**Sexual size dimorphism, spatial segregation and sex-biased bycatch of southern and northern royal albatrosses in pelagic longline fisheries**

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**Abstract**

Bycatch in longline fisheries is a major cause of global declines of albatrosses. Sexual segregation at sea often leads to unequal overlap with different fisheries, resulting in sex-biased bycatch, exacerbating impacts at the population level. In great albatrosses (*Diomedea* spp.), males (the larger sex) tend to spend more time at higher latitudes than females, attributed to competitive exclusion or differences in flight performance, mediated by the pronounced sexual size dimorphism (SSD). Consequently, females are often caught in larger numbers by pelagic longline fisheries in subtropical and temperate areas. Although known for *Diomedea exulans*, this has not been generalised for all great albatrosses. Here we examined the degree of SSD, and developed discriminant functions to determine species and sex in *Diomedea epomophora* and *D. sanfordi*, which are killed in several fisheries in the southern hemisphere. Based on a large sample of bycaught albatrosses caught off Uruguay, both species showed substantial SSD. Discriminant functions assigned species and sexes to otherwise indeterminate individuals with 90-100% accuracy. Based on all birds identified (*n*=128), bycatch in the pelagic longline fishery was female-biased, indicating sexual segregation at sea. These discriminant functions allow species and sexes to be separated, providing critical data for future bycatch assessments.

**Key words**: Discriminant Analysis, Sexual segregation, Seabirds, Southwest Atlantic

**Introduction**

Bycatch in commercial fisheries represents one of the main conservation threats to albatrosses and other seabirds (Croxall et al. 1998, Gales 1998). Albatross life-history strategies (i.e. delayed maturity, low reproductive output and great longevity) make these species particularly vulnerable to any additional source of mortality. Adult survival is the most important demographic parameter influencing population trends (Weimerskirch et al. 1987, Gales 1998). As such, population declines at some colonies associated with reduced adult survival rates have been attributed to bycatch in longline fisheries (Weimerskirch et al. 1987, Croxall et al. 1998). Albatrosses are monogamous and sex ratio in the breeding population is expected to be 1:1. Sexual segregation at sea can therefore have implications for conservation, as sex-specific overlap with fisheries can produce sex-biased mortality (Jiménez et al. 2015); this translates both to an immediate, direct effect on the total number of potential breeders, as well as an indirect effect on fecundity because it affects availability of one sex as partners (Mills & Ryan, 2005).

Sexual segregation in at-sea distribution has been reported in great albatrosses (*Diomedea* spp.), particularly in the wandering albatross (*Diomedea exulans* Linnaeus; Prince et al. 1992, Jiménez et al. 2015), a species that, like others in the genus, exhibits noticeable sexual size dimorphism (SSD) (Shaffer et al. 2001, Cuthbert et al. 2003). On average, males have longer bills (ca. 4%, 170 vs 164 mm) and greater wing span (ca. 4%, 311 vs 299 cm), with ca. 7% more wing area (6260 vs 5860 cm2), and are also 20% heavier (9.4 vs 7.8 kg) than females (Shaffer et al. 2001). Female wandering albatrosses typically forage in sub-Antarctic and subtropical waters, whereas males usually forage further south, in sub-Antarctic and Antarctic zones (Xavier & Croxall 2005, Froy et al. 2015). This partial sexual segregation is attributed either to competition, with larger males excluding the smaller females from access to nearby resources, forcing them to travel further from the colony (Phillips et al. 2008), or the relationship between sexual size dimorphism and flight performance (Shaffer et al. 2001). The latter hypothesis is that as wing loading determines flight speed, the windier regions of the sub-Antarctic and Antarctic are more optimal for males, which have ca. 12% higher wing loading than females, whereas females and fledglings are better adapted for exploiting the lighter winds of subtropical regions. Consequently, bycatch of wandering albatrosses in pelagic longline fisheries, which mainly operate in subtropical regions, is female-biased (Jiménez et al. 2015). Because both hypotheses explaining this latitudinal segregation are mediated by SSD, similar processes and consequences (female-biased bycatch in pelagic longline fisheries) are expected for the other *Diomedea* species.

Large proportions of the global populations of two great albatross species from New Zealand migrate to the southwest Atlantic; the southern royal albatross *Diomedea epomophora* (Lesson) and the northern royal albatross *Diomedea sanfordi*  (Murphy) (Nicholls et al. 2002, Robertson et al. 2003, Moore and Bettany 2005). Separation of these two species was proposed by Robertson and Nunn (1998), and adopted subsequently by both BirdLife International (the listing authority for the World Conservation Union, IUCN) and the Agreement for the Conservation of Albatross and Petrels (ACAP). Northern and southern royal albatrosses are globally threatened according to the IUCN (Endangered andVulnerable, respectively), and >99% of breeding pairs nest at the Chatham Islands and Campbell Island, respectively. The global population trend for southern royal albatross appears to be stable, and for northern royal albatross is unknown (ACAP 2009a, b). During breeding, both species are distributed in New Zealand continental shelf waters (Nicholls et al. 2002, Waugh et al. 2002), while during the non-breeding season, they occur in the southern Pacific, Atlantic and Indian oceans (Nicholls et al. 2002, Robertson et al. 2003, Moore and Bettany 2005). They winter mainly in the southern continental shelf waters of South America, both on the Pacific and Atlantic coasts, and particularly off Argentina and Uruguay (Nicholls et al. 2002, Robertson et al. 2003, Jiménez et al. 2014). This preference for continental shelf habitat contrasts with the wandering albatross, which remains mainly oceanic (Froy et al. 2015). The limited data on body size of southern and northern royal albatrosses suggest that males are larger than females (Westerskov 1960, Tickell 2000), but the size dimorphism has not been tested statistically. In this paper, we use data from royal albatrosses of both species bycaught in pelagic longline fisheries in the southwest Atlantic to first test for sexual size dimorphism, and then apply discriminant analyses to assign sex and species in indeterminate birds. Most of these birds were partially eaten by scavengers, which is common in bycatch studies. We then tested for a biased sex ratio in the complete sample of bycaught birds, and discuss the potential conservation implications. Despite the difference in foraging habitats from the wandering albatross, we predicted comparable latitudinal segregation among sexes in the two royal albatross species, and hence a biased sex ratio in bycatch in pelagic longline fisheries in the north of their ranges.

**Materials and Methods**

This work used data from seabird carcasses collected on pelagic longline vessels by the ‘‘*Programa Nacional de Observadores a bordo de la flota atunera uruguaya*’’ (PNOFA) of the ‘‘*Dirección Nacional de Recursos Acuáticos*’’ (DINARA). These specimens were caught incidentally by Uruguayan commercial and research vessels in 2004-12, and 2009-12, respectively, and Japanese commercial vessels in 2009-11 operating off Uruguay under an experimental fishing license. All vessels fished in shelf break, slope and deeper waters off Uruguay, and Uruguayan commercial vessels also operated in international waters. The temporal distribution of fishing effort, and the captures of royal albatrosses until 2011, are presented in Jiménez et al. (2014). A total of 1599 sets and 3 311 113 hooks were observed during 81 commercial fishing trips by Uruguayan vessels from January 2004 to November 2011. For Japanese vessels, a total of 1114 sets and 2 589 465 hooks were observed in 26 trips in 2009–11. During these sets of observations, a total of 137 royal albatrosses were captured; 68 northern royal albatrosses (NRA), 46 southern royal albatrosses (SRA), and 23 undetermined. We also include data from 10 individuals (three NRA, five SRA and two undetermined) captured incidentally by a Uruguayan research vessel during three surveys (October 2010, July 2011 and July 2012) to assess large pelagic fishes on the shelf break off Uruguay, and 10 individuals (one SRA and nine undetermined) caught incidentally during three commercial fishing trips observed by PNOFA on Uruguayan vessels during May-June, July and September 2012.

Each albatross carcass was referenced and kept frozen in a labelled plastic bag for subsequent analysis in land. Most bycaught birds could be identified as northern or southern royal albatrosses in the laboratory by their plumage. Northern royal albatross has an entirely black upper wing, whereas southern royal has a black upper wing that becomes progressively whiter with age; this white plumage develops first at the leading edge and progresses backwards across the wing towards the trailing edge (Marchant & Higgins 1990, Nicholls et al. 2007, Onley & Scofield 2007). Some bycaught birds were in poor condition, with ruffled feathers or damaged plumage, and species could not be distinguished. The sex was determined directly, where possible, by examining the gonads, unless these were missing as a result of scavengers. Morphometric data were taken from 133 royal albatrosses, including 96, 17 and 20 birds of known species and sex, species only and sex only, respectively. Eighty four, 39 and 10 of these birds were measured by SJ, RF and MA, respectively. Each observer followed the same protocol and has extensive experience with hundreds of bycaught seabirds sampled. All were supervised initially by SJ, reducing the variability among observers. The remaining 24 birds, excluded from analyses, were released alive (2 NRA, 6 SRA and 4 undetermined), not landed (1 NRA and 10 undetermined) or not sampled (1 undetermined). A total of 19 measurements were taken: bill length (Culmen), basal bill depth (BBD), minimum bill depth (MBD), bill depth at unguis (BDU), basal bill width (BBW), basal bill width at commissures (BBWb), head length (HL), maximum head width (MHW), tarsus, middle toe with claw (MTCLAW), middle toe without claw (MTnoC), claw, total length (TL), wing length (WL) and wing cord (WC) from both right and left wings, tail length (Tail) and wing span (WS). Full definitions for all these measurements, and pictures (Fig. S1) of several of them, are shown in the Supplementary Material. Total length, tail length, wing length and cord and wing span were measured with metal rules to the nearest 1 mm. All other measurements were made with a Vernier caliper to the nearest 0.1 mm.

Comparison of mean values between species and sexes were conducted using one-way ANOVA or Student t-tests, after testing for normality (Kolmogorov–Smirnov test) and homogeneity of variance (Levene test). Otherwise, Kruskal-Wallis and Mann–Whitney test were used. Measurements with sample sizes ≤ 8 in one or both groups were not compared statistically. The percentage of dimorphism between sexes in each measurement was calculated as: [(X̅m − X̅f)/ X̅f] ×100, where X̅m and X̅f are mean values for males and females, respectively (Cuthbert et al. 2003). Discriminant function analysis (DFA; Phillips and Furness 1997, Cuthbert et al. 2003) was used to assign species and sex. Nine measurements were initially considered for all functions: Culmen, BBD, MBD, BDU, BBW, HL, MHW, Tarsus and MTNoCL. These were available for 98 birds of known species (58 NRA and 40 SRA), 88 of which were of known sex (females: 42 NRA and 23 SRA, males: 11 NRA and 12 SRA). Therefore, separate DFAs were used to assign species and sex. Eight measurements were excluded: BBWb had low repeatability; MTCLAW and claw were not always available, as the claw was often worn or broken, and MTCLAW was highly correlated with MTNoCL (see below); WL, WC and WS and LT and Tail, as P10 or central rectrices, respectively, were sometimes unreliable because feathers were very worn, broken, missing or re-growing, resulting in small sample sizes (particularly for males). However, some of these were included in the paired comparisons (see Results, Tables I-III). As the right wing of some birds was damaged, measurements from the left wing were used for WL and WC, to maximise sample sizes. Fourteen (12 SRA and 2 NRA) and 71 (21 SRA and 50 NRA) out of these 98 birds were assigned to first-year juveniles (no replacement primaries or rectrices) and immature-adults (moulting primaries or rectrices), respectively. The states of the gonads were noted in 30 of these latter birds, and 27 birds (6 SRA and 21 NRA) were assigned to old immature or adult (granular ovary or enlarged testes).

Backward stepwise DFA was used to establish which characters contribute the most to species and sex classification. In this analysis, characters that contribute least to species or sex discrimination are determined according to a threshold of F values (4.0; significance level of α = 0.05) and successively removed from the analysis until the least number of characters remains. Analyses included all birds for which all nine measurements were available. Each bird was reclassified by calculating the score for each of the two classification groups (e.g. SRA or NRA) and the associated probability, assuming an equal *a priori* probability of belonging to each group. Prior to each backward stepwise DFA, collinearity was investigated by examining variance inflation factors (VIF), and one variable was removed from each pair of highly correlated variables (≥0.9, following Zuur et al. 2007 for DFA). This only occurred in the analysis to assign species; Tarsus and MTOENOCL were highly correlated (0.91) and the latter was removed. The performance of each backward stepwise DFA was also compared with that of a DFA using a jackknifed classification. This classifies each individual using the coefficients derived from all the other birds, eliminating bias and providing a more rigorous estimate of the ability of the functions to separate groups (Phillips and Furness 1997, Thalmann et al. 2007). To separate species (because sample sizes were larger), a second backward DFA based on a random sample of 60 birds (training set) was also performed. The resulting discriminant function was then used to predict the species of the remaining 38 birds. In some cases an alternative DFA was constructed based on fewer measurements than those included in the backward stepwise DFA, particularly when a measurement is not commonly taken by observers, or is difficult to take consistently. However, in order to assign species and sex for the analysis of bycatch composition, those discriminant functions with a higher correct assignment rate were used. Deviations of the sex-ratio from 1 : 1 were tested using Chi square tests with Yates’ correction for continuity. All statistical analyses were conducted in R 2.13.1.

**Results**

Both southern and northern royal albatrosses showed sexual dimorphism, with males larger on average than females in all body measurements tested statistically, although there was always some overlap (Tables I and II). In both species, MBD and MDU, and then HL, showed a higher degree of dimorphism. Southern royal albatrosses were larger, on average, than northern royal albatrosses, but there was considerable overlap between species and sexes (Table III). Pairwise comparisons of mean values showed that male SRA were larger than female NRA in all measurements, but differences between female SRA and male NRA were not significant, with the exception of MBD, BDU and MHW (Table III). There were significant differences between species in mean values for most measurements in comparisons of birds of the same sex, except MBD and BBW (both sexes), BDU (females) and BBW2 (males) (Table III).

The backward stepwise DFA including all 98 birds (58 NRA and 40 SRA) with eight of the nine characters (MTnoC excluded because of collinearity), correctly assigned 95% of the birds to species using a combination of Culmen, BDU and Tarsus (DF1, Table IV). The five misclassified birds included a SRA of unknown sex and four NRAs (three males and one female). After the jackknifing procedure, 94% of birds were assigned correctly. In a backward stepwise DFA including a random sample of 60 birds (36 NRA and 24 SRA), again with eight of the nine characters, the same three characters were retained and 90% of birds were assigned correctly to species (88% after jackknifing). When this equation was applied to the remaining 38 birds (22 NRA and 16 SRA), 89.5 % of them were assigned correctly.

Because Culmen and Tarsus are frequently measured by observers, we constructed another backward stepwise DFA including the original 98 birds, but excluding BDU. The equation (DF2, Table IV) correctly assigned 92% of the birds. Eight NRA (seven males and one female) were misclassified as SRA. After the jackknifing classification, the correct species allocation was again 92%.

For SRA, the analysis including the nine characters measured in 35 sexed birds (23 females and 12 males) showed that a combination of the BDU and HL (DF3, Table IV) correctly assigned sex to 100% of individuals (100% again after the jackknifing classification). A similar analysis based on 53 sexed birds (42 females and 11 males) showed that a combination of BDU and MTnoC (DF4, Table IV) correctly assigned 98% of the birds (also 98% again after jackknifing). Because measuring MTnoC can be problematic (e.g. in living birds), we conducted another backward stepwise DFA based only on head measurements. A combination of three measurements (Culmen, BDU and HL; DF5, Table IV) correctly assigned 98% of the birds to sex (96% after jackknifing). The only misclassification in the first DFA was a male NRA classified as female, and *vice versa* in the other DFA.

By including results obtained with the DFAs, both species and sex were determined for 128 (54 SRA and 74 NRA) of the 133 royal albatrosses caught in the fishery under study. For the remaining five birds (3 NRA and 2 SRA) measurements for applying discriminant functions for sex determination were missing. Bycatch of both species was female-biased; however, the difference from a 1:1 ratio was highly statistically significant in NRA (χ2Yates = 20.55, d.f. = 1, p < 0.01, 57 females and 17 males), but not significant in SRA (χ2 Yates = 2.24, d.f. = 1, p > 0.05, 33 females and 21 males).

**Discussion**

Sexual size dimorphism in both southern and northern royal albatrosses was apparent in all body measurements. The measurements with higher size dimorphism (MBD, BDU and HL) follow the general patterns for the species of Procellariiformes with marked size differences among sexes, such as albatrosses and giant petrels (*Macronectes* spp.), where males often have noticeably bigger bills and heads (Warham 1996). Similar to other species of great albatrosses, such as wandering, Tristan (*Diomedea dabbenena*,Mathews; Cuthbert et al. 2003) and Antipodean (Gibson’s) albatross (*Diomedea antipodensis gibsoni*, Robertson & Warham; Walker & Elliott 1999)*,* and mollymawks (*Thalassarche* spp.; Hedd et al. 1998, Ryan et al. 1999, Gandini et al. 2009), measurements of the depth of the bill (MBD and BDU) of both royal albatross species showed higher dimorphism values. Cuthbert et al. (2003) also found high sexual size dimorphism in the total head length (from the bill tip to the occiput at the rear of the skull), but not culmen, in Tristan albatross, which is comparable to our results for the royal albatrosses.

Interspecific differences in the biogeography of albatrosses have been ascribed to aerodynamic features (Suryan et al. 2008); the hypothesis relating wing loading and wind patterns to sexual segregation (see Introduction) may also explain interspecific segregation at sea. Although there was considerable overlap between species and sexes, SRA was on average larger in body measurements than NRA. Although not measured in the present study, a lower wing loading is expected for NRA, in which case this species might be better adapted for exploiting the lighter winds of subtropical regions. This is supported by our findings, with higher numbers of NRA, particularly females (the smaller sex), bycaught in the northern part of the distribution of royal albatrosses. However, NRA has a considerably lower global population than SRA (ca. 5800 and 7800 annual breeding pairs, respectively; ACAP 2009a, b), and hence the inference that different bycatch rates relate to wing loading would need to be confirmed by analysis of habitat preferences and better data on densities of each species at sea during the non-breeding period.

Assessing the effect of fisheries on seabird populations requires bycaught birds to be identified to species, and provenance (except for endemics), sex and age to be determined (Alexander et al. 1997). An age bias towards young birds is less of a concern than if all bycatch were of adults. Sex- biased mortality in fisheries has reproductive costs beyond the immediate reduction of breeding population, because widowed individuals of the more abundant sex may have difficulties in securing a new partner. Therefore, the impact of the skewed sex ratio on fecundity (mean number of offspring produced per adult) is additive and may persist once bycatch ceases (Mills & Ryan, 2005). The present study provides a valuable tool for onboard scientific observers to separate species and sexes of bycaught royal albatrosses using combinations of two or three morphometric measurements (with accuracies ranging from 90 to 100%), two of which are standard (Culmen and Tarsus) and two are unusual but easy to take (BDU and HL). These discriminant functions were based on birds of a range of ages (see Methods), which can be considered broadly representative of the age structure in the southwest Atlantic; ring recoveries and tracking data indicate that first-year birds are more abundant off Chile, and immatures and adults in the southwest Atlantic (Nicholls et al. 2002, Moore & Bettany 2005, Thomas et al. 2010). Nevertheless, as our analyses included juveniles or younger immatures, which may not have completed growth in skeletal traits (Ryan 1999), it would be useful to confirm the wider application of these DFAs to identify species and sex of royal albatrosses outside the southwest Atlantic by applying them to birds measured at breeding sites. We have done this to some extent, but involving few individuals (see below).

Based on a small sample, Westerskov (1960) suggested that Tarsus may be useful for discriminating royal albatross species. We found overlap among species in this measurement, but it had the greatest standardised discriminant coefficient in both functions based on three (Culmen = 0.448, BDU = -0.484, Tarsus = 0.859) or two (Culmen = 0.372, Tarsus = 0.704) measurements. The power of our discriminant functions for species identification was lower for NRA, particularly males (see results). This is because of the high overlap in measurements of male NRA and female SRA (see Tables I-III). Misidentification in the opposite direction between these two groups may be expected. We applied our DFAs to discriminate species from Culmen and Tarsus (DF2, Table IV) to published data from 10 SRA (5 males and 5 females) from Campbell Island (Westerskov 1960), and sexed nine (90%) correctly. This performance is similar to that within our own sample, either by cross-validation or jackknifing (92%). In addition, two of the bycaught female NRA in our study were ringed (one from Middle Sister Island, Chathams and another from Taiaroa Head), and both were correctly assigned using our two DFAs for species, and the two DFAs for sexing NRA, respectively (Table IV).

Based on the complete dataset of birds identified and sexed by necropsy or discriminant analysis, we showed that both species have female-biased mortality (although not significant in SRA) in pelagic longline fisheries operating in the northern range of their distribution in South America. In subtropical regions, female-biased mortality in seabird bycatch is common, contrasting with male-biased mortality in subpolar regions, a pattern explained by differential at-sea distributions of the two sexes (Bugoni et al. 2011). Therefore, our results strongly suggest that non-breeding NRA and SRA segregate at sea, with females in more northern areas than males. These results have implications for conservation of these globally threatened species. Not only are females likely to be caught in greater numbers in pelagic longline fisheries in other regions, but males are potentially more susceptible to bycatch in fisheries operating in southern regions. However, little is known about the bycatch rates of either royal albatross species and the magnitude of their global bycatch is completely unknown. Both species have been captured incidentally in longline (Gales et al. 1998, Jiménez et al. 2014, this study) and trawl fisheries (Favero et al. 2011, Waugh et al. 2008). Usually few individuals are captured, with the exception of Australian waters in early 1990s (Gales et al. 1998) and recently in the southwest Atlantic (Jiménez et al. 2014), where the bycatch rates for both species in pelagic longline were very high. However, bycatch observer coverage of most fishing fleets is very poor (Phillips 2013). More data are required on fisheries bycatch throughout the at-sea ranges of these and other vulnerable species, and there is a pressing need to determine not only the species, but also the sex and, where possible, the age of captured individuals in order to improve our understanding of impacts of global fishing on their populations.

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**Author contribution**

SJ & RAP determined the basis for the paper, with contributions of AD, OD & AB. AD & SJ designed the sampling on fishing vessels and SJ, MA & RF undertook part of the field work and all the necropsies. SJ undertook the analyses and wrote the first draft with the contribution of RAP. All authors contributed to subsequent drafts.

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ZUUR, A.F., IENO, E.N., SMITH, G.M. 2007. *Analysing Ecological Data*. New York: Springer.**Table I.** Measurements (mean, S.D. and range, in mm) of female and male southern royal albatrosses, and sexual size dimorphism. BBD = basal bill depth; MBD = minimum bill depth; BDU = bill depth at ungis; BBW = basal bill width; BBWb = basal bill width at commissures; HL = head length; MHW = maximum head width; MTnoC = middle toe without claw; TL = total length; WL = wing length; WC = wing cord; Tail = tail length; WS = wing span.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Females | | | | |  | Males | | | | |  | % males larger | t-value | *P* |
|  | Mean | SD | Min. | Max. | n |  | Mean | SD | Min. | Max. | n |  |  |  |  |
| Culmen | 171.0 | 3.7 | 163.4 | 177.5 | 24 |  | 179.1 | 4.7 | 171.5 | 186.0 | 13 |  | 4.7 | -5.80 | < 0.001 |
| BBD | 62.6 | 1.7 | 59.9 | 66.5 | 25 |  | 66.3 | 2.6 | 61.8 | 70.1 | 13 |  | 5.9 | -5.27 | < 0.001 |
| MBD | 34.3 | 1.6 | 30.8 | 36.8 | 25 |  | 37.9 | 1.9 | 34.9 | 41.0 | 13 |  | 10.4 | -6.09 | < 0.001 |
| BDU | 39.4 | 1.2 | 36.7 | 41.4 | 24 |  | 43.6 | 1.4 | 41.2 | 46.2 | 13 |  | 10.6 | -9.51 | < 0.001 |
| BBW | 42.0 | 1.6 | 39.3 | 45.1 | 25 |  | 43.9 | 1.7 | 40.9 | 46.5 | 13 |  | 4.5 | -3.43 | 0.002 |
| BBWb | 55.6 | 2.0 | 52.1 | 58.5 | 24 |  | 59.1 | 4.1 | 53.0 | 64.2 | 13 |  | 6.2 | -3.49 | 0.001 |
| HL | 92.3 | 2.3 | 87.9 | 96.8 | 25 |  | 101.5 | 3.3 | 96.5 | 105.9 | 12 |  | 9.9 | -9.81 | < 0.001 |
| MHW | 79.7 | 1.9 | 76.3 | 82.8 | 25 |  | 85.4 | 2.1 | 82.7 | 88.6 | 13 |  | 7.0 | -8.24 | < 0.001 |
| Tarsus | 123.6 | 2.0 | 119.4 | 126.9 | 24 |  | 130.9 | 3.9 | 125.2 | 137.5 | 13 |  | 5.9 | -7.57 | < 0.001 |
| MTnoC | 146.3 | 3.5 | 137.9 | 152.0 | 25 |  | 156.2 | 3.9 | 151.5 | 164.3 | 13 |  | 6.8 | -8.03 | < 0.001 |
| TL | 1109 | 35 | 1029 | 1149 | 19 |  | 1176 | 35 | 1138 | 1235 | 10 |  | 6.1 | -4.88 | < 0.001 |
| WL | 649 | 15 | 618 | 674 | 14 |  | 674 | 18 | 639 | 696 | 7 |  | 3.9 |  |  |
| WC | 626 | 17 | 595 | 650 | 14 |  | 646 | 15 | 620 | 665 | 7 |  | 3.2 |  |  |
| Tail | 198 | 7 | 190 | 214 | 19 |  | 206 | 8 | 193 | 219 | 11 |  | 4.3 | -3.16 | 0.004 |
| WS | 2969 | 71 | 2855 | 3079 | 13 |  | 3119 | 80 | 3010 | 3220 | 7 |  | 5.0 |  |  |

**Table II.** Measurements (mean, S.D. and range, in mm) of females and males northern royal albatrosses, and sexual size dimorphism. For details of abbreviations see Table I.

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Females | | | | |  | Males | | | | |  | % males larger | t-value | *P* |
|  | Mean | SD | Min. | Max. | n |  | Mean | SD | Min. | Max. | n |  |  |  |  |
| Culmen | 160.4 | 4.7 | 151.4 | 173.7 | 44 |  | 168.9 | 4.0 | 163.2 | 176.7 | 11 |  | 5.3 | -5.56 | < 0.001 |
| BBD | 59.7 | 1.8 | 56.7 | 63.8 | 45 |  | 63.1 | 1.9 | 60.0 | 66.6 | 12 |  | 5.7 | -5.80 | < 0.001 |
| MBD | 34.1 | 1.3 | 31.1 | 37.0 | 45 |  | 36.8 | 2.0 | 33.2 | 40.2 | 12 |  | 8.0 | -5.72 | < 0.001 |
| BDU | 38.9 | 1.2 | 36.0 | 41.0 | 44 |  | 42.3 | 1.6 | 39.4 | 45.7 | 11 |  | 9.0 | -7.82 | < 0.001 |
| BBW | 40.8 | 1.5 | 37.7 | 44.1 | 45 |  | 42.8 | 1.1 | 41.2 | 45.0 | 12 |  | 4.9 | -4.24 | < 0.001 |
| BBWb | 52.9 | 2.2 | 48.6 | 58.5 | 44 |  | 56.4 | 2.6 | 50.7 | 59.9 | 12 |  | 6.6 | -4.65 | < 0.001 |
| HL | 87.6 | 2.8 | 82.2 | 100.6 | 45 |  | 93.9 | 3.5 | 88.9 | 103.6 | 13 |  | 7.1 | -6.76 | < 0.001 |
| MHW | 77.7 | 1.5 | 75.0 | 81.5 | 45 |  | 81.9 | 1.5 | 79.8 | 83.8 | 13 |  | 5.5 | -8.80 | < 0.001 |
| Tarsus | 115.4 | 2.5 | 110.3 | 121.0 | 44 |  | 121.6 | 1.8 | 119.2 | 126.3 | 13 |  | 5.4 | -8.22 | < 0.001 |
| MTnoC | 137.6 | 3.0 | 131.2 | 144.1 | 45 |  | 145.9 | 3.3 | 140.4 | 149.6 | 13 |  | 6.1 | -8.65 | < 0.001 |
| TL | 1057 | 43 | 957 | 1180 | 32 |  | 1116 | 13 | 1092 | 1134 | 8 |  | 5.6 |  |  |
| WL | 630 | 15 | 599 | 647 | 13 |  | 649 | 4 | 645 | 652 | 3 |  | 3.1 |  |  |
| WC | 604 | 15 | 576 | 620 | 11 |  | 628 | 8 | 620 | 635 | 3 |  | 4.1 |  |  |
| Tail | 190 | 6 | 180 | 202 | 27 |  | 200 | 9 | 190 | 217 | 9 |  | 5.1 | -3.58 | 0.001 |
| WS | 2874 | 86 | 2673 | 2971 | 11 |  | 3010 | 6 | 3005 | 3016 | 3 |  | 4.8 |  |  |

**Table III.** Comparison of body size between northern royal albatrosses (NRA) and southern royal albatrosses (SRA). For details of abbreviations see Table I. Significant values are highlighted in bold.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | ANOVA | | Between-species pairwise comparisons (*P*) | | | |
|  | F | *P* | Females vs Females | Males vs Males | Females SRA vs Males NRA | Males SRA vs Females NRA |
| Culmen | 74.83 | **< 0.001** | **< 0.001** | **< 0.001** | 0.488 | **< 0.001** |
| BBD | 45.14 | **< 0.001** | **< 0.001** | **< 0.001** | 0.828 | **< 0.001** |
| MBD | 26.58 | **< 0.001** | 0.977 | 0.180 | **< 0.001** | **< 0.001** |
| BDU | 57.65 | **< 0.001** | 0.583 | **0.027** | **< 0.001** | **< 0.001** |
| BBW | 16.89 | **< 0.001** | 0.793 | 0.129 | 0.425 | **< 0.001** |
| BBWb | 37.00\* | **< 0.001** | **< 0.001** | 0.182 | 0.196 | **< 0.001** |
| HL | 81.39 | **< 0.001** | **< 0.001** | **< 0.001** | 0.348 | **< 0.001** |
| MHW | 73.81 | **< 0.001** | **0.003** | **< 0.001** | **0.001** | **< 0.001** |
| Tarsus | 142.40 | **< 0.001** | **< 0.001** | **< 0.001** | 0.093 | **< 0.001** |
| MTnoC | 121.10 | **< 0.001** | **< 0.001** | **< 0.001** | 0.990 | **< 0.001** |
| TL | 28.15 | **< 0.001** | **0.004** |  |  | **< 0.001** |
| Tail | 15.10 | **< 0.001** | **0.034** | 0.097 | 0.856 | **< 0.001** |

\* Kruskal-Wallis test and Mann–Whitney post hoc comparisons were used.

**Table IV.** Discriminant functions for species and sex determination in southern and northern royal albatrosses. For species determination, scores >0 indicate SRA and <0 NRA. For sex determination, scores >0 indicate male and <0 female.

|  |
| --- |
| **Species determination** |
| D1 = - 31.385213 + (0.0830137 \* Culmen) + (-0.225838 \* BDU) + (0.218976 \* Tarsus) |
| D2 = - 33.361657 + (0.0689926 \* Culmen ) + (0.179565 \* Tarsus) |
|  |
| **Sex determination** |
| *Southern royal* |
| D3 = - 51.595711 + (0.611952 \* BDU) + (0.269481 \* HL) |
| *Northern royal* |
| D4 = - 55.805479 + (0.52554 \* BDU) + (0.242787 \*MTnoC) |
| D5 = - 53.541313 + (0.139945 \* Culmen) + (0.463007 \* BDU) + (0.128741 \* HL) |