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Taxonomy of the Kelp Gull *Larus dominicanus* Lichtenstein Revisited with Sex-Separated Analyses of Biometrics and Wing Tip Patterns

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Frédéric Jiguet, Peter Capainolo, and Alan Tennyson (2012) Taxonomy of the Kelp Gull *Larus dominicanus* Lichtenstein revisited with sex-separated analyses of biometrics and wing tip patterns. *Zoological Studies* **51**(6): 881-892. We investigated geographical phenotypic variations in the Kelp Gull *Larus dominicanus* Lichtenstein, 1823, by separately conducting analyses of biometrics and wing tip patterns in males and females. We attempted to investigate the separate taxonomic status of the recently described *L. d. judithae* and *L. d. melisandae*, define the geographical range of the Antarctic taxon *L. d. austrinus*, and look for variations among populations currently attributed to the nominate *L. d. dominicanus* in South America and New Zealand. Sex-separated analyses confirmed the discriminant structures and wing patterns of *L. d. judithae* (from Indian Ocean sub-Antarctic islands) and *L. d. melisandae* (from Madagascar). We failed to find differences among birds from Antarctica, South Georgia, and the Falklands Is., and suggest that the range of *L. d. austrinus* could extend from the Antarctic Peninsula to these sub-Antarctic islands. Populations sampled in southern Patagonia appeared close to *L. d. austrinus*, although they might also represent populations intermediate between *L. d. dominicanus* and *L. d. austrinus*. The subspecific status of *L. d. antipodus* from New Zealand populations was suggested by phenotypic characters, while a recently published molecular study of Kelp Gull populations suggests well-separated clades for birds breeding in New Zealand, Antarctica, and the Kerguelen Is., while the genetic separation of birds from South America (*L. d. dominicanus*) and Namibia (*L. d. vetula*) needs further study. We recommend further molecular studies of this widely distributed species before making further definitive taxonomic recommendations. http://zoolstud.sinica.edu.tw/Journals/51.6/881.pdf

Key words: Biometrics, Multivariate analyses, Subspecies, Wing pattern.

The range of the Kelp Gull *Larus dominicanus* Lichtenstein, 1823 extends throughout much of the southern hemisphere, with recent modern colonization in the northern hemisphere in Louisiana (USA), Senegal (Jiguet and Defos du Rau 2004), and Morocco (Bergier et al. 2009). The species breeds in South America (including the Falklands and South Georgia, and north to Ecuador on the west coast and to 26°S on the east coast in Brazil), Antarctica (and South Shetlands, South Orkneys, and South Sandwich Is.), the New Zealand region, Australia, southern Africa, southern Madagascar, and the sub-Antarctic Indian Ocean (Kerguelen, Crozet, Heard, Marion, and Prince Edward Is.) (Haase 1996, Higgins and Davies 1996). Early studies of geographical variations in this species did not show biometric differences among populations (Dwight 1925, Higgins and Davies 1996). However, the Kelp Gull was customarily divided into 2 subspecies (Brooke

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and Cooper 1979), with *L. d. vetula* (Bruch, 1853) breeding in South Africa and Namibia, recognized by its dark iris and dull bare parts in breeding adults (Brooke and Cooper 1979, Jiguet et al. 2001, Jiguet 2002), while the nominate form bred at all other locations. A study of geographical variations in biometrics and plumage patterns led Jiguet (2002) to propose recognizing 4 subspecies within the Kelp Gull complex: nominate *L. d. dominicanus* in South America and surrounding islands (including the Falklands and South Georgia), New Zealand (including the Chathams and New Zealand sub-Antarctic islands), and Australia; *L. d. vetula* in southern Africa; *L. d. judithae* Jiguet, 2002 in the southern Indian Ocean; and *L. d. melisandae* Jiguet, 2002, in Madagascar. Birds breeding on the Antarctic Peninsula were described under the name *L. d. austrinus* Fleming, 1924, while birds breeding in New Zealand and adjacent islands were described under the name *L. d. antipodus* G.R. Gray, 1844, but these were considered to be junior synonyms of *L. d. dominicanus* by Jiguet (2002).

Recently, Sternkopf (2011) produced a phylogenetic tree including individuals from various breeding populations to investigate the colonization history of the species. Based on sequences of 3 mitochondrial genes, this phylogeny, obtained with a Bayesian approach, included individuals sampled in Namibia (n = 20), Chile (20), Argentina (20 from Punta Tombo), Kerguelen islands (5), the Antarctic Peninsula (20), the Chatham Is. (5), and the New Zealand mainland (23 from Wellington). The combination of the 3 mitochondrial genes allowed Sternkopf (2011) to propose a well-resolved genetic structure for the mitochondrial (mt)DNA of these birds. Individuals of a similar geographical origin were generally grouped together (Fig. 1), with only a few exceptions. Figure 1 reproduces Sternkopf's tree, retaining only well-supported branches with posterior probability (PP) values of > 0.9. On this tree, Namibian birds partly mixed with Chilean birds (4 Namibian birds within the Chilean group) which are sister taxa to all others. The separation of the Argentine group from the Namibian-Chilean group was only weakly supported (with a PP of 0.82), so all of these could possibly form a single monophyletic group (i.e., African and South American birds; the nominate type locality is Brazil). There are clearly 2 distinct mtDNA lineages in South America, with the Argentinean lineage being more closely related to lineages found eastwards. All other individuals were included in a well-supported clade (with a PP of 1) which differentiated approximately 95,000 yr ago. Subsequently a Kerguelen clade separated (with a PP of 1), then an Antarctic clade (with a PP of 1), and then a Chatham Is. and New Zealand clade (with a PP of 1). According to this tree topology of mtDNA, *L. d. dominicanus* is paraphyletic, as Chilean gulls are more closely related to their Namibian counterparts than to Argentinean gulls, and *L. d. judithae* is currently recognized as a valid subspecies, even though it is one of the most phenotypically distinct subspecies (Jiguet 2002). If *L. d. judithae* is effectively a distinct subspecies, it would also be appropriate to recognize the Antarctic and New Zealand birds as 1 or 2 distinct subspecies, with available names being *L. d. austrinus* and *L. d. antipodus*, respectively. This would be reasonable if individuals from these populations also phenotypically differ from other populations.

In this paper, we investigated phenotypic variations in the Kelp Gull in greater detail, by separately analyzing males and females of various geographical origins, considering biometrics and wing tip patterns. Sex-separated analyses were motivated by the existence of a sexual size dimorphism in large gulls (Dwight 1925) as found in other bird species (Boulord et al. 2011). Compared to data used by Jiguet (2002), we obtained larger sample sizes of specimens by compiling data from 4 different museum collections. We attempted to reassess the taxonomic status of *L. d. judithae* and *L. d. melisandae*, and further investigate populations currently considered to belong to the nominate *L. d. dominicanus* of South America,

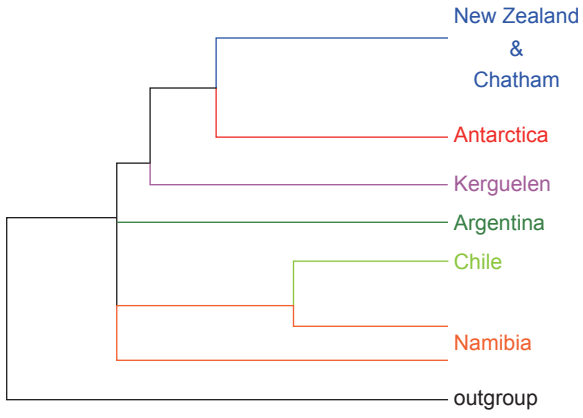

Fig. 1. Phylogenetic tree of the Kelp Gull *L. dominicanus* simplified from Sternkopf (2011) obtained with a Bayesian approach from sequences of 3 mitochondrial genes; only branches supported by bootstrap values of > 0.9 were retained. The outgroup includes European taxa of large white-headed gulls (Sternkopf 2011).

Antarctica, and New Zealand. We conclude by making taxonomic recommendations.

MATERIALS AND METHODS

Study material

Birds used in the analyses were specimens of adult Kelp Gulls held at the Muséum national d'Histoire naturelle, Paris, France (MNHN), the Natural History Museum, Tring, UK (BMNH), the American Museum of Natural History, New York, NY, USA (AMNH), and the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ). We considered only adult specimens of known sex (i.e., reported on the label attached to the specimen), and with all outer primaries fully grown, to allow recording of the full wing pattern. This analysis included 123 males and 120 females.

Biometrics and wing patterns

We measured the maximum wing chord, tarsus length, culmen length (from feathers to the tip), bill depth at the gonys, and bill depth at the base of the nostrils (to the nearest millimeter) on all specimens. We also recorded 2 wing plumage characters (Fig. 2), as in Jiguet (2002): (1) the number of white mirrors on the 2 longest primaries (primaries numbered ascendantly; recorded as 1 if present on P10 only; 1.5 if present on P10 and very restricted on P9; and 2 if obviously present on both P9 and P10); and (2) the number of white tongues between the black tip and sooty-black base on the median primaries from P5 outwards (ranging 1- -4). These data were taken by the different co-authors: Frédéric Jiguet at MNHN and BMNH, Peter Capainolo at AMNH, and Alan Tennyson at NMNZ. The 3 museums hold specimens of various studied populations, so that measurement differences between observers should not have strongly structured the dataset (Perktas and Gosler 2010).

Fig. 2. Wing of a Kelp Gull *L. d. judithae* showing the location of mirror on the outermost primaries and of tongues on the inner primaries.

Geographical variations

Multivariate statistics (principal component analysis (PCA), multiple analysis of variance (ANOVA), and discriminant analysis) of the biometric and wing plumage variables were used to look for geographical variations. Separate analyses were conducted for males and females, as gulls show an obvious sexual size-dimorphism (Dwight 1925). We performed parametric discriminant analyses and error rate estimates (EREs) in classification (Mathsoft 1999) to test how birds from geographically distinct origins could be discriminated. This technique provides an upper limit of error count estimates, and cross-validation is necessary. The cross-validation technique uses functions computed from all data except for the case being classified. Each observation is systematically dropped, the discriminant function is re-estimated, and the excluded observation is classified. All EREs presented in this study are based on posterior probabilities (see McLachlan 1992 and Mathsoft 1999 for more details). We performed various discriminant analyses by considering different groups of specimens.

Kelp Gulls in South America, Antarctica, and New Zealand

We first performed discriminant analyses for 103 males and 92 females by considering the following 8 groups of specimens, according to their collection locations: (1) eastern South America (23°- -34°S: northern Argentina and Brazil, which includes the type locality of the nominate *L. d. dominicanus*); (2) western South America (2°- 41°S: Ecuador, Peru, and northern and central Chile); (3) Patagonia (51°- -56°S: southern Argentina and southern Chile); (4) the Falkland Is. (52°S); (5) South Georgia (55°S); (6) Antarctica (64°- -65°S; (7) New Zealand (North and South Is.); and (8) New Zealand sub-Antarctic islands (Macquarie, Campbell, Antipodes, and including the temperate Chatham Is.). It should be noted that

there is a latitudinal gap of specimens available from South America, both on the west and east coasts: between 41°S and 51°S in western South America and between 34°S and 51°S in eastern South America. We began with a model using 8 groups, and then performed stepwise backward pooling of populations by regrouping the 2 groups that displayed the smallest differences in means, i.e., that had the lowest probability of differences in means (using Hotelling's T-squared test for differences in means between each group). We then re-ran the model with 7 groups. The process was repeated until no 2 populations significantly differed in means, using the probabilities given by the Hotelling's T-squared test corrected for multiple analyses of the same dataset (using Bonferroni's correction).

Second, we performed discriminant analyses for males and females to test the validity of the *L. d. austrinus* subspecies. In these analyses, we grouped birds according to the results obtained in the 1st analyses described above.

Third, specimens were grouped corresponding to the 4 subspecies (Jiguet 2002), plus Antarctic and New Zealand birds, which were sometimes recognized as *L. d. austrinus* and *L. d. antipodus*, respectively.

All statistical analyses were performed using the S-PLUS package (Mathsoft 1999). Statistical tests were considered significant at $p < 0.05$.

RESULTS

Male Kelp Gulls in South America, Antarctica, and New Zealand

The 1st model analyzed the 8 geographic groups (see "Materials and Methods"). The mean ERE for the 1st discriminant analysis was 41.9%. We pooled together the 2 groups with the smallest differences in means, to perform a stepwise backward pooling of populations. Hotelling's T-squared test for differences in means between each group indicated that the 1st pooling should be eastern and western South American specimens ($F_{7,89} = 0.79$, $p = 0.59$). The resulting discriminant analysis had a mean ERE of 39.2%. The 2nd step was to group Falklands and South Georgian specimens ($F_{7,90} = 1.12$, $p = 0.36$; with a resulting ERE of 32.9%). The 3rd step was to group specimens originating from mainland New Zealand (North and South Is.) and surrounding sub-Antarctic islands ($F_{7,91} = 1.16$, $p = 0.33$; with a resulting ERE of 30.0%). The 4th step was to group the Antarctic and Patagonian specimens ($F_{7,92} = 1.97$, $p = 0.07$; with a resulting ERE of 29.7%). The 5th step was to group the Falklands/South Georgian birds with the Antarctic/Patagonian specimens ($F_{7,93} = 2.48$, $p = 0.02$, not significant after Bonferroni's correction; with a resulting ERE of 21.4%). Results of this final model for males are presented in table 1. The multivariate ANOVA was highly significant for this final model (Wilk's lambda = 0.284, $F_{21,268} = 7.01$, $p < 0.001$). Hotelling's T-squared test for differences in means between each of the 3 groups was highly significant (New Zealand and northern South America: $F_{7,94} = 5.31$; New Zealand and southern South America/Antarctica: $F_{7,94} = 14.70$; northern South America and southern South America/Antarctica: $F_{7,94} = 9.49$; all $p < 0.001$).

A PCA was performed to test the geographical variation in the variables measured (with the 1st component explaining 88.8% of the variance, and the 2nd component explaining 9.5%), and the results are presented in figure 3.

Table 1. Results of a discriminant analysis performed on 103 adult male Kelp Gulls, using 5 biometric and 2 plumage characters. Classifications and posterior errors in classification are presented for each group, including top values from a plug-in classification table and bottom values from a cross-validation table. The mean posterior error was 0.214 (for both the plug-in and cross-validation tables)

Geographical origin	Northern South America	Southern South America/ Antarctica	New Zealand	Posterior error
Northern South America (east and west coasts)	13	3	7	0.408
	12	4	7	0.421
Southern South America/ Antarctica	2	38	4	0.136
	2	37	5	0.125
New Zealand	4	4	28	0.186
	5	5	26	0.192

Female Kelp Gulls in South America, Antarctica, and New Zealand

Again, we first analyzed the 8 groups according to geographical origins (see "Materials and Methods"). The mean ERE for the 1st discriminant analysis was 40.2%. We then pooled together the 2 groups as for males. Hotelling's T-squared test for differences in means between each group revealed that the 1st pooling should be specimens originating from mainland New Zealand (North and South Is.) and surrounding sub-Antarctic islands ($F_{7,78}$ = 0.59, p = 0.78). The resulting discriminant analysis had a mean ERE of 33.8%. The 2nd step was to group eastern and western South American specimens ($F_{7,79}$ = 0.66, p = 0.71; with a resulting ERE of 31.9%). The 3rd step was to group Falklands and Antarctic specimens ($F_{7,80}$ = 1.39, p = 0.22; with a resulting ERE of 30.2%). The 4th step was to group the 'Antarctic' group with South Georgian specimens ($F_{7,81}$ = 2.52, p = 0.02, not significant after Bonferroni's correction; with a resulting ERE of 29.6%). There was no reason to further pool the 'Antarctic' group with Patagonian specimens in the case of females, as the means

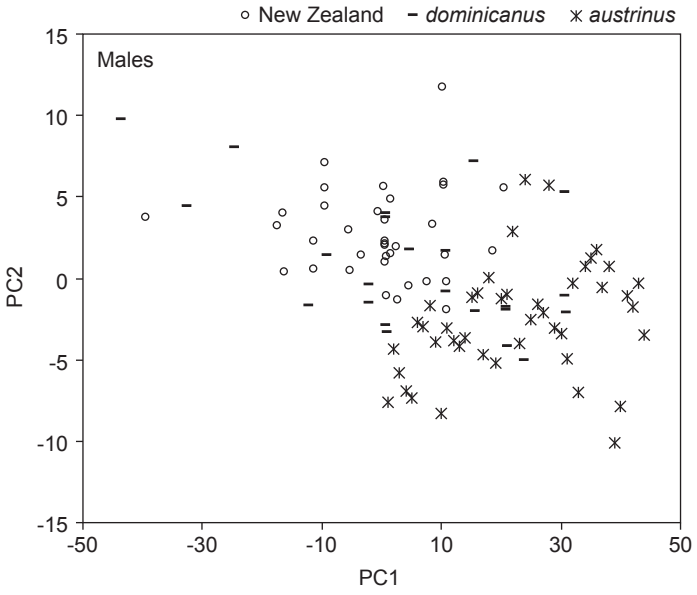

Fig. 3. Scatterplots of the 1st 2 principal components (PC1 and PC2) by pairs, resulting from a PC analysis performed on 103 adult male Kelp Gulls, using 5 biometric and 2 plumage characters, for birds originating from Antarctica to Patagonia, northern South America, and New Zealand.

Table 2. Results of a discriminant analysis performed on 92 adult female Kelp Gulls, using 5 biometric and 2 plumage characters. Classifications and posterior errors in classification are presented for each group, including top values from a plug-in classification table and bottom values from a cross-validation table. The mean posterior errors were 0.296 for the plug-in table and 0.310 for the cross-validation table

Geographical origin	Northern South America	Patagonia	South Georgia/ Falklands/ Antarctica	New Zealand	Posterior error
Northern South America	14	1	1	8	0.458
	12	1	3	8	0.452
Patagonia	0	8	1	2	0.211
	1	5	2	3	0.406
South Georgia/ Falklands/ Antarctica	0	3	13	3	0.371
	0	3	13	3	0.321
New Zealand	4	1	3	30	0.180
	5	1	3	29	0.188

of the 2 groups significantly differed ($F_{7,82}$ = 3.92, p < 0.001). Results of the final model for females are presented in table 2. The multivariate ANOVA was highly significant for the final model (Wilk's lambda = 0.270, $F_{21,236}$ = 6.50, p < 0.001). For the final model with 4 groups (Table 2), Hotelling's T-squared tests for differences in means between each of the 4 groups were highly significant (all p < 0.001, except for the Antarctic and Patagonian groups, $F_{7,82}$ = 3.92, p = 0.001).

A PCA was performed to investigate geographical variations in the variables measured (with the 1st component explaining 86.2% of the variance and the 2nd component 10.0%), and the results are shown in figure 4.

Validity of the subspecies *L. d. austrinus* sensu lato

Analyses of biometrics and wing patterns indicated that it was pertinent to pool birds originating from Antarctica (from where the subspecies *L. d. austrinus* was described), South Georgia, the Falklands, and Patagonia. We conducted discriminant analyses to test how this group (*L. d. austrinus* sensu lato), differed from the nominate *L. d. dominicanus* which originated from northern South America. The multivariate ANOVA was highly significant for the 2 models (males: Wilk's lambda = 0.479, $F_{7,59}$ = 9.16, p < 0.001; females: Wilk's lambda = 0.387, $F_{7,46}$ = 10.4, p < 0.001). Classification matrices resulting from these analyses are presented in table 3. Specimens of the group *L. d. austrinus* sensu lato were correctly classified with a posterior error rate of < 10%.

Validity of the subspecies *L. d. judithae* and *L. d. melisandae*

For this analysis, specimens were separated into 6 groups: South America (nominate *L. d. dominicanus*, 2°- -41°S in South America; 23 males and 24 females), Antarctica (*L. d. austrinus* sensu lato as defined in this study, i.e., 51°- -65°S in South America to Antarctica; 43 males and 30 females), Madagascar (*L. d. melisandae*; 4 males and 6 females), southern Africa (*L. d. vetula*; 6 males and 10 females), sub-Antarctic Indian Ocean islands (*L. d. judithae*; 12 males and 13 females), and New Zealand (35 males and 37 females). This was primarily done to test the robustness of the subspecific status of the subspecies *L. d. judithae* and *L. d. melisandae* using sex-separated analyses (cf. Jiguet 2002). The multivariate ANOVA was highly significant (males: Wilk's lambda = 0.109, $F_{35,469}$ = 9.30, p < 0.001; females: Wilk's lambda = 0.098, $F_{35,456}$ = 9.63, p < 0.001). Results of the discriminant analyses separately performed for males and females are presented in

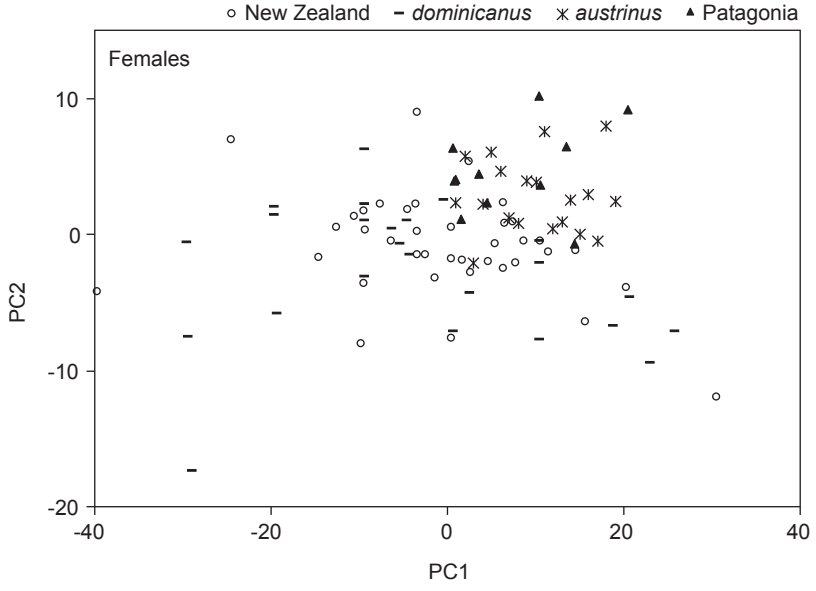

Fig. 4. Scatterplots of the 1st 2 principal components (PC1 and PC2) by pairs, resulting from a PC analysis performed on 92 adult female Kelp Gulls, using 5 biometric and 2 plumage characters, for birds originating from Antarctica to the Falklands, Patagonia, northern South America, and New Zealand.

tables 4 and 5, respectively. Using re-substitution and error count estimates, no individual from *L. d. judithae* and only 2 *L. d. melisandae* (1 male and 1 female of 10 specimens) were mis-classified. Cross-validation EREs gave the same results. The large majority of *L. d. austrinus* specimens were correctly classified (posterior error rates of 19% in males and 13% in females). All *L. d. vetula* females were mis-classified, and only 1 *L. d. vetula* male was correctly classified. Nominate birds and *L. d. antipodus* from New Zealand showed poor correct classification rates, with most errors being attributed to the New Zealand group.

DISCUSSION

Subspecies are allopatric non-discrete taxa defined as geographic segments of a species that differ from each other to a reasonably practical degree but with less than totality (e.g., at least 70% - -75%; Smith et al. 1997). Subspecies can interbreed and exhibit intergradations in contact zones, but maintain a practical level of distinction in 1 or more characters outside contact zones. Herein, we considered that populations merit a distinct subspecific taxonomic status if > 80% were correctly classified by the multivariate analyses. When interpreting an available molecular study

Table 3. Results of a discriminant analysis performed on 67 male and 54 female Kelp Gulls *L. dominicanus*, using 5 biometric and 2 plumage characters. Classifications and posterior errors in classification are presented for each group, including top values from a plug-in classification table and bottom values from a cross-validation table. The mean posterior errors were 0.114 for the plug-in table and 0.133 for the cross-validation table for males, and 0.131 for the plug-in table and 0.128 for the cross-validation table for females

Group	Sex	*L. d. austrinus* sensu lato	*L. d. dominicanus*	Posterior error
L. d. austrinus sensu lato	Males	42	2	0.070
		41	3	0.082
	Females	27	3	0.094
		26	4	0.094
L. d. dominicanus	Males	3	20	0.199
		4	19	0.230
	Females	4	20	0.178
		5	19	0.171

Table 4. Results of a discriminant analysis performed on 123 adult male Kelp Gulls *L. dominicanus*, using 5 biometric and 2 plumage characters. Classifications and posterior errors in classification are presented for each group, including top values from a plug-in classification table and bottom values from a cross-validation table. The mean posterior errors were 0.233 for the plug-in table and 0.247 for the cross-validation table

Subspecies	*L. d. antipodus*	*L. d. austrinus*	*L. d. dominicanus*	*L. d. judithae*	*L. d. melisandae*	*L. d. vetula*	Posterior error
L. d. antipodus	25	3	4	3	0	0	0.320
	21	5	5	3	1	0	0.424
L. d. austrinus sensu lato	2	37	2	1	0	1	0.148
	1	36	3	2	0	1	0.129
L. d. dominicanus	7	3	13	0	0	0	0.365
	7	4	12	0	0	0	0.364
L. d. judithae	0	0	0	12	0	0	-0.287
	0	0	0	12	0	0	-0.356
L. d. melisandae	0	0	1	0	3	0	0.308
	0	0	1	0	3	0	0.178
L. d. vetula	1	2	2	0	0	1	0.815
	1	2	2	0	0	1	0.862

based on mtDNA (Sternkopf 2011), we suggest that monophyletic groups should be considered as possible subspecies, even if the tree of haplotypes might not be the true tree of the population lineages. Studies of biometrics and plumage patterns using discriminant approaches have previously proven to be useful in segregating birds belonging to different subspecies (Bretagnolle et al. 2000, Jiguet 2002). Taxonomy and phylogeny of large white-headed gulls have received increased interest in recent research work, especially in attempts at understanding evolutionary processes that led to rapid speciation in this group (Chu 1998, Liebers et al. 2001 2004, Crochet et al. 2002, Pons et al. 2005, Sternkopf et al. 2010). Most published studies examined northern hemispheric taxa; the taxonomy of the Kelp Gull has received less attention. Crochet et al. (2002) and Liebers et al. (2004) confirmed that this taxon was a member of the group of large white-headed gulls, but geographical variations in phenotypic patterns of the Kelp Gull have only recently been studied over its wide breeding range (Jiguet 2002). Although sex-related size dimorphism is known in gulls (Dwight 1925), Jiguet (2002) based his conclusions on sex-mixed analyses. In this study, we performed sex-separated analyses to test the validity of the taxonomic treatment proposed by Jiguet (2002) and to further investigate geographical variations and taxonomic positions of populations breeding in South America and New Zealand, including some islands well isolated from continental coasts.

The nominate form *L. d. dominicanus* was described from the 'coast of Brazil'. By analyzing 5 biometric measures and 2 plumage characters, we failed to find differences between birds breeding on the eastern (Brazil, northern Argentina) and western coasts (from Ecuador to central Chile) of South America. The phenotypes of the birds of these 2 coasts are similar, so they could be considered the same subspecies. However, we noted that the tree presented by Sternkopf (2011) suggests that the Chilean birds are closer to *L. d. vetula*, while the Argentine birds of that study were sampled at Punta Tombo, 44°2'S, and thus were out of the latitudinal range covered by our specimens. Using the molecular results of Sternkopf and our phenotypic results, the taxonomic treatment of the African, and eastern and western South American birds could be 3-fold: (a) a single subspecies *L. d. dominicanus* breeding in southern Africa and southern America; (b) 2 subspecies: *L. d. dominicanus* breeding on the eastern South American coast, and *L. d. vetula* breeding in southern Africa and northern Chile; and (c) *L. d. vetula* breeding in southern Africa, *L. d. dominicanus* breeding from central Argentina to Brazil, and a 3rd subspecies breeding on the western coast of South America; the name *L. d. verreauxii* Bonaparte 1855 is available for Chilean birds (Jiguet 2002). Further results from nuclear genes, not only mitochondrial genes, are necessary before reaching a more-definitive conclusion. The African subspecies *L. d. vetula* was not well discriminated from the nominate *L. d. dominicanus* in our biometric study, as was the case in the sex-mixed analyses (Jiguet 2002).

Table 5. Results of a discriminant analysis performed on 120 adult female Kelp Gulls *L. dominicanus*, using 5 biometric and 2 plumage characters. Classifications and posterior errors in classification are presented for each group, including top values from a plug-in classification table and bottom values from a cross-validation table. The mean posterior errors were 0.284 for the plug-in table and 0.277 for the cross-validation table

Subspecies	*L. d. antipodus*	*L. d. austrinus*	*L. d. dominicanus*	*L. d. judithae*	*L. d. melisandae*	*L. d. vetula*	Posterior error
L. d. antipodus	20	5	5	5	0	2	0.409
	19	6	5	5	0	2	0.411
L. d. austrinus sensu lato	5	23	1	1	0	0	0.190
	5	22	2	1	0	0	0.190
L. d. dominicanus	6	5	10	0	1	2	0.448
	6	5	9	0	1	3	0.424
L. d. judithae	0	0	0	13	0	0	-0.426
	0	0	0	13	0	0	-0.437
L. d. melisandae	0	0	1	0	5	0	0.089
	0	0	1	0	5	0	0.097
L. d. vetula	6	1	1	0	0	2	0.743
	7	1	2	0	0	0	0.725

However, both taxa were very well discriminated using the bare part colors (dark iris, grayish green legs, and orange-yellow orbital ring in *L. d. vetula*; yellow to brown iris, yellowish to yellow legs, and red orbital ring in *L. d. dominicanus*; Jiguet et al. 2001) and are widely accepted (Brooke et al. 1982, Steele and Hockey 1990), so we propose to maintain recognition of *L. d. vetula* as a valid subspecies, based on distinctive colors of its bare parts. Bare part colors were not considered in the present study.

In 1924, Fleming attributed a subspecific status to Antarctic populations, but its validity was refuted by Dwight (1925), before Jiguet (2002) proposed that it be reconsidered. In the present work, populations from the Antarctic Peninsula, Antarctic islands, South Georgia, and the Falklands (and also from Patagonia for males only) were shown to be closely similar in biometrics and wing patterns. All populations breeding from Antarctica to the Falklands could be assigned to the subspecies *L. d. austrinus* from a phenotypic point of view, while the taxonomic affinities of birds breeding in Patagonia (Tierra del Fuego) are not yet clear, although the highest probability is that they are closest to those breeding on adjacent sub-Antarctic islands. It is possible that birds occurring in Patagonia are intermediate between *L. d. austrinus* and *L. d. dominicanus*, but previous work (Jiguet 2002) and this study failed to find any clinal latitudinal variations in general phenotypic patterns in South America. It should however be noted that we had no available specimens from 41°--51°S in South America, and that the 2 subspecies of *L. d. dominicanus* and *L. d. austrinus* might meet somewhere within this belt. Regardless, the validity of *L. d. austrinus* is supported by the level of discrimination we obtained for specimens collected in northern and central South America, and those from Patagonia to Antarctica, for both males and females. The 2 identified groups seem to be largely homogeneous and well discriminated from each other. Genetically, birds from the Antarctic Peninsula are well separated from South American birds, with birds from the Kerguelen islands (subspecies *L. d. judithae*) interposed. Pending further information on molecular phylogenetic relationships between all the Antarctic and sub-Antarctic populations, and as Kelp Gulls from Antarctica do not share a common mtDNA lineage with birds from South American islands and Patagonia, the evidence indicates that *L. d. austrinus* is a distinct subspecies occurring on the Antarctic Peninsula and nowhere else.

The taxonomic position of populations breeding in New Zealand needs clarification, but there is some evidence to support their recognition as a distinct subspecies. For example, New Zealand populations differ from other populations in that adult birds have either only 1 white mirror (on the outermost primary, P10) or 2 white mirrors (on the 2 outermost primaries, P10 and P9); note that adult New Zealand birds are known to switch from 1 pattern to the other during molting (Kinsky 1963). In South American populations of the nominate *L. d. dominicanus*, birds with 2 mirrors are very rare, while they represent about 30% of birds breeding in New Zealand (Kinsky 1963, Higgins and Davies 1996, Jiguet 2002). At the other extreme, individuals of populations breeding on sub-Antarctic islands in the southern Indian Ocean (subspecies *L. d. judithae*) always have 2 white mirrors (Jiguet 2002, this study). In this study, birds from New Zealand were well discriminated from the nominate *L. d. dominicanus* and *L. d. austrinus* (e.g., 80% correctly classified in the discriminant analyses), but the situation was less clear when considering all subspecies in a single analysis, especially because birds with 2 mirrors on the outer primaries were classified as *L. d. judithae*. An extra point worth mentioning is that different Kelp Gull populations have different species of parasitic chewing feather lice. *Quadraceps ornatus fuscolaminulatus* (Enderlein, 1908) is found on birds from Kerguelen, Macquarie, and Campbell islands, whereas *Q. punctatus sublingulatus* Timmermann, 1952 is found on birds from the North and South I. of New Zealand (R. Palma, pers. comm.). However, chewing feather lice of gulls from other populations and subspecies (especially the nominate) need to be investigated before drawing further conclusions from this criterion. The phylogenetic study provided by Sternkopf (2011) indicated that birds from New Zealand and the adjacent Chatham Is. form a well-separated and -defined clade; these birds were close to but genetically distinct from the Antarctic birds of the subspecies *L. d. austrinus*. If, as mtDNA suggests, *L. d. judithae* and *L. d. austrinus* are valid subspecies, then New Zealand birds must fall outside the nominate form *L. d. dominicanus*, in order to maintain its monophyly. New Zealand breeding populations should therefore be considered a separate subspecies, namely *L. d. antipodus*, while the potential subspecific status of some populations breeding on surrounding islands, like those on the Chathams, requires further investigation. This taxonomic treatment

is also supported by the correct classification of more than 80% of individuals from New Zealand in the discriminant analyses performed on birds from South America, Antarctica, and New Zealand.

Phenotypically, birds breeding in Madagascar (*L. d. melisandae*) and on sub-Antarctic islands in the southern Indian Ocean (*L. d. judithae*) were very well discriminated from other populations. We thus found similar results to Jiguet (2002), with additional support based on a separate analysis of males and females. This work therefore adds credibility to the validity of the 2 subspecies described for these populations (Jiguet 2002), with analyses of mtDNA confirming the monophyly of a Kerguelen (*L. d. judithae*) clade (Sternkopf 2011), while the possible molecular differentiation of *L. d. melisandae* still needs to be investigated.

Using the usual calibration of 2% sequence divergence per million years for the cytochrome-*b* gene (Shields and Helm-Bychowski 1988) as a crude approximation, haplotypes of European large-white headed gull taxa would have diverged between 10^6 and 170,000 yr ago (Crochet et al. 2002, Sternkopf 2011). Note that the species are likely to be even younger than that (Edwards 1997); the low level of genetic divergence suggests that species of the *L. fuscus* clade evolved comparatively recently, a fact that would account for the many controversial species limits in this group. Concerning the Kelp Gull, Sternkopf (2011; see fig. 3.28 therein) proposed that Namibian and Chilean haplotypes diverged 78,000 yr ago, Argentine and Chilean/Namibian haplotypes 144,000 yr ago, Kerguelen haplotypes 88,000 yr ago, and Antarctic and New Zealand haplotypes 67,000 yr ago. These long periods of range fragmentation support considering all clades identified here as potential phylogenetic subspecies, despite poor phenotypic differentiation between some well genetically separated populations which presumably reflect the recent divergence of their haplotypes. Unlike the rule in the northern hemisphere where there are numerous large white-headed taxa (Liebers et al. 2001, Crochet et al. 2002), the Kelp Gull is the only large white-headed gull that breeds in the southern hemisphere, and its broad range probably facilitated its subspeciation. However, further molecular results obtained from different mitochondrial or nuclear DNA are necessary to confirm the distinctiveness of these lineages (Zink 2004) and to reassess the sole available molecular-based phylogeny (Sternkopf 2011). Hopefully this would resolve some of the current mismatches between morphological and molecular data (Iamsuwansuk et al. 2012) and eventually discuss the subspecific or specific status of some of the Kelp Gull taxa (Mantelatto et al. 2011).

Table 6. Morphometrics and wing pattern of Kelp Gull *L. dominicanus* taxa: wing length, culmen length, bill height at the gonys, numbers of mirrors and tongues on the primaries, given as the mean (minimum-maximum recorded, if different from the mean). *L. d. austrinus* is here restricted to the Antarctic Peninsula

(a) Males/Subspecies	*n*	Wing length (mm)	Tarsus length (mm)	Culmen length (mm)	Gonys height (mm)	No. of mirrors	No. of tongues
L. d. dominicanus	23	416 (390-464)	64.6 (58.8-72.1)	53.9 (47.9-61.2)	20.6 (18.6-23.5)	1	2.6 (1-4)
L. d. vetula	6	422 (408-440)	64.1 (57.6-72.0)	53.8 (48.4-57.3)	22.1 (19.8-24.7)	1.1 (1-1.5)	2.5 (2-3)
L. d. austrinus	8	431 (380-446)	62.0 (58.4-64.1)	49.3 (46.0-51.9)	20.4 (19.3-22.5)	1	3.0 (2-4)
L. d. antipodus	35	421 (400-460)	67.7 (61.3-76.4)	53.3 (46.5-58.4)	21.4 (16.8-25.3)	1.2 (1-2)	2.3 (1-3)
L. d. judithae	12	406 (365-428)	62.8 (54.8-66.9)	47.8 (43.9-50.5)	21.5 (20.4-23.3)	2	2.5 (2-3)
L. d. melisandae	4	405 (96-420)	62.0 (58.0-70.0)	56.0 (53.8-57.7)	19.7 (19.2-20.2)	1	1.5 (1-3)

(b) Females/Subspecies	*n*	Wing length (mm)	Tarsus length (mm)	Culmen length (mm)	Gonys height (mm)	No. of mirrors	No. of tongues
L. d. dominicanus	24	396 (370-425)	63.2 (54.6-74.0)	49.9 (45.3-58.9)	19.2 (16.7-23.0)	1	2.7 (2-4)
L. d. vetula	10	405 (373-420)	62.5 (56.6-71.9)	50.9 (47.5-57.2)	20.2 (19.4-22.1)	1	2.3 (2-3)
L. d. austrinus	4	421 (410-429)	60.1 (55.1-64.0)	45.9 (43.7-47.3)	19.2 (18.6-19.8)	1	3
L. d. antipodus	37	399 (360-430)	61.8 (52.3-71.6)	48.3 (45.0-53.4)	19.6 (17.9-22.0)	1.2 (1-2)	2.3 (1.5-3)
L. d. judithae	13	385 (362-398)	58.3 (55.7-63.1)	44.3 (41.8-47.9)	19.2 (18.0-21.1)	2	2.6 (2-3)
L. d. melisandae	6	405 (380-420)	62.0 (58.3-69.7)	52.6 (49.6-55.0)	18.5 (17.4-19.5)	1	1.3 (1-3)

CONCLUSIONS

In conclusion, we propose first to recognize as subspecies those geographical populations for which genetic and phenotypic data are available and congruent: *L. d. judithae* Jiguet, 2002 (southern Indian Ocean), *L. d. austrinus* Fleming, 1924 (restricted to the Antarctic Peninsula), and *L. d. antipodus* G.R. Gray, 1844 (New Zealand). Second, we recognize the subspecific status of the Malagasy Kelp Gull because of its phenotypic differences, despite the lack of genetic information: *L. d. melisandae* Jiguet, 2002 (Madagascar). Third, we propose maintaining the taxonomic status quo for populations with poor phenotypic differentiation, as studied here, regardless of whether genetic data are available. Therefore, the current taxonomy should be maintained for *L. d. dominicanus* Lichtenstein, 1823 (Brazil) and *L. d. vetula* (Bruch, 1853) (Southern Africa). Morphological similarities may have resulted from convergence due to environmental constraints and do not necessarily indicate a common ancestry. We recommend waiting for further molecular phylogenetic studies of these gull populations, to reexamine the paraphyly of the current *L. d. dominicanus-vetula* group, before reassessing their taxonomic treatment. Table 6 proposes information on biometrics and wing patterns of the different subspecies as recognized here.

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