petrels have two breeding habitats: small coral islets of the southern lagoon, where they breed on at least 12 islets (total population of *c.* 100 pairs: Pandolfi & Bretagnolle 2002); and the mountains of the main island, with nesting areas between sea-level and 1200 m, and as far as 20 km inland (V.B. pers. obs.). We conducted fieldwork from December 2002 to March 2003 and from November 2003 to February 2004 on a small 3.9-ha islet of the southern lagoon of New Caledonia (22°33'S, 166°47'E). This islet has the largest breeding population of Tahiti Petrels in the southern

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lagoon and differs from the other islets in being a rocky hill (40 m asl) that is covered with trees, shrubs and grasses. Besides Tahiti Petrels, two other species of Procellariids breed there: *c.* 500 pairs of Wedge-tailed Shearwater *Puffinus pacificus* and fewer than 50 pairs of Black-winged Petrel *Pterodroma nigripennis*.

Nest contents could be determined and monitored through a gallery that was dug from the surface to the burrow, just beneath the incubation chamber. The hole was covered with sticks and sealed with a piece of synthetic mattress held in place with stones. To minimize disturbance, we checked burrows with an infrared miniature camera (Panasonic), modified by A. Hughes. We banded adults and measured their wing (flattened) and tail (± 1 mm). We measured bill length (culmen), bill depth (at gonys) and tarsus with a caliper (± 0.1 mm). Body weight (± 10 g) was measured with a *Pesola* spring balance, and feathers were collected for DNA analyses. We measured eggs (length and width) with the same caliper and weighed them and the chicks, initially with an electronic balance (up to 200 g, ± 0.1 g), and later with the *Pesola* balance. We also took the same measurements on bird skins at the American Museum of Natural History (New York), Museum National d'Histoire Naturelle (Paris) and British Museum of Natural History (Tring).

Molecular sexing was based on DNA extracted from one feather bulb for each individual using a rapid simple alkaline extraction method (Malagó *et al.* 2002). We determined sexes by polymerase chain reaction (PCR) amplification of part of two CHD genes present on the sex chromosomes (Fridolfsson & Ellegren 1999), and separated PCR products by electrophoresis for 60 min at 100 V in a 1.8% agarose gel stained with ethidium bromide. Birds were sexed according to the presence of the PCR products of CHD-Z (700 bp, both sexes) and CHD-W (450 bp, females only).

Statistical analysis

We first used univariate statistics (analysis of variance, ANOVA) on each biometric character, and then used quadratic discriminant function analysis (DFA). We used quadratic DFA rather than linear DFA because the criterion of homoscedasticity was not met. DFA is a multivariate technique that combines variables to maximize separation between groups (Pimentel 1979, James & MacCulloch 1990). It also provides a quantitative check on the

discriminatory power of the discriminant functions in allocating single observations into the a priori group with the closest centroid in multivariate space (Footitt & Mackauer 1980). Two estimates of classification power were calculated. The first, which is simply derived from resubstitution of all individuals, provides an apparent error rate (the error count) but has an optimistic bias. The second estimate was obtained by a cross-validation technique (a jackknife procedure) and is probably more realistic. The stepwise discriminant function was also used for detecting those biometric parameters that were the most informative with regard to sex discrimination, taking into account correlation between variables.

Body measurements were fitted to several growth curve models (Ricklefs 1983, Zach *et al.* 1984) using a program written using the statistical package SAS 8.0 with PROC NLIN (SAS 1999). The use of a non-linear least-squares regression procedure assumes that residuals are randomly distributed, independently of chick age (Zach *et al.* 1984). We compared two models (logistic and Gompertz), and chose the best model with regard to residual distribution, estimated visually by plotting residuals vs. age.

RESULTS

Sexual dimorphism and geographical variation

We caught and ringed 70 adult birds, of which 60 could be sexed by genetic analysis (no DNA could be extracted from the feathers of ten birds). Average biometric parameters of these birds were compared with those obtained from museum specimens, by subspecies (Table 1). Heavily unbalanced sample sizes (most live birds from New Caledonia and most specimens from Polynesia) precluded a detailed analysis of biometric differences between dead and live birds. Statistically comparing nine museum specimens and 60 live birds from New Caledonia by use of a two-way ANOVA (sex and nature of bird as factors) indicated that the nature of the bird significantly affected only tarsus ($F = 5.11$, $P = 0.03$, $n = 69$; see also Fig. 1), whereas culmen, bill depth and tarsus were sexually dimorphic (all other parameters and all interactions non-significant). Owing to tarsus shrinkage, we conducted separate analyses for skins and live birds. All but one parameter was sexually dimorphic in live birds, and a stepwise discriminant analysis revealed that culmen, bill depth and tarsus were the most discriminant. In

Table 1. Biometry of *Pseudobulweria r. trouessarti* (from New Caledonia) and *P. r. rostrata* (from Polynesia).

	Mean \pm sd	Range	Mean \pm sd	Range	F	P
New Caledonia (alive)	Males ($n = 31$)		Females ($n = 29$)			
Culmen (mm)	37.4 \pm 1.2	35.2–39.9	35.4 \pm 1.3	32.25–39.6	38.13	< 0.001
Bill depth (mm)	15.4 \pm 0.6	12.7–16.5	14.4 \pm 0.49	13.5–15.45	41.88	< 0.001
Wing (mm)	302.4 \pm 7.5	274–318	297.5 \pm 8.6	282–318	5.53	< 0.05
Tail (mm)	122.5 \pm 4.0	114–133	120.4 \pm 4.5	113–128	3.83	ns
Tarsus (mm)	50.2 \pm 1.4	47.2–52.95	48.7 \pm 1.17	45.8–50.85	21.78	< 0.001
Body weight (g)	442.2 \pm 32.6	393–520	417.9 \pm 40.5	360–520	6.59	< 0.05
New Caledonia (skins)	Males ($n = 4^*$)		Females ($n = 5^*$)			
Culmen (mm)	37.7 \pm 1.2	36.1–38.7	35.3 \pm 0.9	34.6–36.8	10.693	< 0.05
Bill depth (mm)	15.2 \pm 0.7	14.6–16.2	14.7 \pm 0.4	14.2–15.2	1.876	ns
Wing (mm)	295.5 \pm 11.0	285–306	294.8 \pm 4.3	290–301	0.017	ns
Tail (mm)	117 \pm 4.7	112–123	122 \pm 5.1	116–129	2.261	ns
Tarsus (mm)	48.8 \pm 0.6	48.4–49.7	48.0 \pm 1.8	45.0–49.5	0.775	ns
Body weight (g)	373.3 \pm 32.1	350–410	391.7 \pm 20.2	370–410	0.699	ns
Polynesia–Marquesas (skins)	Males ($n = 15$)		Females ($n = 14$)			
Culmen (mm)	36.2 \pm 1.0	33.7–38.2	35.4 \pm 1.2	33.1–37.4	4.207	= 0.05
Bill depth (mm)	14.6 \pm 0.6	13.2–15.4	13.9 \pm 0.5	12.9–15.0	10.210	< 0.05
Wing (mm)	297.0 \pm 8.4	278–307	294.4 \pm 6.0	285–308	0.892	ns
Tail (mm)	119.8 \pm 4.3	114–130	120.2 \pm 4.1	115–128	0.070	ns
Tarsus (mm)	47.9 \pm 2.0	43.3–50.2	47.4 \pm 2.1	43.4–51.0	0.464	ns

* $n = 3$ for body weight (each sex).

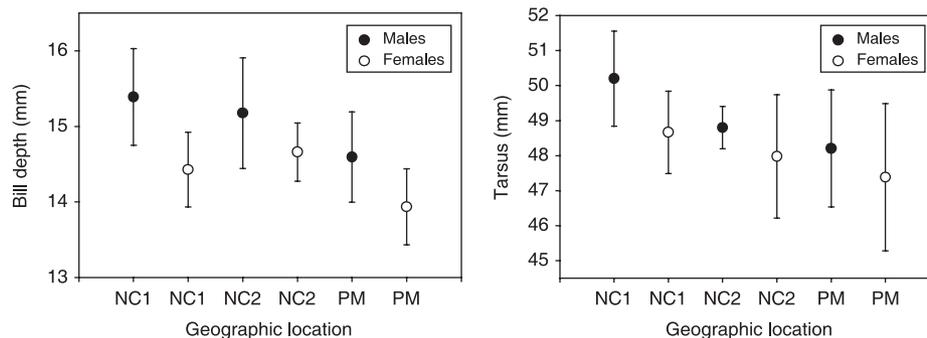


Figure 1. Variation in mean (and standard deviations) tarsus and bill depth according to sex, subspecies and nature of specimen (live vs. skins). NC1 = live bird from New Caledonia; NC2 = specimen from New Caledonia; PM = specimen from Polynesia and Marquesas; see Table 1 for sample sizes.

skins, however, only bill parameters revealed significant sexual dimorphism (Table 1).

We tested geographical variation by comparing skins from New Caledonia ($n = 9$) with those from French Polynesia ($n = 29$, grouping birds from Tahiti and Marquesas that did not differ statistically on any of the parameters, all $P > 0.5$). Two-way ANOVA (with subspecies and sex as factors) indicated that subspecies differed only in bill depth ($F = 9.41$, $P = 0.0040$) and sexes differed only in culmen ($F = 14.1$, $P = 0.0006$) and bill depth ($F = 7.58$, $P = 0.0094$). All other F -values (including all interactions) were

non-significant. However, neither sexual dimorphism nor geographical variation was important enough to allow a high rate of correct classification using discriminant analyses. For instance, based on live birds from New Caledonia alone, the error rate in sex determination was 8% (cross-validation error rate was 18%, $n = 60$) when we used all biometric parameters, including body weight, whereas the error rate for subspecies discrimination was 16% for males ($n = 50$) and 24% for females ($n = 48$; body weight excluded; error rate and cross-validation provided similar percentage of correct classification).



Figure 2. Photograph of Tahiti Petrel chick (14 days old). Note the dark triangle on the white belly that has been found on the two chicks surveyed.

Breeding biology

In February 2002, we found two Tahiti Petrel burrows and ringed the pairs concerned, but no egg or chick was found. In December 2002, the same pairs occupied the burrows, which contained an egg and a chick, respectively. Burrows were 120 and 83 cm from entrance to back of the incubation chamber. We found an egg (60.5×44.3 mm) on 3 December 2003, and weighed it several times to obtain a regression of egg density with age: $\text{density} = -0.0024(\text{age in days}) + 0.9574$ ($R^2 = 0.98$, $n = 4$). At hatching (12 January 2003), the chick weighed 60.6 g. The two equations provided by Warham (1990: 322–323) suggested that the incubation period was 54.2 and 56.5 days, based on hatch weight. Hatchlings had the same colour pattern as adults, except for a strikingly dark grey triangle on the white belly (Fig. 2) that remained visible during the entire chick-rearing period.

We monitored both burrows and measured chicks regularly. Based on the size of the first chick, of known age, we estimated that the other was 8 days old when found. The pulli were fed between dusk

and midnight on 17 occasions out of 19 nights that we attended the nests. For the first chick, 9–20 days old, the average meal was 52.1 ± 21.2 g (i.e. 16% of its body weight, $n = 8$), whereas for the second, 11–69 days old, meal size was 64.9 ± 30.1 g (14% of body weight, $n = 9$). Lags between successive meals were 1 day ($n = 10$) and 2 days ($n = 2$) for the first chick and 1 day ($n = 6$), 2 days ($n = 3$), and 3, 4 and 5 days (one each) for the second chick. Weight loss when unfed averaged 1.56 g/h ($\text{sd} = \pm 0.61$, $n = 11$) for the first chick and 1.32 g/h ($\text{sd} = \pm 1.09$, $n = 15$) for the second chick. Growth curves for wing, tarsus, culmen, bill depth and body weight are based on logistic equations (Fig. 3).

In Tahiti, data published from 1997 to 2002 in the local ornithological journal *Te Manu* (P. Raust pers. comm.) on fledged Tahiti Petrels attracted to lights suggest a fledging season spread throughout the year (Fig. 4). These data suggest a peak in laying dates (based on a total breeding period of 165 days) between March and July.

Inter- and intraspecific competition for burrows

The Wedge-tailed Shearwater nests in sympatry with Tahiti Petrels, and sizes of burrow entrances of the two species are essentially identical (P.V. and V.B. pers. obs.). Interspecific competition appeared very strong between them: in four burrows (out of *c.* 20), a Petrel was the first recorded occupant but a Shearwater was found later on. A burrow occupied by an incubating male Petrel that left its egg was occupied 2 days later by another pair of Petrels; 13 days later, the second male occupied the burrow with a new female; 2 days later, the first male was back with the new female, and they stayed together for at least 4 days; on the following day, however, a pair of Shearwaters finally occupied the burrow and no Petrel occupied it again. An adult Petrel and a pair of Shearwaters struggled for one egg that the Petrel finally incubated for the next 12 days, but surprisingly the hatchling was a Shearwater (which had disappeared by our next visit, 14 days later). The burrow of a Shearwater chick was occupied by a male Petrel that prevented the chick from being fed on two consecutive nights. We also witnessed fights between Shearwaters and Petrels, some of which presumably led to death: in one burrow with a nesting pair of Petrels and one with a downy Shearwater chick, mummified bodies of an adult Shearwater and a fledged Petrel, respectively, were found in the nest chamber.

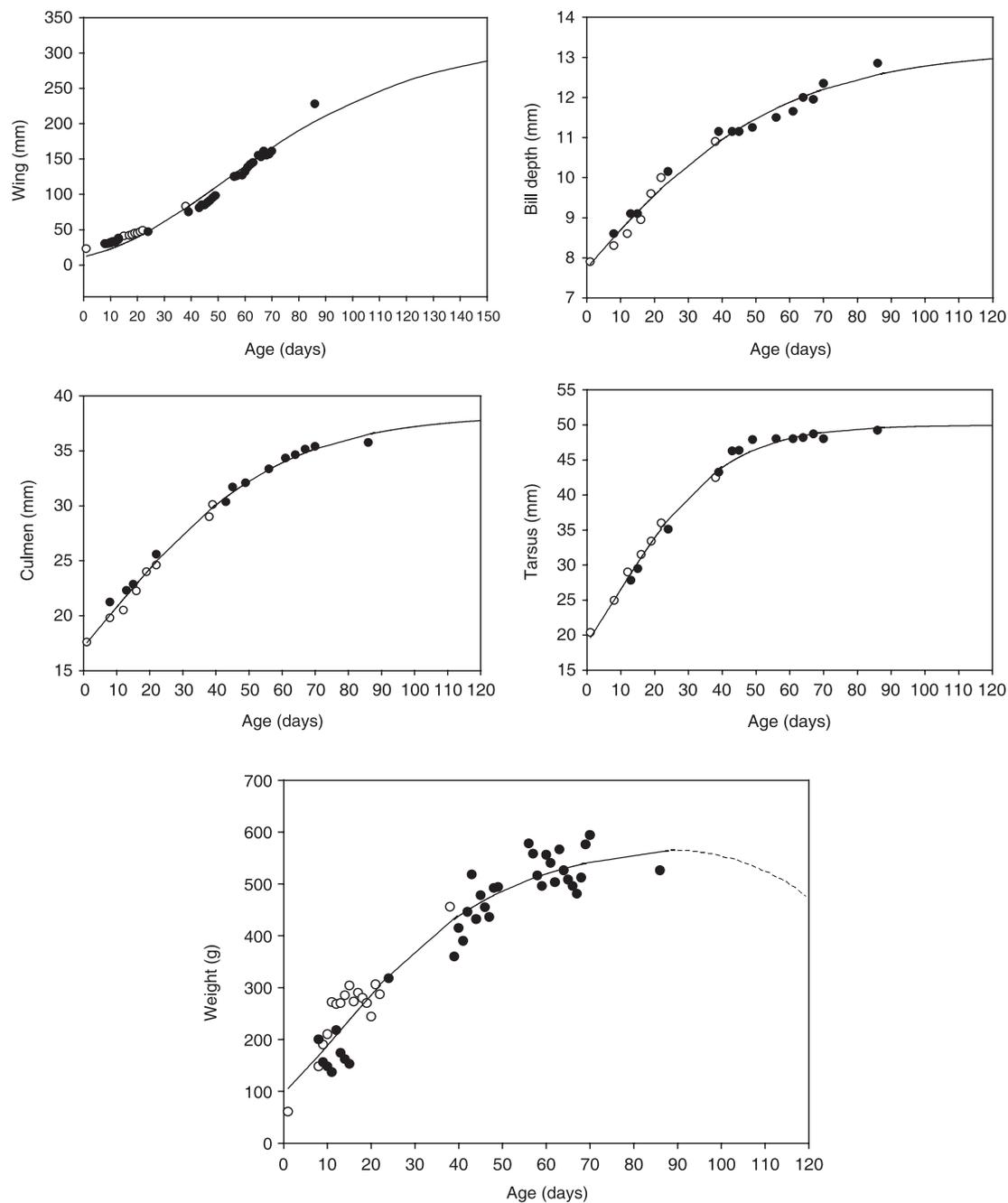


Figure 3. Growth curves of wing, tarsus, culmen, bill depth and body weight (white dots for the first chick and black dots for the second chick). For body weight, after it has reached a plateau (about 70 days), it decreases before first flight (this is symbolized by the dotted line, which was drawn by hand).

DISCUSSION

Until now, the breeding biology of the Tahiti Petrel was unknown (as was the case for all *Pseudobulweria* species). Only breeding periods were suspected: from March to October in Polynesia (Holyoak &

Thibault 1984, Brooke 2004), and June to October (De Naurois 1978) or January to May in New Caledonia (Hannecart & Létocart 1980). Based on data from this study and from museum specimens (adults collected on eggs or chicks for which egg-laying was back-calculated), egg-laying is now documented to

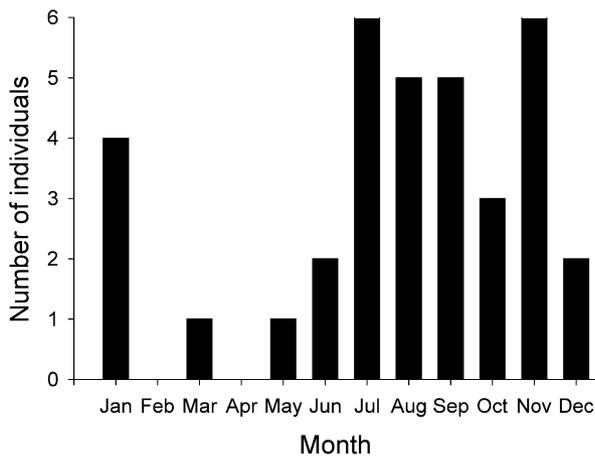


Figure 4. Fledging dates ($n = 35$) for the Tahiti Petrel on Tahiti (see text).

occur in New Caledonia in March, June, July, August, October, November and December. Our data from the southern lagoon, however, suggest a more restricted breeding period, in the austral summer, with egg-laying occurring only in October–December. Several dozen Tahiti Petrels were actively displaying at night (V.B. pers. obs.) with no trace of breeding in May 1986; eight adults were calling in May 1997 and a pair visited a burrow that was empty in July 1997 (M. Pandolfi Benoit pers. comm.): so, Tahiti Petrels also visit their breeding colonies after breeding, as is the case of many Procellariidae of various genera (reviewed by Warham 1996).

In Polynesia, laying dates of Tahiti Petrels are also spread throughout the year, although they peak between March and July, at least on Tahiti. Museum specimens from the Marquesas Islands indicate laying in July, August and October. Laying dates therefore occur through the year in both subspecies, but peaks are apparent and differ between localities. For comparison, the Fiji Petrel is believed to fledge in the austral spring (based on the type specimen), suggesting a laying period in autumn (Watling & Lewanavanua 1985), and the Reunion Petrel is a summer breeder (Attié *et al.* 1997, Le Corre *et al.* 2003).

Neither incubation length nor chick rearing duration could be calculated precisely during this study and had to be estimated from egg characteristics using allometric equations available for petrels: 55 days for the incubation length and about 110–120 days for the fledging period. These values are similar to those of the Hawaiian Petrel *Pterodroma sandwichensis* (Warham 1990, Brooke 2004), which

has a similar body weight: incubation 55 days and chick rearing 111 days. Interestingly, growth curves for Tahiti Petrels are also very similar to those for the Hawaiian Petrel (Simons 1985; see Fig. 3 for comparison).

Sexual dimorphism in biometry was established by De Naurois and Erard (1979), although it was based on a small sample. They concluded that only bill depth differed, especially for Polynesian birds. Our study actually indicates the reverse (i.e. New Caledonia birds are more sexually dimorphic than Polynesian birds, probably because the former have much deeper bills than the latter) and that characteristics other than bill depth also differ (all parameters but tail in live birds; bill depth and culmen in museum specimens). We detected geographical variation only for bill depth (we failed to detect any statistical difference in tarsus between the two subspecies as reported by De Naurois & Erard 1979). Small sample sizes (only nine birds from New Caledonia) and tarsus shrinkage, however, may explain this difference. Nevertheless, the morphometric difference between the two forms is very slight (as is also the case for genetic markers: Bretagnolle *et al.* 1998) and further questions the validity of the two subspecies.

The breeding population of the Tahiti Petrel on our study islet was estimated at about 20 pairs (Pandolfi Benoit & Bretagnolle 2002). During this study, we found 20 burrows (most were not active) and caught 70 birds, which suggests that the breeding population is slightly larger. This is the largest breeding unit of the southern lagoon. Threats include boats and human landing for recreational purposes (see also Pandolfi Benoit & Bretagnolle 2002), Ship Rats *Rattus rattus* that were successfully eradicated in 1998, Peregrine Falcons *Falco peregrinus* that catch Black-winged Petrels (active by day) but not Tahiti Petrels, and Wedge-tailed Shearwaters. With half a million breeding pairs in the southern lagoon (Pandolfi Benoit & Bretagnolle 2002), the latter species, which lays at the same time as the Tahiti Petrel, is a very strong competitor. This probably explains why Tahiti Petrels are so rare on coralline islets, and relatively more abundant on this rocky islet, as Shearwaters prefer deep soils, not found on steep slopes. Similarly, Shearwaters are present only on the coast of the main island, completely avoiding the inland areas favoured by Tahiti Petrels. On the mountains of Grande-Terre (the main island), the breeding population of Tahiti Petrels was tentatively estimated at 1000–5000 pairs (Bretagnolle 2001), but it presumably faces high predation rates from rats, cats, dogs

and pigs. Therefore, although facing strong adverse competition from Shearwaters, the New Caledonian southern lagoon population of the Tahiti Petrel is probably the only secure population in the long term, perhaps at the world level, because every breeding locality known to date holds several invasive mammalian species.

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