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Assortative mating, sexual size dimorphism and sex determination in a seabird with plumage polymorphism

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ABSTRACT

Intraspecific plumage polymorphism in seabirds is often attributed to advantages in foraging activities and escape from predators, but its role in sexual selection is not well understood. The Trindade petrel (*Pterodroma arminjoniana*) presents morphs varying from pale to whole dark, with no apparent sexual size dimorphism (SSD). We tested assortative mating in Trindade petrels based on plumage colours and body size. In addition, genders of Trindade petrels were identified molecularly aiming to test SSD based on morphometrics, which was also used to generate a discriminant function for sex assignment. Within-pair consistency in plumage colour (i.e. birds paired with mates of the same morph) was detected in 9 out of 10 pairs, but not in morphometric traits. Minimum bill depth and bill depth at unguis were traits significantly larger in males. The best model was adjusted with Bill depth at unguis, wing chord and body mass, with global discriminatory power of 78.4%. Our results suggest that plumage colours may be sexually selected in Trindade petrels, which brings evolutionary implications on the persistence of plumage polymorphism. Discriminatory power of the best discriminant function was similar to those found in other Procellariiformes and also among datasets obtained by distinct researchers, demonstrating its robustness.

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Introduction

Environment-mediated selection has been shown to be a major factor shaping bird phenotypes within and between populations (Grant and Grant 2002; Nunes et al. 2018; Nunes and Bugoni 2018). For instance, range-wide seabird species may develop population-specific characteristics in phenotypic traits to optimize the use of local resources (Jakubas et al. 2014, Colombelli-Négrel 2016, Nunes et al. 2016). Between-sex morphometric differences may also occur in order to enhance feeding efficiency and avoid intrapopulation resource competition (González-Solís et al. 2000; Shaffer et al. 2001). Complementarily, population-level phenotypes may also be influenced by sexual selection, which results from mate choice or intrasexual competition for mates (Andersson 1994).

Assortative mating is a nonrandom pattern of mate choice, which can be positive if similar phenotypes mate or negative if mating occurs between dissimilar phenotypes (Burley 1983). Seabirds may mate assortatively in relation to phenotypic traits such as body measurements (Forero et al. 2001; Einoder et al. 2008), ornaments (Jones and Hunter 1993; Rull et al. 2016) and colour morphs (Phillips and Furness 1998). This behaviour can result from selection acting directly

or indirectly on the mate choice and is often treated as a mechanism of premating reproductive isolation (Jiang et al. 2013). Nonrandom mating has several evolutionary implications, such as increasing homozygosity and selection against immigrants (Redden and Allison 2006). In this context, knowledge on mating strategies can shed light on the drivers of population differentiation in strongly structured metapopulation systems with low genetic diversity, as usually observed in seabirds (Milot et al. 2007; Ramírez et al. 2013; Nunes and Bugoni 2018).

Seabirds mostly display greyscale plumages and are less colourful than non-marine birds (Schreiber and Burger 2001). Nonetheless, intraspecific plumage polymorphism can be observed in three out of six seabird Orders (i.e. Procellariiformes, Suliformes and Charadriiformes) (Phillips and Furness 1998; Le Corre 1999; Carlos and Voisin 2008) while this is rare in other bird groups (Galeotti et al. 2003). Different colour morphs are a consequence of differential deposition of melanins (Ducrest et al. 2008) and genetically polymorphic phenotypes occur independently of age, sex, or individual and environmental condition (Roulin and Bize 2007). Furthermore, local adaptation has been suggested as a potential mechanism of maintenance

of plumage polymorphism (Dreiss et al. 2012). In this way, plumage polymorphism in seabirds has been suggested to play a relevant role in trophic interactions, representing an advantage when escaping from predators or catching prey. For example, plumage colour of red-footed boobies *Sula sula* has been suggested to be a defensive camouflage, reducing the detection by kleptoparasites, such as frigatebirds (Le Corre 1999). Similarly, the plumage morph in Arctic skua *Stercorarius parasiticus* may act to reduce the conspicuousness by prey, increasing its chase success (Caldow and Furness 1991; Arcos 2007). Alternatively, sexual selection has also been raised as potential mechanism acting in the maintenance of plumage polymorphism (Roulin and Bize 2007; Roulin 2016). Individuals of different colour morphs may be adapted to specific environmental conditions and those locally adapted are preferred to mate. The colour morph may be a clue of partners able to perform better parental care and the mate choice may even allow the pairs to produce offspring of higher genetic quality (Roulin and Bize 2007; Roulin 2016). In addition, mating preference is context-dependent, may vary temporally and spatially (Roulin and Bize 2007), and the evidences of nonrandom mating based on colour are contradictory among seabird species (Davis and O'Donald 1976; Baião and Parker 2008).

The sexual selection hypothesis, besides the intersexual food competition and reproductive role division, has also been invoked to explain the sexual size dimorphism (SSD) (Hedrick and Temeles 1989). In general, SSD in seabirds is male-biased, but a few species present females larger than males (Schreiber and Burger 2001). For example, albatrosses and petrels have been demonstrated to hold male-biased SSD with bill and wing length as the most sexually dimorphic traits (Bugoni and Furness 2009; Carey 2011; Mischler et al. 2015). However, the Procellariiformes Order comprises ~150 species (Gill and Donsker 2018) distributed worldwide and thus exposed to a range of selective pressures, which could contribute to biases in SSD patterns from a single expected pattern. In this context, the group of gadfly petrels (*Pterodroma* spp.) is an interesting group for studying variations in SSD, as it is the most diverse genus among Procellariiformes (35 species) (Gill and Donsker 2018) and present species-specific differences regarding body size, bill shape and spatial distribution (del Hoyo et al. 1992).

Efficient sex determination of birds with the absence of apparent sexual dimorphism in the field is challenging and a variety of techniques, such as cloacal inspection, vocalization and morphometric sexing,

had been employed (O'Dwyer et al. 2006; Totterman 2012). Morphometric measurements may enable a quick sex determination through an inexpensive and non-invasive technique, but its accuracy depends on the degree of dimorphism and the geographical body size variation may limit its applicability (Einoder et al. 2008; Carey 2011; Jakubas et al. 2014). In addition, inter-researcher differences in the way measurements are taken may decrease its accuracy, and therefore it is recommended that a single researcher perform all morphological measurements (Carey 2011) which can make difficult its applicability even within the same research group.

The Trindade petrel *Pterodroma arminjoniana* (Giglioli & Salvadori, 1869) is a medium-sized and surface-nesting seabird with polymorphic plumage, which breeds on the Trindade Island, South Atlantic Ocean, and the Round Island, Indian Ocean (Brown et al. 2010). In Trindade Island, ca. 1130 pairs breed all year round with two marked egg-laying peaks in September–October and February–March (Fonseca-Neto 2004; Luigi et al. 2009). Both female and male seem to share equally the breeding duties, as well as explore similar foraging areas and food resources during the breeding (Luigi et al. 2009; Leal et al. 2017) and non-breeding (Krüger et al. 2016; Ramos et al. 2017) seasons. Sexual differences in plumage and vocalization are apparently absent and previous results indicate the absence of SSD (Luigi et al. 2009). Most of the population of Trindade Island (62.1%, $n = 713$ birds sampled from 1998 to 2007) has dark grey upperparts, white below and in forehead-sides (pale morph), 28.2% are wholly dark brown birds (dark morph) and 9.7% show some degree of intermediate colouration (Luigi et al. 2009).

In this study, we tested assortative mating in Trindade petrels based on plumage colour and body size. Since there are more pale and dark-morph petrels breeding on Trindade Island, and few individuals with intermediate colouration, we expect to find evidence of non-random mating based on plumage colour. Furthermore, males and females have strong overlap on morphometric traits (Luigi et al. 2009) and thus we expect to find evidences of random mating based on body size. This strong overlap also suggests the absence of SSD in Trindade petrels, distinct from the general pattern of male-biased SSD in Procellariiformes (Serrano-Meneses and Székely 2006). Bill is the most sexually dimorphic structure in seabirds and SSD has been detected in some bill measurements, such as bill depth and head-bill length (Bugoni and Furness 2009; Carey 2011; Mischler et al. 2015), although these traits were not assessed by Luigi et al. (2009). In

this context, we used body measurements not considered previously in order to test SSD in Trindade petrels and to generate a discriminant function. From this, we hypothesized that there is SSD in bill measurements. Finally, we developed a discriminant function to sex determination and tested its robustness when applied to datasets obtained by distinct researchers, aiming to check its usefulness for other studies.

Material and methods

Study area

Sampling was carried out on Trindade Island (20°30'S; 29°19'W), which is located in the South Atlantic Ocean, 1140 km off the South American coast (Barth 1958). Trindade is a volcanic island with an area of 8 km² (Barth 1958) surrounded by oligotrophic deep waters up to ~5500 m depth (Leal and Bouchet 1991). It has a tropical oceanic climate with an average air temperature between 22°C in winter and 27°C in summer (Pedroso et al. 2017). The island is under influence of the Brazil Current, a western boundary current that flows southward and has temperature and salinity above 20°C and 36, respectively (Silveira et al. 2000).

Sampling

Nests of Trindade petrels were visited regularly, checked visually and data was obtained by LB in 2008 and GRL in 2014. Nests are visited by other Trindade petrels, mainly during the prospecting phase, therefore only pairs which male and female had been observed attending the egg and/or chick were taken into account to investigate the assortative mating. Trindade petrels were captured on their nests by hand or hand net and a metal ruler was used to take body measurements for wing chord and tail length (at the nearest mm). A calliper was used to measure tarsus length, middle toe length with nail, middle toe length without nail, bill length, nostrils-to-bill-tip length, head length, bill depth at nostrils, minimum bill depth and bill depth at unguis, with 0.1 mm precision. In addition, a spring scale was used to measure the body mass (in g), with ~5 g precision. Bill measurements followed descriptions from Zino and Zino (1986).

The plumage morph of each individual was identified as follows: pale morph, dark grey upperparts and whitish breast/vent; intermediate morph, dark grey upperparts and breast/vent mottled or uniformly dusky; and dark morph, wholly dark brown (Flood and Fisher 2013) (Figure 1). Finally, blood samples

(~0.05 mL) were taken from the tarsal vein using sterile syringe/needle and preserved in absolute ethanol or on FTA® cards. After sampling, petrels were banded with uniquely numbered metal rings and released back in their respective nests.

Molecular sexing

In the lab, DNA was extracted following the 5 M sodium chloride protocol (Medrano et al. 1990) and CHD genes were amplified with the 2550F and 2718R primers and PCR conditions described by Fridolfsson and Ellegren (1999). Molecular sexing of Trindade petrels using PCR amplification of the CHD genes was carried out through a 3% agarose electrophoresis, so that males were identified by two overlapped bands (i.e. one visible band), and females by two bands of distinct fragment length (i.e. two visible bands).

Researcher bias assessment

Petrels could not be resampled in the field by different researchers to test the researcher bias. Therefore, 19 Atlantic petrels *Pterodroma incerta* skins previously deposited in the Bird Collection of the Universidade Federal do Rio Grande-FURG (Coleção de Aves da FURG – CAFURG) were measured both by LB and GRL in order to test the researcher bias in the morphometric dataset of Trindade petrels. Atlantic petrels were sampled for morphometrics as referred above, except for body mass, so that the two researchers carried out sampling independently. Most Atlantic petrels were emaciated and came from a mass inland displacement of birds mediated by a hurricane (Bugoni et al. 2007).

Data analysis

Binomial test was performed to verify the assortative mating based on the plumage colour. Paired sign test and Spearman's rho (ρ) correlation were used to assess the assortative mating based on the body size.

To investigate the sexual size dimorphism, firstly outliers were identified by using standard deviations as a criterion: morphometric data outside \pm two standard deviations from the mean were removed from the dataset, while body mass values outside \pm one standard deviation were removed, in order to avoid biased information by individual daily fluctuations. To evaluate the homogeneity of variances and if data was normally distributed, Bartlett and Shapiro–Wilk's tests were performed with the original and log-transformed datasets. However, as data do not comply with these

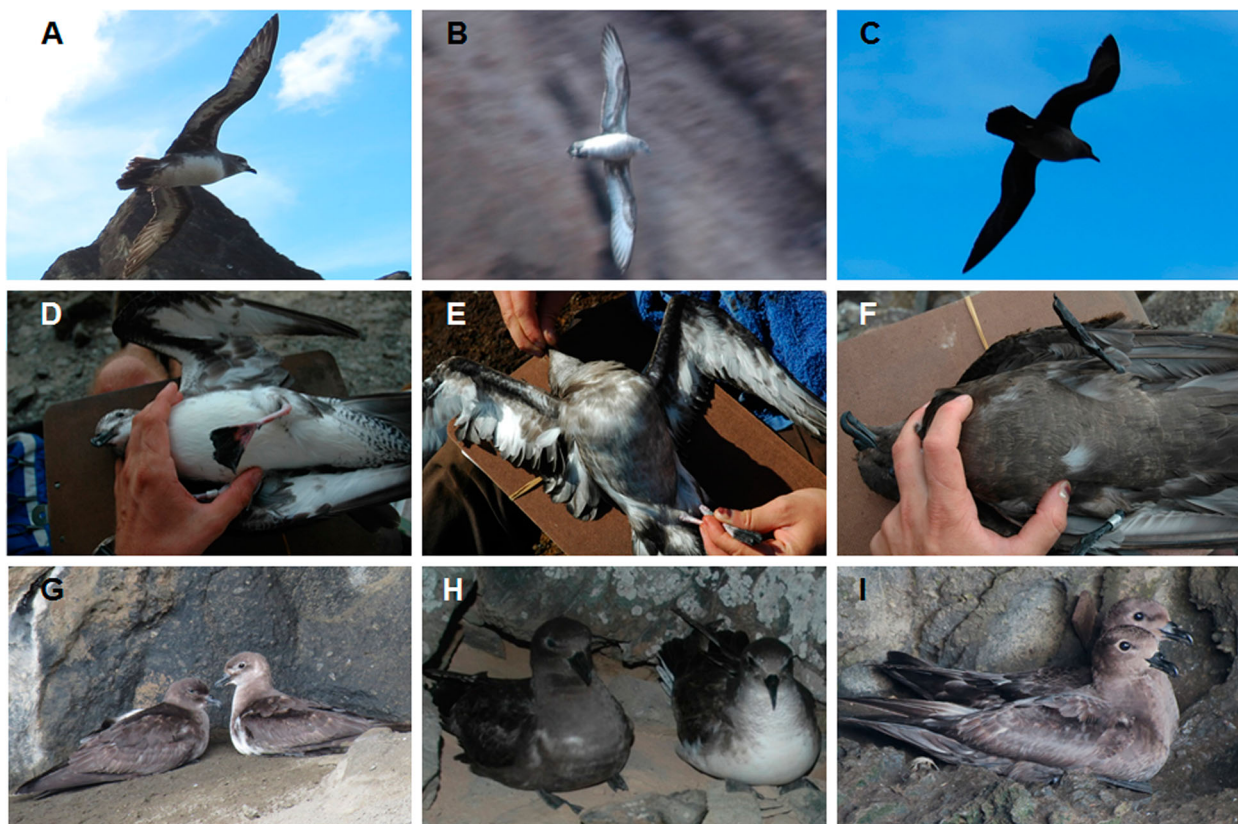


Figure 1. Plumage morphs and breeding pairs of Trindade petrel *Pterodroma arminjoniana*. Underside in flight and in a detailed view of pale morph (A, D), intermediate morph (B, E) and dark morph (C, F). Pale–pale pair (G), pale–dark pair (H) and dark–dark pair (I)

assumptions univariate intersexual differences were assessed through Mann–Whitney–Wilcoxon tests (U). Bonferroni correction for multiple comparisons was used to adjust P -values (Zar 2010). Sexual size dimorphism index was calculated as the ratio between the average values for males and females for each trait. Spearman’s rho (ρ) was used to assess correlation between SSD indices generated from LB’s and GRL’s datasets, and also to test within-pair morphometric correlation. Regarding the experiment with Atlantic petrels, Spearman’s correlation was used to test for consistency of measurements between researchers, and the paired sign test was applied to assess differences between measurements of each sampler.

Generalized linear models (GLM) were fitted to the dataset by assuming a binomial distribution, in order to generate a discriminant function to separate genders based on biometric data. For this, Spearman’s correlation was used to test for multicollinearity, so that correlated variables were removed from the analysis. Model selection followed a stepwise regression procedure, starting with the saturated model and removing variables aiming to reach the best fitted model (Burnham and Anderson 2002). Akaike’s Information Criterion (AIC) was used for ranking models, assuming

the smaller AIC value the better. Validation was carried out with the same dataset used to fit the model ($n = 57$; collected by LB), with a sample obtained from random selection without replacement containing 50% of the full LB’s data set (jackknife method), and with the smaller dataset ($n = 24$; collected by GRL). Cutpoint (C) was calculated from discriminant scores (D) of the LB’s dataset, following the equation proposed by Hair et al. (2009) for groups with different sizes:

$$C = \frac{(Nf * Zm) + (Nm * Zf)}{Nf + Nm}$$

where N is the sample size for males (m) and females (f), and Z is the centroid (mean of discriminant scores) for each sex. All statistical analyses were carried out using the software R (R Core Team 2017).

Results

Assortative mating

Ten pairs were sampled for assortative mating among the Trindade petrels (Table I). None of the traits measured was significantly correlated or were significantly different within pairs and SSD index of all

Table I. Body measurements (in mm, except body mass in g) of ten pairs of Trindade petrels (*Pterodroma arminjoniana*) sampled breeding on Trindade Island (Brazil). Percentage of males larger for each measurement, sexual size dimorphism index (SSD) and the results of Spearman's correlation and paired sign tests are also presented.

	Males	Females	Males Larger (%)	Sign test		SSD	Spearman	
				s	P		ρ	P
Bill length	30.7 ± 9.2	30.3 ± 9.1	40.0	4	0.75	0.99 ± 0.04	0.24	0.49
Nostrils-to-bill-tip length	22.8 ± 6.8	21.6 ± 6.5	30.0	3	0.34	0.98 ± 0.06	0.20	0.57
Bill depth at nostrils	13.2 ± 4.0	14.6 ± 4.4	60.0	6	0.75	1.03 ± 0.09	-0.61	0.05
Minimum bill depth	9.6 ± 2.9	9.5 ± 2.9	66.7	6	0.50	1.05 ± 0.09	-0.17	0.66
Bill depth at unguis	11.6 ± 3.5	11.8 ± 3.5	77.8	7	0.17	1.02 ± 0.08	-0.46	0.17
Tarsus length	38.7 ± 11.6	40.3 ± 12.1	50.0	5	1.00	1.01 ± 0.04	0.49	0.14
Middle toe with nail	52.2 ± 15.7	50.9 ± 15.3	30.0	3	0.34	0.98 ± 0.04	-0.30	0.39
Middle toe without nail	45.4 ± 13.6	44.1 ± 13.2	60.0	6	0.75	0.99 ± 0.04	-0.19	0.59
Wing chord	298 ± 89.4	291 ± 87.3	20.0	2	0.10	0.97 ± 0.05	0.57	0.07
Tail length	118 ± 35.4	112 ± 33.2	55.6	5	1.00	1.01 ± 0.04	0.28	0.42
Head length	78.1 ± 23.4	76.7 ± 23	40.0	4	0.75	1.00 ± 0.04	-0.32	0.35
Body mass	375 ± 112.5	435 ± 130.5	44.4	4	1.00	0.99 ± 0.10	0.06	0.86

measurements have been close to one (Table I). However, males tend to be larger mainly in bill height measurements (>60% of males were larger than females). Interestingly, there was within-pair consistency of plumage colour for nine out of ten pairs sampled, (binomial test; $P < 0.05$) with five pale-pale pairs, four dark-dark pairs, and one pair with a dark female and an intermediate male.

Researcher bias

Only two out of eleven traits of the Atlantic petrels were not significantly correlated between measurements taken by the two researchers and the tail length was the least correlated measurement (Table II). Complementarily, seven traits were significantly different when comparing measurements obtained by each researcher. From this, Trindade petrels datasets were analysed separately regarding sexual size dimorphism in order to avoid researcher bias.

Sexual size dimorphism

In general, male-biased dimorphism was detected, ranging from 0.1% (bill length) to 6% (body mass) in the LB's dataset, although wing chord was larger for

females in this dataset, and from 1% (tail length) to 7% (body mass) in the GRL's dataset (Table III). Minimum bill depth and bill depth at unguis were shown to be significantly male-biased in both datasets, while body mass was significant only in the LB's dataset, and head length only in the GRL's dataset. Nevertheless, SSD indices were significantly correlated among datasets from both researchers (Figure 2).

Discriminant function

Due to the inconsistency between measures taken by each researcher, detected from the experiment with Atlantic petrels, GLMs were adjusted only using the LB's dataset due to its larger sample size and the validation was carried out using GRL's dataset. The best adjusted model included bill depth at unguis, wing chord and body mass, and successfully identified the gender of 78.4% of the LB's birds, of which 74.2% of males and 85.0% of females were correctly assigned. Cutpoint (C) was estimated at 0.321, by the discriminant function as:

$$D = (\text{bill depth at unguis} * 3.383) + (\text{mass} * 0.036) + (\text{wing} * -0.095) - 22.678$$

Table II. Body measurements (in mm) of Atlantic petrels (*P. incerta*) skins ($n = 19$) taken by two different researchers (LB and GRL). Results of Spearman's correlation and paired sign tests are also presented.

Trait	Mean ± SD		Spearman		Sign test	
	LB	GRL	ρ	P	s	P
Bill length	36.48 ± 1.47	37.04 ± 1.67	0.82	<0.001	15	0.002
Nostrils-to-bill-tip length	26.96 ± 1.21	28.03 ± 1.58	0.78	<0.001	16	0.001
Bill depth at nostrils	15.42 ± 1.06	16.27 ± 1.01	0.80	<0.001	16	0.004
Minimum bill depth	11.29 ± 0.57	11.78 ± 0.61	0.75	<0.001	18	<0.001
Bill depth at unguis	14.86 ± 1.16	14.03 ± 0.78	0.29	0.236	3	0.007
Tarsus length	44.24 ± 1.85	44.23 ± 1.19	0.62	0.005	8	0.814
Middle toe with nail	59.79 ± 1.24	58.95 ± 2.00	0.47	0.045	6	0.167
Middle toe without nail	52.46 ± 1.77	52.79 ± 1.98	0.52	0.021	8	0.647
Wing chord	314.32 ± 7.72	306.16 ± 7.18	0.81	<0.001	0	<0.001
Tail length	122.89 ± 4.32	121 ± 4.08	0.18	0.468	5	0.143
Head length	89.26 ± 2.35	92.23 ± 2.26	0.71	<0.001	18	<0.001

Table III. Body measurements (in mm, except body mass in g) of Trindade petrel (*Pterodroma arminjoniana*) taken by LB and GRL on Trindade Island (Brazil). SSD = male:female (means). *P*-values of paired sign tests adjusted with Bonferroni correction; *n* = 33 males and *n* = 24 females in LB's dataset; *n* = 17 males and *n* = 7 females in GRL's dataset

Trait	LB					GRL				
	Mean ± SD		SSD	<i>U</i>	<i>P</i>	Mean ± SD		SSD	<i>U</i>	<i>P</i>
	♀	♂				♀	♂			
Bill length	29.11 ± 0.97	29.15 ± 0.91	1.00	402.5	0.881	29.45 ± 1.19	30.26 ± 0.69	1.03	32.5	0.091
Nostrils-to-bill-tip length	21.04 ± 1.02	21.23 ± 0.90	1.01	353.5	0.459	21.96 ± 1.05	22.61 ± 0.99	1.03	36.0	0.144
Bill depth at nostrils	14.00 ± 0.72	14.28 ± 0.64	1.02	303.5	0.088	13.96 ± 0.86	14.37 ± 0.35	1.03	38.0	0.181
Minimum bill depth	9.44 ± 0.43	8.89 ± 0.37	1.05	167.5	< 0.001	9.41 ± 0.45	9.91 ± 0.39	1.05	26.5	0.038
Bill depth at unguis	10.98 ± 0.33	11.42 ± 0.46	1.04	179.0	< 0.001	10.74 ± 0.35	11.36 ± 0.39	1.06	5.0	0.001
Tarsus length	37.15 ± 1.13	37.43 ± 1.60	1.01	355.0	0.474	37.88 ± 0.94	38.89 ± 1.20	1.03	30.5	0.070
Middle toe with nail	51.00 ± 2.08	51.82 ± 1.90	1.00	418.5	0.931	49.31 ± 2.13	50.53 ± 1.53	1.02	38.5	0.192
Middle toe without nail	86.00 ± 1.60	45.64 ± 1.81	1.01	359.0	0.405	42.39 ± 2.31	43.74 ± 1.25	1.03	35.0	0.126
Wing chord	290.0 ± 6.70	288.52 ± 7.20	0.99	439.5	0.395	291.59 ± 7.65	298.71 ± 7.83	1.02	30.5	0.069
Tail length	114.17 ± 2.87	115.67 ± 4.03	1.01	297.0	0.110	114.47 ± 4.56	116.00 ± 4.58	1.01	45.5	0.390
Head length	75.07 ± 1.85	75.71 ± 2.03	1.01	334.5	0.223	74.72 ± 2.00	77.54 ± 1.00	1.04	9.0	0.001
Body mass	351.73 ± 32.12	373.48 ± 30.41	1.06	234.5	0.028	365 ± 32.36	389.29 ± 38.02	1.07	34.5	0.118

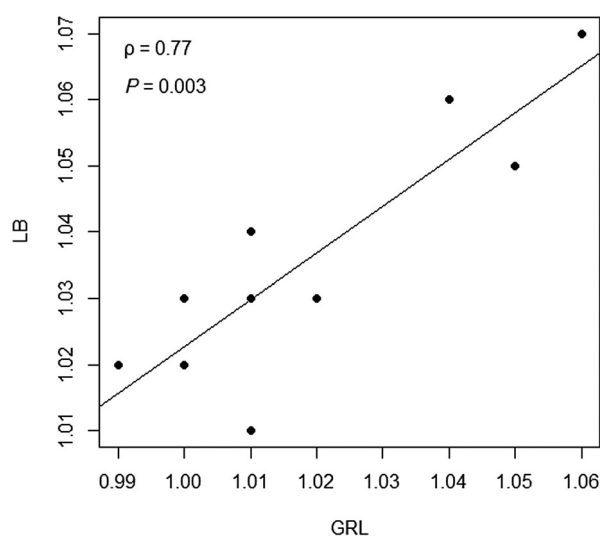


Figure 2. Correlation between sexual size dimorphism (SSD) indexes (male:female) obtained by two researchers (LB and GRL) for 12 morphometric measurements taken on distinct individuals of Trindade petrels *Pterodroma arminjoniana* (*n* = 81). Three morphometric measurements had identical SSD values making the points overlapped in the figure.

Therefore, when $D > 0.321$ individuals were assigned as males, and when $D < 0.321$ as females. Cross-validation correctly identified 71.4% and 71% of samples for both genders considering the GRL's and the resampled (i.e. jackknife) datasets, respectively.

Discussion

Assortative mating

Our results demonstrate assortative mating in Trindade petrels based on plumage colour, but not based on morphometrics, indicating a preference for mates of same plumage morph. Despite the absence of assortative mating based on plumage colour in red-footed

boobies (Baião and Parker 2008) and northern fulmars *Fulmarus glacialis* (Hatch 1991), evidences of sexual selective pressure acting on plumage polymorphism in seabirds had been reported for Arctic skua (Phillips and Furness 1998). The genetic compatibility hypothesis proposes that colour polymorphism may be used as a cue to select the most genetically compatible mate, which may produce more high-quality offspring (Saino and Villa 1992; Roulin 2004). Furthermore, the expression of colour morphs may be correlated with other phenotypic traits (i.e. physiological and behavioural), which also may influence the mate choice (Roulin and Ducrest 2011). In Arctic skua, mating type and its influence on breeding variables, such as breeding phenology or fecundity, may vary between year and colonies (Phillips and Furness 1998), remaining unclear the potential advantages of this behaviour. Trindade petrels of different morphs are recorded in both laying peaks, breeding under different environmental conditions, and also sharing the same crevice (authors', unpub. obs.), which may indicate the absence of local adaptation. However, studies addressing breeding success, ectoparasite load, microhabitats for nesting and at sea foraging of the different morph pairs, can help to understand the assortative mating based on plumage polymorphism in Trindade petrels and other seabirds.

Sexual size dimorphism

Male-biased SSD was detected in Trindade petrels, in conflict with previous results (Luigi et al. 2009), through the inclusion of measures not considered in early studies. Male-biased SSD is the pattern expected for Procellariidae (Serrano-Meneses and Székely 2006) and bill dimensions are the most sexually dimorphic traits in Procellariiformes (Bugoni and Furness 2009;

Navarro et al. 2009; Carey 2011; Mischler et al. 2015). Thus, male-biased dimorphism in bill dimensions had already been reported for Gould's *P. leucoptera*, Providence *P. solandri* and Grey-faced *P. gouldi*, gadfly petrels (O'Dwyer et al. 2006; Bester et al. 2007; Bourgeois et al. 2017). Since the bill is mainly a feeding structure, intersexual differences in size and shape could be related to differences in feeding ecology (González-Solís 2004). SSD can result from differences in ecology in order to avoid the intersexual competition for resource or even due to different breeding roles (Hedrick and Temeles 1989; Serrano-Meneses and Székely 2006). However, no intersexual differences in at-sea distribution and diet parameters were detected for Trindade petrels in different phases of the breeding period (Leal et al. 2017) and both sexes seem to share equally the duties during breeding (Luigi et al. 2009).

In birds, bill size and shape may also be associated to other functions, such as territorial defense (Mínguez et al. 2001; Nunes et al. 2018) and mate acquisition (Coulter 1986). Trindade petrels display strong nest site fidelity (Luigi et al. 2009) and thus a deeper bill can represent an advantage when defending territories. This is particularly important due to limited nest sites (authors', unpub. obs.), and the overlap between birds nesting along the two seasons. Indeed, as breeding lasts 8 months, and thus temporal and spatial overlap is unavoidable (Ramos et al. 2017). A hypothesis that explains SSD as a consequence of sexual selection, establishes that smaller males are favoured when competition occurs through aerial display, and larger males when they display or fight on the ground (Serrano-Meneses and Székely 2006). Trindade petrels initially perform aerial display but continue their display and courtship on the ground (Luigi et al. 2009; Flood and Fisher 2013). Thus, it is possible that sexual selection is the main force acting to favour male petrels with more ability to defend nests (i.e. males with larger bill).

Sex discrimination

Our results demonstrated a discriminatory power to identify the gender successfully (~78%) similar to other seabirds in which the same method was applied, such as tropicbirds (Nunes et al. 2013), terns (Fletcher and Hamer 2003) and other petrels (O'Dwyer et al. 2006; Mischler et al. 2015; Bourgeois et al. 2017). This demonstrates that even with some significant differences between sexes in Trindade petrels, there is a large overlap in the range of body size traits.

The accuracy of sex determination through morphometry depends on the degree of dimorphism

and in highly dimorphic species such as the southern giant petrel *Macronectes giganteus* (Copello et al. 2006), the Balearic shearwater *Puffinus mauretanicus* (Genovart et al. 2003) and the great black-backed gulls *Larus marinus* (Mawhinney and Diamond 1999), the discriminant function is able to predict sex correctly in > 90% of the individuals. Due to the small dimorphism degree in gadfly petrels (Serrano-Meneses and Székely 2006), other techniques as body condition at the time of laying, cloacal inspection and vocalization may be more effective in sexing *Pterodroma* spp. in the field (O'Dwyer et al. 2006; Totterman 2012). Although our data do not allow a better sexual determination due to the small sample size of pairs, when within-pair comparisons are performed, the sex determination through morphometrics may improve up to 10% the accuracy of sexing (Fletcher and Hamer 2003; Carey 2011; Bourgeois et al. 2017). Sexual differences in vocalization are apparently absent in Trindade petrels (Luigi et al. 2009) and the technique of cloacal measurement at the time of laying can only be applied during a limited period of breeding. Thus, morphometrics may be useful for sex assignment of this species in the field, however, within-pair comparisons would improve its accuracy and results should be considered with caution.

The model applied in the datasets of both samplers (LB and GRL) had similar discriminatory power, even with inconsistencies and systematic error between measures taken by both researchers. Differences between measurements of the same traits by different samplers are common ('researcher error') and could make direct comparison difficult. However, our results demonstrated that even with significant differences between measures taken by each researcher, the model maintained its performance with similar discriminatory power. This demonstrated that this equation is robust enough to be applied by different researchers in the field.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Ethical approval

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