GEOGRAPHIC VARIATION IN MORPHOLOGY AND ALLOZYMES OF SOUTH AMERICAN IMPERIAL SHAGS

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ABSTRACT.—To evaluate the hypothesis that Pleistocene glaciations in southern South America effected differentiation in the Imperial Shag (*Phalacrocorax atriceps*), I analyzed geographic variation in plumage, skeletal size and proportions, and allozymes in populations from seven South American localities. Alar bar size, crest length, and the size of the white dorsal patch vary geographically among juveniles but not adults, and the alar bar and white dorsal patch are both present all year in adults. Geographic variation in osteology is marked, with males showing more interpopulational differentiation than females. Coastal populations follow Bergmann's rule, while freshwater Fuegian lake shags are smaller than coastal populations even though the geographically nearest coastal population is the largest one in body size. Shags from the lowest latitude, in central Chile, have relatively long culmens, conforming to Allen's rule. All populations except that from Chubut Province are very similar in allozyme frequencies, and the very low genetic distances between populations are noncongruent with the greater degree of morphological differentiation, particularly between lake and coastal populations. The genetically differentiated Chubut population was probably somewhat isolated on the Patagonian Massif, a circumstance unrelated to Pleistocene glaciations. Chilean shags were probably not long reduced during glaciations to a small isolate, because they can form colonies on unglaciated headlands; they are only slightly differentiated from Atlantic populations. The treatment of the Falkland Islands population as a distinct subspecies is supported by plumage characters. The freshwater Fuegian shags must have differentiated since glacial recession. The populations from the southern Atlantic coast and coastal Tierra del Fuego, which were probably contiguous throughout the Pleistocene, differ from each other only clinally in size. Unlike the cases of other Fuego-Patagonian species studied, Pleistocene vicariance events appear to have had little influence on the evolutionary history of the Imperial Shag. This is probably related to life-history traits of this species such as coloniality, vagility, longevity, trophic generalism, and cold tolerance. *Received 17 November 1992, accepted 12 May 1993.*

SPECIATION DUE TO Pleistocene glacial vicariance events is widely accepted as a plausible mechanism promoting speciation for many birds (Mengel 1964, Moreau 1966, Bermingham et al. 1992). However, in Patagonia, Pleistocene glaciations apparently pushed forests north in Chile into a small refugium, and east of the Andes into what is now the steppe region of Argentina; no avian speciation is hypothesized to have resulted from these changes in distribution of the forest (Vuilleumier 1985). Although coastal Patagonian birds occupy a linear habitat unlike that of forest birds, presumably at the height of major glaciations their habitat similarly receded along the Pacific coast to a refuge on northern Chiloé Island and possibly farther north (Fig.

1; Devillers and Terschuren 1978). On the Atlantic side of Patagonia, the ranges of marine littoral birds must have repeatedly changed with sea level rise and fall because of the relatively gradual slope of the continental shelf, but more habitat would probably have been available there during glacial maxima than at present. Pleistocene glaciations thus would have isolated Pacific and Atlantic populations of marine littoral birds, increasing the opportunity for differentiation between the resultant isolates (Devillers and Terschuren 1978, Humphrey and Péfaur 1979, Livezey 1986, Rasmussen 1987, Corbin et al. 1988). Among avian marine littoral taxa whose current distributions make them amenable to testing evolutionary hypotheses on the effects of Pleistocene glaciation in Patagonia, the steamer-ducks (*Tachyeres*; Livezey 1986) and the Rock Shag (*Phalacrocorax magellanicus*; Rasmussen 1987) exhibit patterns of geographic variation that are best explained as having re-

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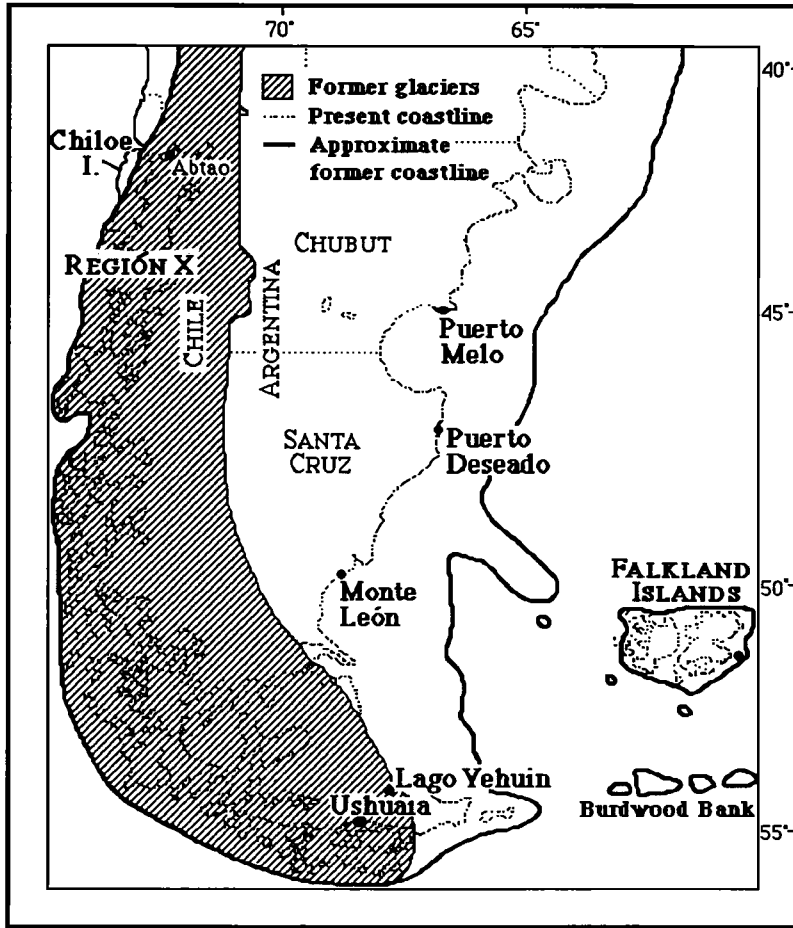
Fig. 1. Principal collection localities (signified by black dots) for specimens used in study superimposed on a map showing presumed maximum extent of glaciers and coastline during height of last glaciation (ca. 30,000 ybp; modified from Devillers and Terschuren 1978).

sulted from isolation of populations during glacial events, while the origin and present distribution of the two morphs of the Imperial Shag (*P. atriceps*) cannot be explained on that basis (Rasmussen 1991). This however does not preclude the possibility that other aspects of within-species evolution in the Imperial Shag were influenced significantly by the Pleistocene glaciations of southern South America.

To address the question of whether Pleistocene vicariance events effected differentiation in the Imperial Shag, I analyzed patterns of geographic variation in plumage (first separating out age and temporal variation), skeletal size and shape, and allozymes for seven populations from southern South America. If prolonged isolation due to vicariance has been an important

factor, one would predict stronger differentiation of the Pacific isolate from the Atlantic populations than that found among the Atlantic populations. Although the relationships between the two morphs of the Imperial Shag have been examined in detail (e.g. Behn et al. 1955, Devillers and Terschuren 1978, Siegel-Causey 1986, Rasmussen 1991), very little is known of geographic variation in the species within southern South America; presently all continental shags, both of the white-cheeked "*atriceps*" and the black-cheeked "*albiventer*" morphs, are treated as *P. atriceps atriceps*, and the monomorphic black-cheeked Falkland Island population as *P. atriceps albiventer* (Devillers and Terschuren 1978). Several closely related forms that are often considered specifically

distinct (del Hoyo et al. 1992) occur on island groups in much of the subantarctic and the Antarctic Peninsula. Previous studies of geographic variation in South American Imperial Shags utilized only external characters, which are highly variable interpopulationally, individually, seasonally, and among age classes (Bernstein and Maxson 1981). In considering the extent to which patterns of geographic variation within the species may have resulted from Pleistocene glaciations, I examined life-history traits of the Imperial Shag that could have influenced its evolutionary reaction to such events. The north-south orientation of the localities provided the opportunity to examine the data for adherence to the relevant ecogeographic rules (Zink and Remsen 1986)—Bergmann's rule, which predicts the correlation of intraspecific increase in body size with higher latitudes; and Allen's rule, which predicts that populations of a species will have shorter extremities at higher latitudes.

METHODS

Most specimens used in plumage, multivariate morphometric, and electrophoretic analyses were collected between 1979 and 1987 at seven localities (Fig. 1). Additional skin specimens were borrowed from or examined at museums listed in Acknowledgments.

Plumage analysis.—Plumage characters were evaluated for 144 specimens and 48 sight records (40 males, 65 females, 87 sex unknown) primarily from the seven major localities, but some were from additional, nearby localities. "King" and "Blue-eyed" morphs were combined at each locality of co-occurrence for analysis of plumage characters; no "King Shags" had the white dorsal patch. For analysis of plumages, birds that lacked juvenal feathers were classed as adults (*n* = 94); those that had not yet commenced the first prebasic body molt were considered juveniles (*n* = 75); and those in first prebasic body molt were classed as subadults (*n* = 23) and were not used in further analyses because they combined juvenal and adult plumage characters. The length of the white alar bar of one wing of each adult Blue-eyed Shag was measured in millimeters using dividers. Because alar bars of juveniles are generally ill-defined, they were not measured but instead were subjectively categorized as follows: (1) none; (2) slight (narrow and barely perceptible); (3) moderate (average width); or (4) large (wide). The length of alar bar when present in juveniles exhibited little variation and was not characterized. Wild juveniles in Chile were examined with a 40× spotting scope from about 50 m for determination of the alar-bar category. Size of dorsal patch was measured for adults (dorsal patch area = length

× width). In juveniles, an indication of the dorsal patch was often present, but it was never clearly demarcated from the surrounding feathers. Length of taut crest was measured from its base with dividers.

Skeletal specimens.—Thirty-five osteological measurements from 212 skeletal specimens obtained at seven localities (Fig. 1) were analyzed in this study (*n* for each locality and sex given in Appendix). For most statistical comparisons, the small sample from the Falkland Islands was excluded. Within 3 h of collection, masses of shag specimens were taken to the nearest 50 g with a Pesola scale, and muscle/skeleton masses were taken after removal of skin and viscera. Lengths of culmen, tarsus, tail, and wing (arc) were measured to the nearest millimeter. Specimens were sexed by inspection of gonads.

Tissue samples.—Between 1984 and 1987, tissue samples (liver, heart muscle, and pectoral muscle) were collected from each specimen (except for 10 specimens from Puerto Melo, and 20 of 46 specimens from Puerto Deseado, for which only liver was sampled): Región X, 20; Monte León, 26; Falkland Islands, 3; Lago Yehuin, 15; Ushuaia, 26. Tissues were preserved in liquid nitrogen 1 to 3 h after collection and, thereafter, were stored at −73°C. Starch-gel electrophoresis followed standard methods. Loci were considered monomorphic if they were not polymorphic in assays of at least 22 specimens, a minimum of two from each locality. Monomorphic loci were: ACON-M; ADH; ADK; AKP; ALD-1, -2; EAP; F-1,6-DP; FUM-1, -2; GDH; GOT-M; αGPDH-1, -2; GPI; ICD-1, -2; LAP-1; LDH-1, -2; MDH-1, -2; MPI; NP; PGM-1; PK-1; SDH-A; SOD-A, -B. All polymorphic loci were examined for all 146 individuals, and accuracy of scoring was double checked with repeated runs. In cases where adventitious banding was suspected, another slice of the same gel was counterstained for verification.

Statistical analyses.—Skeletal measures used in all multivariate analyses are listed in the Appendix. Based on previous analyses that showed that the two morphs did not differ (Rasmussen 1991), "King" and "Blue-eyed" shags were pooled at each locality of co-occurrence for statistical analyses. Untransformed data are given in tables of means, and for multivariate analyses data were natural log-transformed. Geographic variation in skeletal characters was examined using principal-components analysis (PCA) and two-way analyses of variance (ANOVAs) of the resultant scores, and discriminant-function analyses (DFAs). Variance-covariance matrices were used in PCA, and tests were done for absence of correlation among variables, significance of eigenvalues, and presence of regions of sphericity. For multivariate analyses, up to 10% of the total values for each incomplete specimen were estimated using the BMDP missing-data program (Dixon 1985). For each DFA, canonical-variate scores were standardized by multiplication of the scores by the pooled within-groups standard deviations. The Monte León population was excluded from
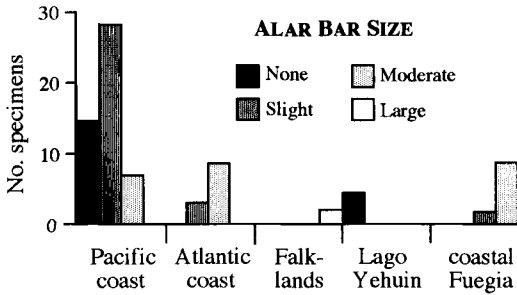
Fig. 2. Geographic variation in prominence of alar bar size in juvenile Imperial Shags. Darker bars indicate less developed alar-bar categories.

DFAs because some specimens were juveniles. For analysis of clinal variation, the Lago Yehuin sample was excluded. When originally unsexed specimens could be unequivocally sexed using DFA (Rasmussen 1991), they were included in further analyses. Computer statistical analyses used are part of the BMDP package (Dixon 1985).

Allozyme analyses.—Nomenclature of individual loci for proteins with multiple loci followed Harris and Hopkinson (1976); where homology was uncertain the most anodally migrating locus was denoted 1, the next 2, etc. Within a locus, the most anodally migrating allele was designated the a allele, the next b, etc. Observed and calculated heterozygosities, percent polymorphic loci, Nei's (1978) modified genetic distance, Rogers' (1972) genetic distance, and Wright's (1978) F-statistics were obtained using BIOSYS-1 (Swofford and Selander 1989). Gene flow among populations was qualitatively estimated using Slatkin's (1981) graphic method.

RESULTS

Geographic and temporal variation in plumage.— Presence and degree of development of the alar bar is geographically variable among populations in juvenile Imperial Shags (Fig. 2), but in adults, length does not vary seasonally or geographically (Figs. 3A and 4A). Only 1 of 88 adult specimens examined entirely lacked an alar bar. At any season, virtually all adults have a measureable crest (Fig. 3B), while juveniles normally do not, except for the two from the Falklands (Fig. 4B). The white dorsal patch is absent in juvenile Imperial Shags from Puerto Deseado and Monte León ($n = 27$), and in one juvenile from Cape Horn. In juvenile Imperial Shags from Chile ($n = 5$), three lack any trace of a dorsal patch, one has the area slightly paler than the surrounding feathers, and one has a small
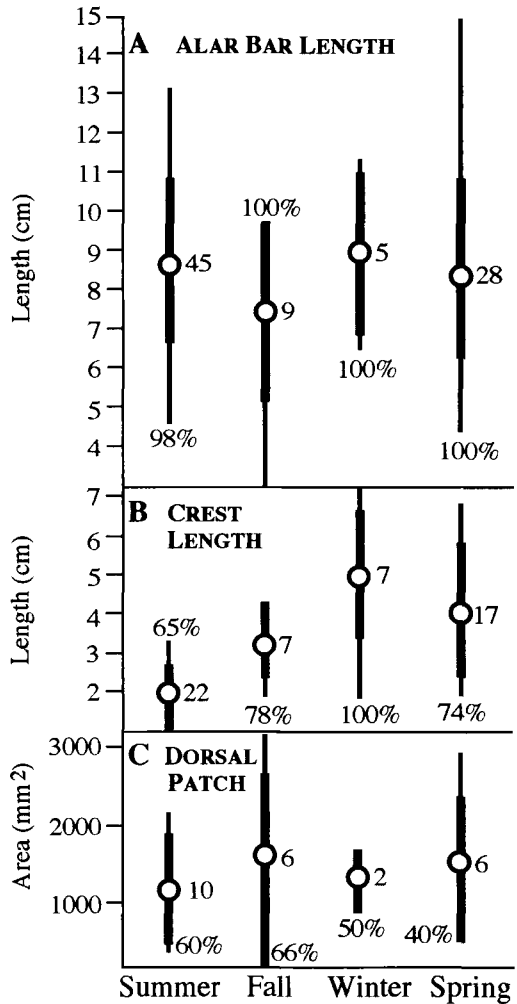

Fig. 3. Temporal variation in plumage among adult Imperial Shags (austral summer = December–February; fall = March–May; winter = June–August; spring = September–November). For each season, circle denotes mean length, heavy bar is standard deviation, thin bar is range, number beside mean is n with feature, and percent figure is percent of specimens examined with feature. (A) Length of alar bar; (B) length of crest; (C) dorsal patch size.

measureable dorsal patch. In juveniles, the dorsal patch is not sharply demarcated from the surrounding feathers as it is in adults. The dorsal patch is present in about one-half of the adult "Blue-eyed Shags" and occurs in similar proportions during each season (Fig. 3C); however, it is unclear if individuals lose the patch seasonally. No "King Shags" examined had a dorsal patch.
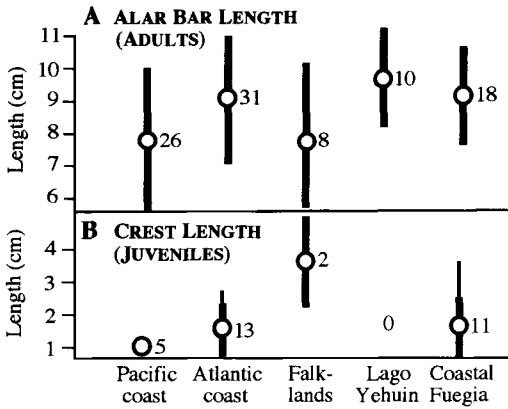
Fig. 4. Geographic variation among Imperial Shags in: (A) length of alar bar in adults; and (B) crest length in juveniles. Conventions as in Figure 3.

Geographic variation in skeletal size and shape.— The sexes are significantly different in all osteological measures except ischial terminus width (Appendix). Interaction effects are significant in only five measures, indicating that the degree of sexual dimorphism is similar in Imperial Shags throughout southern South America. Means of all external measurements differ highly significantly among localities for both sexes (Appendix). In general, males from Lago Yehuin are the smallest among males in each measurement, while males from Ushuaia are the largest. Males from Región X, at the lowest latitude, have external culmen lengths significantly longer than males from Puerto Melo, Lago Yehuin (both $P < 0.01$; approximate test of equality of means; Sokal and Rohlf 1981: 409–410), and Puerto Deseado ($P < 0.05$), and their skeletal culmen lengths are significantly longer than those from Puerto Melo, Monte León, and Lago Yehuin (all $P < 0.01$), as well as Puerto Deseado ($P < 0.05$). Culmen length of the larger-bodied Ushuaia males, from the highest latitude, does not differ from that of Región X males ($P > 0.05$). Females from Región X have the external culmen longer than those from Lago Yehuin ($P < 0.01$) and shorter than those from Ushuaia ($P < 0.05$); skeletal culmen length for Región X females is longer than those from Puerto Melo and Monte León ($P < 0.01$). Females from Lago Yehuin are generally smaller than any other population, except in cranial width.

Length of the nasal gland impression shows a latitudinally clinal trend among coastal pop-
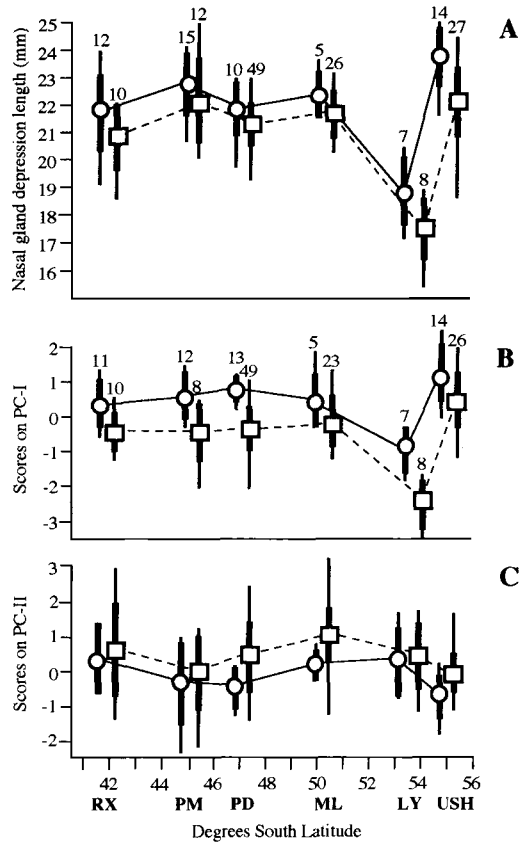

Fig. 5. Latitudinal variation in Imperial Shags for each sex: (A) nasal gland impression length; (B) PC-I scores; and (C) PC-II scores (RX = Región X, PM = Puerto Melo, PD = Puerto Deseado, ML = Monte León, LY = Lago Yehuin, USH = Ushuaia). Means shown as circles for males, squares for females; heavy bars are standard deviations; thin bars ranges; *n* for each locality-sex group given above range bar (*n* for PC-II is same as for PC-I).

ulations in both sexes (Fig. 5A; Spearman rank correlation of five populations: males, $r = 0.828$, $P < 0.05$; females, $r = 0.828$, $P < 0.05$); the Lago Yehuin population differs dramatically from coastal populations in this feature.

In a PCA of both sexes of Imperial Shags at six continental localities (sexes were analyzed together but graphed separately for ease of interpretation), 75% of the variance is explained by the first three components (Table 1). Principal component I (PC-I) is a strong size axis, on which all variables are large and positive except ischial terminus width, the only variable that does not differ between the sexes and, thus, is proportionately larger in females than in

males (Appendix). PC-II is a contrast between general size and lacrimal width, with interorbital width and lacrimal height being uncorrelated. Both of these uncorrelated variables differ greatly among populations, especially between Lago Yehuin and other populations. PC-III is a contrast axis of five cranial variables against culmen length and most postcranial variables.

Males from Ushuaia generally have large positive scores on PC-I (Fig. 5B), reflecting their large body size; they are larger than males from Región X, Chile (GT2-method, difference between means = 0.86, $P < 0.05$; Sokal and Rohlf 1981:248–250) and Lago Yehuin (difference between means = 2.26, $P < 0.05$), but do not differ from other groups ($P > 0.05$). All males from Ushuaia have negative scores on PC-II, due primarily to their large lacrimal widths. Males from Lago Yehuin all have negative scores on PC-I, showing their small body size; their mean component scores are significantly smaller than for males of all other groups (all $P < 0.05$). Males from Lago Yehuin have positive or low negative scores on PC-II, reflecting their narrow lacrimals. Males from Puerto Melo, Puerto Deseado, Monte León, and Región X tend to be intermediate both in body size and lacrimal width and their PC-I scores do not differ significantly at $P > 0.05$.

Females from Ushuaia generally have the highest PC-I scores for their sex and are significantly larger than all other groups (all $P < 0.05$). Females from Lago Yehuin have the lowest PC-I scores and do not overlap with other groups; they are significantly smaller than all other populations (all $P < 0.05$). Females from Región X and the three Atlantic coastal localities are intermediate in size and their PC-I scores do not differ ($P \leq 0.05$).

When the freshwater Lago Yehuin population is excluded, PC-I scores are significantly correlated with latitude for both sexes among coastal populations (Fig. 5B; males, $n = 55$, $b = 0.060$, $r = 0.416$, $P < 0.01$; females, $n = 116$, $b = 0.083$, $r = 0.436$, $P < 0.01$). Both sexes from Lago Yehuin have much lower PC-I scores than do the respective sexes of coastal populations. PC-II is not correlated with latitude for either sex ($P > 0.05$), and means of the Lago Yehuin population do not differ from those of other populations in this component (Fig. 5C).

In a canonical analysis of males from five continental localities (Monte León excluded), the total jackknifed percent correctly identified was 90.2%, much higher than the 20% expected if assignment was random. The most useful variables for discriminating the populations on canonical variable I (CV-I) are cranial height contrasted against interorbital width and ulna length (Table 1). CV-II of males is a contrast between lengths of frontal, ulna, and femur against humerus length. Among males from Ushuaia, 92.9% were correctly identified. Males from Puerto Melo and Puerto Deseado are not well discriminated from each other, and the 95% confidence limits for the means of the two groups overlap (Fig. 6A). Among males from Puerto Melo, 73.3% were identified correctly, as were 92.3% from Puerto Deseado, 100% from Región X, and 100% from Lago Yehuin.

In an equivalent canonical analysis of females from the same localities, the total correctly identified was 73.6% (Table 1). CV-I of females appears to be a contrast between culmen length and tibiotarsus length; CV-II is a contrast between ulna and tibiotarsus length. For females from Región X, Puerto Melo, and Puerto Deseado, the 95% confidence limits for the mean scores overlap each other (Fig. 6B). Región X females were identified correctly (jackknifed) in 80.0% of the cases, those from Puerto Melo in 66.7%, from Puerto Deseado in 69.4%, and from Ushuaia in 77.8%. Females from Lago Yehuin ($n = 8$) cluster separately from all other groups and 87.5% were correctly identified.

In all except one of the comparisons (Región X vs. Lago Yehuin), the Mahalanobis' D between males of each population exceeds that for females (Table 2). Mahalanobis' Ds between Lago Yehuin and each coastal population are generally much larger than among coastal populations.

Geographic variation in allozymes.—Only 9 (24%) of the 38 presumptive genetic loci I examined were variable (Table 3). Alleles fixed in one population are all present in at least one other population. In the three cases in which an allele is found in only one population, that allele is found in low frequencies (≤ 0.05). Over all populations, the mean calculated heterozygosity is 2.1% and mean observed heterozygosity is 2.2% (Table 4). Heterozygosity values for the seven populations of Imperial Shags ($H = 1.4$–2.9%) are relatively low even for birds ($\bar{H}_c = 6.5\%$, $n = 79$ species; $\bar{H}_o = 4.4\%$, $n = 86$, range 0–17.5%; Evans 1987). Alleles of EST-1 and PEP-E tend to occur in proportions contrary to Hardy-

TABLE 1. Component loadings for variables on components I–III from PCA, and standardized coefficients for canonical variables I–III from canonical analyses.

| Variable | Component loadings | | | Standardized coefficients | | | | | |
	I	II	III	Males[a] I	Males[a] II	Males[a] III	Females[b] I	Females[b] II	Females[b] III
Cranial w	0.623	0.382	0.043	—	—	—	0.37	0.00	-0.26
Cranial h	0.618	0.183	0.159	-0.90	0.15	0.33	—	—	—
Interorbital w	0.793	0.044	0.499	1.00	0.49	-0.48	0.40	0.24	0.47
Frontal l	0.649	0.244	0.007	-0.24	-1.00	-0.30	0.05	-0.52	-0.15
Rear skull l	0.825	0.289	-0.018	0.53	-0.33	0.33	—	—	—
Lacrimal h	0.668	0.100	0.274	—	—	—	—	—	—
Lacrimal w	0.757	-0.648	-0.077	—	—	—	0.47	0.20	0.10
Culmen l	0.677	0.218	-0.272	-0.31	-0.33	-0.94	0.59	-0.16	-0.94
Culmen w	0.686	0.158	0.158	—	—	—	0.31	0.43	-0.03
Culmen h	0.736	0.228	0.383	—	—	—	0.38	0.51	0.02
Quadrate l	0.778	0.337	-0.096	0.18	0.35	-0.51	—	—	—
Sternal w	0.737	0.306	-0.157	0.37	-0.31	-0.42	—	—	—
Interacetabular w	0.586	0.309	0.043	—	—	—	0.31	-0.32	0.34
Sacral l	0.731	0.363	-0.164	-0.64	-0.49	0.42	—	—	—
Preacetabular iliac wing	0.685	0.238	-0.032	0.50	0.19	0.31	—	—	—
Antitrochanter w	0.746	0.387	-0.153	-0.34	0.41	0.59	0.13	-0.27	0.25
Ischial terminus w	0.279	0.183	-0.193	-0.38	-0.40	0.35	—	—	—
Furculum l	0.834	0.348	-0.137	—	—	—	0.32	-0.17	0.48
Scapula l	0.751	0.383	-0.124	0.57	-0.01	0.61	—	—	—
Coracoid l	0.808	0.350	-0.247	0.44	0.01	0.32	—	—	—
Coracoid articular l	0.716	0.204	-0.130	—	—	—	—	—	—
Humerus head w	0.654	0.248	-0.287	-0.66	1.79	-0.06	0.08	0.97	0.06
Humerus l	0.785	0.387	-0.204	0.89	-0.89	0.29	—	—	—
Ulna l	0.752	0.413	-0.231	—	—	—	—	—	—
Carpometacarpus l	0.750	0.395	-0.246	0.11	0.45	-0.72	—	—	—
Manus digit 2 phalanx l	0.671	0.304	-0.178	0.14	-1.02	0.58	0.11	-0.57	-0.13
Femur l	0.797	0.324	-0.253	—	—	—	0.64	-0.88	0.41
Tibiotarsus l	0.749	0.405	-0.230	—	—	—	—	—	—
Tarsometatarsus l	0.789	0.386	-0.253	—	—	—	—	—	—
Pes digit 4 phalanx l	0.726	0.334	-0.233	—	—	—	—	—	—
Eigenvalue	15.508	3.145	1.344						
Percent variance explained	52.93	16.46	5.46						
			ANOVA[c]						
Locality F	59.90***	5.64***	18.37***						
Sex F	37.45***	10.65**	3.10ns						
Interaction F	0.99ns	1.23ns	0.71ns						

[a] Wilks' lambda = 0.002, approximate F-statistic = 8.71, df = 68 and 159, $P < 0.001$.
[b] Wilks' lambda = 0.040; approximate F-statistic = 8.41, df = 52 and 347, $P < 0.001$.
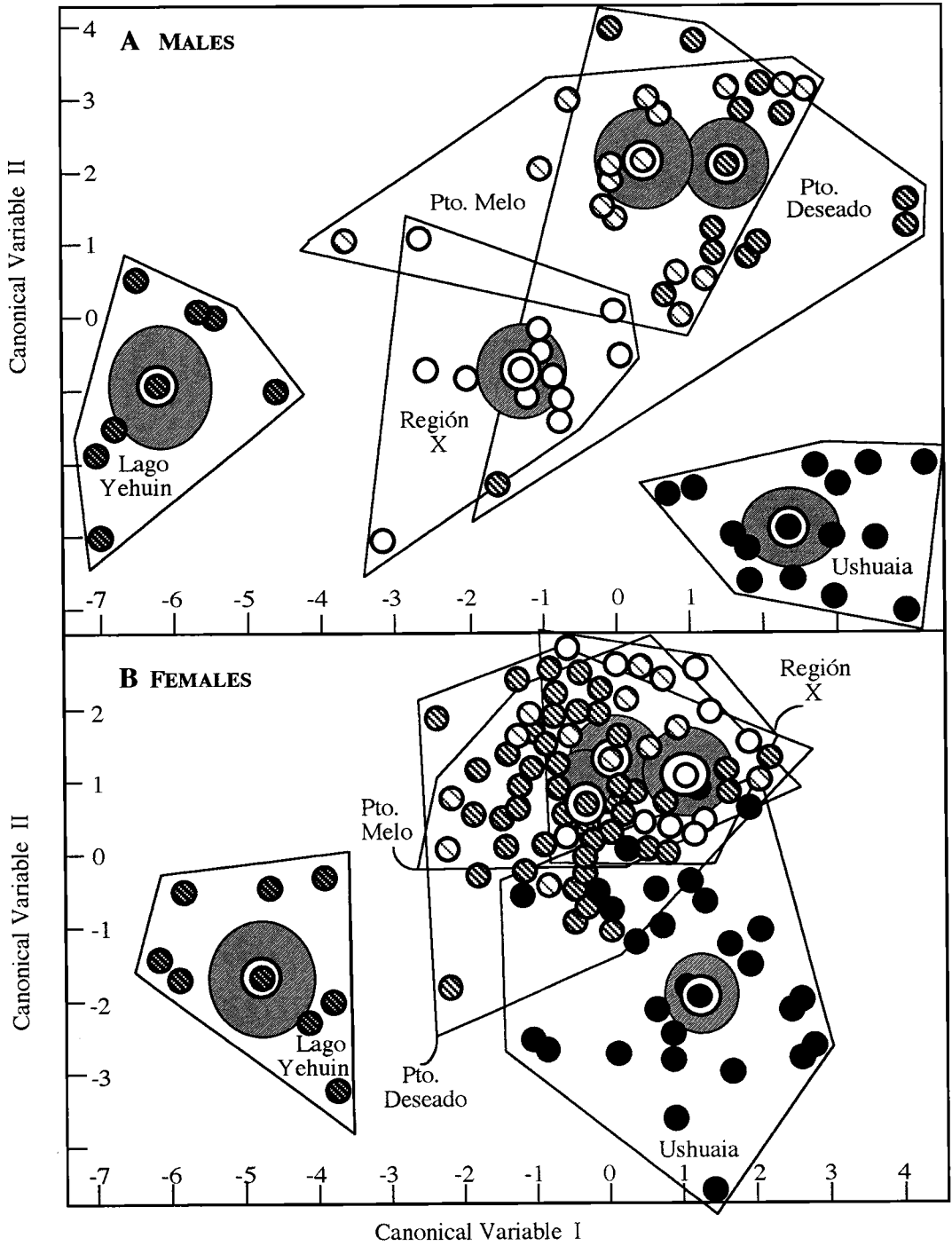[c] Two-way ANOVA. ns, $P > 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

Fig. 6. Plot of means (symbols in large open circles), individual scores (circles) and 95% confidence limits of the means (solid gray shapes) on CV-I and CV-II for (A) male and (B) female Imperial Shags from all continental localities except Monte León.

TABLE 2. Mahalanobis' Ds (females to upper right, males to lower left) for canonical variables I and II of five populations of Imperial Shags.[a]

Locality	Región X, Chile	Puerto Melo	Puerto Deseado	Lago Yehuin	Ushuaia
Región X, Chile	—	1.10^{ns}	1.44^{ns}	$6.34***$	$2.74**$
Puerto Melo	$3.42***$	—	0.68^{ns}	$5.52***$	$3.26***$
Puerto Deseado	$4.03***$	1.10^{ns}	—	$4.93***$	$2.91**$
Lago Yehuin	$5.00***$	$7.47***$	$8.44***$	—	$5.98***$
Ushuaia	$4.43***$	$5.39***$	$4.96***$	$9.12***$	—

[a] Levels of significance from F-matrix (^{ns}, $P > 0.05$; *, $P \le 0.05$; **, $P \le 0.01$; ***, $P \le 0.001$); df for males = 17 and 40; df for females = 13 and 89.

Weinberg predictions and, in one population each, G-6-PD and PEP-B deviate from Hardy-Weinberg equilibrium. Both Nei's and Rogers' genetic distances were low, generally being highest between Puerto Melo and other populations (Table 4). Slatkin's (1981) qualitative gene-flow-estimation method gives a concave curve, indicating high gene flow among populations.

F_{st} values, which measure genetic differentiation among populations, are relatively small (Table 3), with the exceptions of EST-D and G-6-PD. These loci contribute heavily to raising the F_{st} value, which without their contributions would have been 0.044. These two loci are the only ones surveyed to have differentiated geographically. EST-D and G-6-PD represent 13.7% and 10.3%, respectively, of the possible among-deme variability in allelic frequencies. The mean F_{st} indicates that about 6% of the allelic variability is distributed among populations, with the rest being within populations. The mean F_{st} value over all polymorphic loci is not significantly different from zero ($t = 1.63$, df = 8, $P > 0.05$).

DISCUSSION

Patterns of geographic variation.—Juvenile Imperial Shags vary geographically in presence and degree of development of the alar bar, a character that is least well developed or not present in birds from Chile and Lago Yehuin, and reaches its maximum size in birds from the Falkland Islands. Adults, however, show little variation in length of the alar bar, either temporally or geographically. This matches Bernstein and Maxson's (1981) finding that the alar bar is present all year in the Antarctic Shag (*P.* [*atriceps*] *bransfieldensis*), and contradicts the interpretation that in the "King Shag" the alar

bar occurs only late in the breeding season, being lost again prior to breeding, with the reverse sequence occurring in the "Blue-eyed Shag" (Watson 1975). This confusion could have arisen due to the preparation of some study skins with the scapulars covering the alar bars.

Specimens and photographs from the austral spring support Watson's (1975) conclusion that adults of the "King Shag" morph usually have longer, fuller crests at maximum development than do adults of the "Blue-eyed Shag" morph; I found no photos or specimens of the "Blue-eyed Shag" morph with crests as large as those in many "King Shags." Two juveniles from the Falkland Islands possess long, well-developed crests; a larger sample size is needed to determine if this is typical for Falkland juveniles. Bernstein and Maxson's (1981) observation that the Antarctic Shag retains the white dorsal patch all year also pertains to the "Blue-eyed" morph of the Imperial Shag, rather than being a character of the nuptial plumage only (Watson 1975, Devillers and Terschuren 1978).

Differentiation in skeletal size and shape among populations is more marked in males than in females. This pattern has been found for several other species of birds (Baker and Moeed 1979, Ross and Baker 1982, Livezey 1986), and may reflect the operation of sexual selection on males and the influence of reproductive constraints on females. The strong positive correlations of component I scores (which is a size axis for both sexes) with increasing latitude shows that coastal populations adhere to Bergmann's rule.

Genetic distances between populations of Imperial Shags were very low, all distances being well below the average Nei's D (0.044) between species of birds (Barrowclough 1980). Over all populations, the mean number of alleles per locus was 1.15 and, over all loci, the mean per-

cent polymorphic loci was 14.28%. These values are lower than the mean values for 103 avian species (Evans 1987). The mean F_{st} value (6.2%) was larger than the average for local avian populations (2.2%) of five species reported by Barrowclough (1983), and somewhat higher than the mean (4.8%) for 23 species reported by Evans (1987), indicating a level of population structuring higher than usual for conspecifics. The mean F_{st} indicates modest genetic structuring in the Imperial Shag, but in terms of genetic distances, only those between Puerto Melo and other populations suggest a significant degree of genetic differentiation. Results from morphometric and allozyme data sets for Imperial Shags show a lack of concordance, as they do for many other bird species for which these suites of data have been compared (e.g. Zink 1983, 1986, 1988, Karl et al. 1987, St. Louis and Barlow 1987). However, low levels of genetic differentiation do not diminish the evolutionary significance of morphological divergence.

Effects of Pleistocene vicariance events on evolution in South American Imperial Shags. —In the late Cenozoic, repeated glacial cycles occurred in southern South America, one sometime between 7 and 4.6 million years before present (mybp), one at about 3.6 mybp, and others between 2 mybp and 10,000 years before present (ybp; Mercer 1976, 1983). Subsequently, minor Holocene glacial cycles primarily affected montane regions. The last major glaciation reached its maximum around 30,000 ybp, when the 2,000-km-long ice sheet was 140 km wide in the north and more than 400 km wide and 1000 m thick in southern Patagonia (Clapperton 1984; Fig. 1). The southern part of the ice cap was grounded offshore in the Pacific Ocean and, as far north as 43°S, glaciers calved into the sea (Mercer 1976). The western coast of Patagonia, the southernmost islands, the Andes, and steppes on the east flank of the mountains were ice covered, while eastern Tierra del Fuego remained unglaciated (Porter et al. 1984), and the Falkland Islands were glaciated only at the highest elevations (Clapperton and Sugden 1976). Glacial recession occurred between 14,000 and 10,000 ybp (Heusser and Flint 1977), and in coastal Chile this resulted in a fjord landscape (Heim 1951, Ruddiman and Duplessy 1985), while on the eastern slope of the Andes, numerous glacial lakes were formed (Clapperton 1984). Because in southern Chile piedmont glaciers moved into coastal fjords in narrow lobes (White 1988), ice-free areas such as nunataks may well have existed between the lobes even during the height of the glaciations. Evidence of other refugia, such as those in northwestern Isla Chiloé (Villagrán 1988), may well be found in the vast, largely unstudied fjord region of Chile, as they have been in topographically similar regions of southeastern Alaska and western British Columbia (Warner et al. 1982, Mann 1986).

To understand the effects these glacial events must have had, I consider life-history traits of the Imperial Shag and its very close relative, the Antarctic Shag (*P. [atriceps] bransfieldensis*; Siegel-Causey and Lefevre 1989), which now occurs in a relatively inhospitable climate. To survive, Antarctic Shags must have access both to roosting cliffs and ice-free water within several kilometers of one another. They are largely resident under fairly severe environmental conditions, but move locally when seas freeze (Parmelee et al. 1977, Glass 1978). Some South American Imperial Shags (mostly juveniles) migrate north in the winter, but most are resident (Doello-Jurado 1917, Vaz-Ferreira 1950, Narosky et al. 1988). Thus, subsistence of nonbreeding Imperial Shags would have been possible along the Pacific coast of Patagonia because, although glaciers calved into the sea south of 43°S, the sea itself remained unfrozen.

Nesting in glaciated areas is often considered to be impossible for nearly all avian species (Devillers and Terschuren 1978, Humphrey and Péfaur 1979, Vuilleumier 1985, Livezey 1986). However, the Antarctic Shag is said to sometimes build nests directly on the ice (Menegaux 1909), and presence of snow and ice does not delay its breeding (Shaw 1986, N. P. Bernstein in litt.); it has bred successfully even when ice-covered seas prevented breeding by other seabirds (Parmelee et al. 1978). This suggests that South American Imperial Shags could have nested in glaciated areas, although successful nesting colonies could not have occurred on rapidly advancing glaciers. Thus, the cold-tolerant Imperial Shags, dependent only on the existence of ice-free water and relatively stable nesting areas, could have survived in small numbers in refugia between glacial lobes or even on static glaciers. Entire colonies of shags suddenly desert long-established nesting sites to initiate new colonies elsewhere (Parmelee and MacDonald 1975, Voisin 1984), and show low between-year nest-site or colony fidelity, a relatively high divorce rate, and a high adult sur-

TABLE 3. Allele frequencies[a] and F_{st} values across alleles at each locus for Imperial Shags.

Locus	Allele	Región X	Puerto Melo	Puerto Deseado	Monte León	Falkland Islands	Lago Yehuin	Ushuaia	F_{st}
EST-1	a/b	0/1.0	0.100/0.900ns	0.022/0.967***	0/1.0	0/1.0	0/1.0	0/0.960***	0.051
	c/d	0/0	0/0	0.011/0	0/0	0/0	0/0	0	
EST-D	a/b	0.125/0.875ns	0.500/0.500ns	0.174/0.826ns	0.154/0.846ns	0.167/0.833ns	0/1.0	0.135/0.865ns	0.137
GOT-S	a/b	0.125/0.875ns	0/1.0	0.011/0.989ns	0.058/0.942ns	0/1.0	0.033/0.967ns	0/1.0	0.058
G-6-PD	a/b	0/1.0	0/1.0	0.011/0.978***	0/1.0	0/0.833ns	0/1.0	0.019/0.962ns	0.103
	c	0		0.011	0	0.167	0	0.019	
PEP-B	a/b	0.025/0.975ns	0/1.0	0.054/0.946***	0.115/0.885ns	0/1.0	0/1.0	0/1.0	0.061
PEP-C	a/b	0.875/0.125ns	1.0/0	0.978/0.022ns	0.981/0.019ns	0.833/0.167ns	0.800/0.200ns	0.827/0.173ns	0.068
PEP-D	a/b	0/0.925ns	0.050/0.950ns	0/0.989ns	0/0.981ns	0/1.0	0/1.0	0/0.962ns	0.030
	c	0.075	0	0.011	0.019	0	0	0.038	
PEP-E	a/b	0.950/0.050ns	1.0/0	0.967/0.033***	0.904/0.096*	1.0/0	0.933/0.067***	0.923/0.077**	0.027
6-PGD	a	1.0/0	1.0/0	0.989/0.011ns	1.0/0	1.0/0	0.967/0.033ns	0.981/0.019ns	0.016

a X^2 tests for departure from Hardy-Weinberg equilibrium: ns, $P > 0.05$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$).

TABLE 4. For each population of Imperial Shags: mean calculated heterozygosity per locus (unbiased estimate; $\hat{H}_c$); mean direct-count (observed heterozygosity per locus ($\hat{H}_o$); Hardy-Weinberg expected heterozygosity; mean number of alleles per locus; and percent loci polymorphic ($\hat{P}$). For genetic distances, Nei's (1978) above diagonal; Rogers' (1972) below.

Locus	Región X	Puerto Melo	Puerto Deseado	Monte León	Falkland Islands	Lago Yehuin	Ushuaia	Mean
$\hat{H}_c$ ± SE	0.025 ± 0.011	0.021 ± 0.015	0.014 ± 0.007	0.022 ± 0.010	0.026 ± 0.015	0.016 ± 0.009	0.025 ± 0.011	0.021
$\hat{H}_o$ ± SE	0.025 ± 0.011	0.029 ± 0.022	0.018 ± 0.008	0.020 ± 0.009	0.026 ± 0.015	0.014 ± 0.011	0.021 ± 0.010	0.022
H-W expected ± SE[a]	0.025 ± 0.111	0.021 ± 0.015	0.018 ± 0.008	0.022 ± 0.010	0.026 ± 0.015	0.016 ± 0.009	0.025 ± 0.011	—
Alleles/locus ± SE	1.16 ± 0.06	1.08 ± 0.04	1.29 ± 0.09	1.16 ± 0.06	1.08 ± 0.04	1.11 ± 0.05	1.21 ± 0.08	1.15
$\hat{P}$[b]	0.158	0.079	0.237	0.158	0.079	0.105	0.184	0.143
Genetic distances								
Región X	—	0.004	0.000	0.000	0.000	0.000	0.000	
Puerto Melo	0.023	—	0.003	0.003	0.002	0.008	0.004	
Puerto Deseado	0.011	0.016	—	0.000	0.000	0.001	0.001	
Monte León	0.010	0.020	0.007	—	0.000	0.001	0.001	
Falkland Islands	0.012	0.021	0.012	0.016	—	0.000	0.000	
Lago Yehuin	0.014	0.026	0.014	0.015	0.013	—	0.000	
Ushuaia	0.010	0.021	0.010	0.013	0.009	0.009	—	

a Unbiased estimated (Nei 1978).

b 0.99 criterion.

vival rate (Brothers 1985, Shaw 1986). Thus, if their colony were overrun by advancing glacial ice, shags likely would recolonize a more suitable location, and total nesting failure in any given year probably would not extirpate a local population. Compared to most seabirds, Imperial Shags are relatively sedentary and, in their wide range in the subantarctic and Antarctic, they are prone to allopatric differentiation. However, they have been recorded far offshore (Ardley 1936, Tickell 1972, Thurston 1982, Bourne and Curtis 1985), and their present distribution in several Andean lakes and throughout the high latitudes of the Southern Hemisphere demonstrates their long-distance dispersal capabilities over land and water, so there is little doubt that Imperial Shags would be fully capable of long-distance movements to new areas upon loss of their previous habitat.

The population of Imperial Shags from Región X differs from Atlantic coastal populations only in that the culmen is relatively longer. Juveniles tend to lack the mottled alar bar, unlike juveniles of the Atlantic populations; adults are monomorphic for the "*P. atriceps*" phenotype. The longer culmen of Región X birds, from the lowest latitude sampled, conforms to Allen's rule, which predicts longer extremities at lower latitudes; no such pattern occurs in tarsus length. Because these differences are relatively minor, it is inadvisable to treat Región X birds as a distinct subspecies. The colonial Imperial Shag would have been able to breed in large numbers in small suitable areas in Chile, so even if glaciation had forced their isolation in a small refugium (which seems unlikely, see above), shag numbers there would not necessarily be small, unlike species with large single-pair territories such as the forest birds of Patagonia (Vuilleumier 1985). Thus, neither reduced heterozygosity nor strong differentiation would be predicted for this population of shags.

In coastal central Chile and Andean lakes, Imperial Shags usually nest on cliffs, while in coastal Argentina and Tierra del Fuego they nest on flat surfaces (Rasmussen 1989, Rasmussen et al. 1992, 1993); the cliff-nesting habit coincides almost exactly with areas that were formerly extensively glaciated. As montane glaciers typically follow valleys, it may be that the cliff-nesting habit in these populations of Imperial Shags arose from the necessity of nesting on unglaciated coastal cliffs during glacial episodes.

Late Pleistocene and Holocene climates in southern South America have ranged from very cold to only slightly warmer than at present (Heusser 1974, Markgraf 1984, Villagrán 1985, 1988, Heusser et al. 1988). Presently, Imperial Shags winter north to 37°S on the Chilean coast (Jehl 1973) and to 35°S on the Uruguayan coast (Devincenzi 1929). They have nested: north in Chile to 38°S (Bullock 1935); in the Andes to 41°S; and on the Atlantic side from about 44°S south to at least 55°S and probably as far as 56°S. Antarctic Shags have been found as far south as 67°50′S. Imperial Shags are as abundant on the arid Atlantic coast as on the extremely mesic Pacific coast of Patagonia. Their current distributions demonstrate that the Imperial Shag and its near relatives are not greatly affected by cold conditions and differing precipitation levels, suggesting that the distributions of South American Imperial Shags would not have been heavily impacted by the climatic fluctuations that occurred during the Pleistocene, since the areas they inhabited did not experience greatly warmed temperatures. Because Imperial Shags are for the most part inshore, opportunistic feeders (Rasmussen et al. 1993), they would be less affected by shifting ocean currents than is the Guanay (*P. bougainvillii*), whose population plummets dramatically during El Niño years when the current is far offshore and its principal prey fish is unavailable.

During glacial maxima, the isostatic lowering of sea levels (Milliman and Emery 1968, Dillon and Oldale 1978) exposed much of the vast Argentine continental shelf, so the Atlantic coast of Patagonia was considerably farther east than at present. During the last glaciation, the distance between the Atlantic coast and the Falkland Islands was reduced by about 50% to less than 300 km (Fig. 1; Urien and Zambrano 1973). Therefore, populations of Imperial Shags on the Atlantic coast could have significantly expanded during glacial maxima, and gene flow might have been facilitated between Falkland Island and mainland populations.

The Falkland Island population has a relatively high level of heterozygosity for this group, even though it is an island population, suggesting that no bottleneck event has occurred. Despite this, the juvenal plumage of the Falkland Islands population appears to be distinct, with two character states (long crest and very large alar bars) not found in continental juveniles. The adult plumage is monomorphic;

no white-cheeked, white-backed birds have ever been recorded there. However, while a larger sample size is needed, the three skeletal specimens available from the Falklands are similar to coastal Atlantic birds in size, and their allozyme frequencies do not differ. Of the numerous bird species known as vagrants to the Falklands (Woods 1975), most were probably blown there by westerly winds; 19 of these species normally occur only from northern Patagonia north. The fact that the Puerto Melo population is more similar to the Falkland population than it is to Fuegian and Chilean populations, the virtual homogeneity of the "King Shag" morph in both populations, and the trend toward vagrants of other bird species on the Falklands coming from the northwest suggest that vagrant shags occurring in the Falkland Islands would most likely be from Chubut. If gene exchange from Santa Cruz Province occurred, one would expect to find the occasional "Blue-eyed Shag" morph, which is numerically dominant in Santa Cruz, on the ornithologically well-known Falkland Islands. The Falkland population, *P. atriceps albiventer*, is the only South American population treated as subspecifically distinct by Devillers and Terschuren (1978); since juvenal plumage characters support this taxonomy, the subspecific designation should be retained for this population. As these islands harbor 14 endemic subspecies of birds and one endemic flightless species, it is not surprising that the Imperial Shag population there also merits treatment as a distinct subspecies.

The Ushuaia population clearly falls at the large end of a latitudinal cline in size among coastal South American Imperial Shags. This population shows no other major differences from Atlantic populations, with which it has probably been in continuous or nearly continuous contact.

The Puerto Melo population shows virtually no differentiation in plumage and skeletal size or proportions from the other Atlantic populations, other than its near homogeneity of plumage pattern. However, it shows the greatest divergence in allozyme frequencies from the other populations, especially from populations in Tierra del Fuego and Región X. Imperial Shags appear to be relatively isolated at Puerto Melo, on the edge of the ancient Patagonian massif in Chubut Province, Argentina (Urien and Zambrano 1973, Cei 1979), as is the White-headed Flightless Steamer-Duck (*Tachyeres leucoce-*

phalus; Livezey 1986), and a small, resident, possibly differentiated population of Falkland Skuas (*Catharacta antarcticus;* Devillers 1978). South of the massif, a 300 km expanse of sandy coastline unsuitable for nesting by Imperial Shags stretches along Golfo San Jorge between Bahía Bustamante, in central Chubut Province, to Cabo Blanco, northern Santa Cruz Province (Punta 1989). Bahía Bustamante and areas to the north are inhabited almost entirely by the "King Shag" morph, while Cabo Blanco and areas farther south are predominantly inhabited by the "Blue-eyed Shag"; this phase segregation strongly suggests the relative isolation of the northern population. The very few "Blue-eyed Shags" reported from Chubut Province may be vagrants from the mixed population of Santa Cruz Province.

Some populations of Imperial Shags probably survived the glacial periods in lakes that no longer exist. Several freshwater populations of Imperial Shags occur now (Navas 1970, Rasmussen et al. 1992), all in glacial lakes that were uninhabitable during glacial maxima. Ephemeral periglacial lakes were created in many areas (Caldenius 1932, Heusser and Flint 1977), and any of these lakes that held appropriate prey could have served as refugia for Imperial Shags. Although Imperial Shags may ascend rivers to feed such as at Puerto Deseado, they are not known to nest along rivers, which thus are unlikely to have served as glacial refugia.

The shags of Lago Yehuin differ from coastal Imperial Shags in proportions and certain cranial characters; based on this and the morphometric differentiation demonstrated in my study, this form is clearly a taxon distinct from coastal populations, and is being treated in more detail elsewhere (Rasmussen and Humphrey in prep.). In terms of plumage and allozymes, however, no differentiation from coastal populations was detected. Allozyme heterozygosity is very low in this form, suggesting that the population might have undergone a genetic bottleneck, which would be predicted given the small size of the lake and especially of the nesting island. The Lago Yehuin population is anomalous for its small body size at such a high latitude; small size may have been selected for because its primary prey fishes, the small *Galaxias* (Rasmussen and Humphrey in prep.), are unprofitable for birds of large body size. This is paralleled by the situation in a tiny, newly described insular Bahamian race of the Double-crested Cormo-

rant (*P. auritus heuretus*; Watson et al. 1991), which appears to prey on smaller fishes than do the widespread mainland forms. The small nasal-gland depressions of the Lago Yehuin shags suggest that they would be intolerant of marine conditions for long periods of time. Because both lakes from which they are known (Lago Yehuin and Lago Fagnano) were glaciated from 20,000 to 10,000 ybp, the shags that now inhabit the lake must either have lived elsewhere during the glaciation or have become differentiated from the parental populations in the last 10,000 years. Shags, with their relatively long generation times, would require a longer period for change to occur than do the small birds known to exhibit rapid phenotypic differentiation (Johnston and Selander 1964, Conant 1988, Grant and Grant 1990).

Patterns of geographic differentiation observed in the Imperial Shag in the South American portion of its range cannot be readily explained as having resulted from isolation due to Pleistocene glaciations and related environmental perturbation. That the Imperial Shag seems to have been relatively unaffected by the glaciation may be attributed to its life-history characteristics such as longevity, relative vagility, cold tolerance, generalist feeding, and colonial breeding. This contrasts with most other birds, especially forest birds that would have had to await forest regeneration prior to recolonization and reestablishment of gene flow. Of species with more similar ecological requirements, the Rock Shag was apparently affected much more strongly by isolation due to glacial vicariance than were the coastal populations of the Imperial Shag, as plumage characters (both in adults and juveniles) differ strikingly between Pacific and Atlantic populations (Rasmussen 1987). This would be predicted based on the Rock Shag's smaller size, its more sedentary habits, and its absence from extremely cold regions. As another example, the even more sedentary steamer-ducks (*Tachyeres*) seem to have been split into Atlantic and Pacific populations by the Pleistocene glaciations; colonization of the Falkland Islands probably occurred during the period of lowered sea levels (Livezey 1986).

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APPENDIX. Untransformed data for Imperial Shags from each locality presented as $\bar{x} \pm$ SD (n). Linear measures in millimeters and mass in grams.

Variable (significance[b])	Sex	Región X	Puerto Melo	Puerto Deseado	Monte León	Falkland Islands	Lago Yehuin	Ushuaia
Body mass (***, ***, *)	M	2,254.17 ± 91.60 (12)	2,425.38 ± 184.82 (13)	2,371.25 ± 203.54 (12)	2,200.00 ± 278.39 (5)	2,250.00 ± 353.55 (2)	2,117.86 ± 136.98 (7)	2,802.00 ± 225.30 (15)
	F	1,975.00 ± 174.64 (11)	1,851.25 ± 96.87 (8)	2,071.76 ± 126.44 (54)	2,066.15 ± 300.11 (26)	2,000.00 (1)	1,881.25 ± 88.39 (8)	2,378.39 ± 185.14 (28)
Muscle/skel mass (***)	M	1,292.50 ± 78.22 (10)	1,377.78 ± 94.44 (9)	1,426.50 ± 69.40 (10)	1,336.00 ± 156.46 (5)	—	1,220.50 ± 135.77 (6)	1,596.50 ± 107.60 (10)
	F	1,094.44 ± 101.38 (9)	1,050.00 ± 65.95 (5)	1,161.06 ± 68.75 (33)	1,152.00 ± 143.21 (25)	—	1,091.43 ± 179.18 (7)	1,273.06 ± 86.13 (18)
External culmen 1 (***)	M	61.10 ± 1.37 (10)	56.17 ± 1.17 (6)	57.82 ± 2.32 (11)	57.40 ± 3.65 (5)	—	55.14 ± 2.79 (7)	60.80 ± 0.84 (5)
	F	57.00 ± 2.91 (10)	53.75 ± 0.96 (4)	54.64 ± 1.97 (33)	55.30 ± 2.85 (23)	—	51.62 ± 2.07 (8)	60.62 ± 2.45 (16)
Tarsus 1 (***)	M	59.10 ± 2.88 (10)	62.67 ± 2.58 (6)	64.45 ± 1.97 (11)	62.20 ± 3.11 (5)	—	61.29 ± 3.73 (7)	64.80 ± 4.44 (5)
	F	56.70 ± 2.26 (10)	58.25 ± 2.36 (4)	61.58 ± 2.30 (33)	62.48 ± 3.98 (23)	—	57.87 ± 2.53 (8)	62.41 ± 3.37 (17)
Wing chord 1 (***)	M	293.30 ± 4.64 (10)	287.33 ± 6.19 (6)	304.27 ± 5.50 (11)	296.40 ± 6.19 (5)	—	283.57 ± 3.64 (7)	307.00 ± 2.24 (5)
	F	281.70 ± 6.04 (10)	275.50 ± 6.61 (4)	284.12 ± 5.05 (32)	289.87 ± 10.42 (23)	—	271.12 ± 4.76 (8)	286.41 ± 26.30 (17)
Tail 1 (***)	M	127.87 ± 10.82 (8)	119.00 ± 3.16 (6)	125.18 ± 4.00 (11)	131.60 ± 3.71 (5)	—	118.14 ± 5.67 (7)	126.80 ± 3.70 (5)
	F	117.70 ± 6.77 (10)	112.00 ± 6.83 (4)	120.21 ± 8.08 (33)	131.00 ± 9.52 (23)	—	103.43 ± 2.44 (7)	118.00 ± 6.77 (17)
Cranial w (***, ***, ns)	M	36.17 ± 0.71 (12)	36.99 ± 1.18 (15)	37.35 ± 0.87 (13)	36.56 ± 1.10 (5)	36.80 ± 0.57 (2)	36.57 ± 0.58 (7)	38.07 ± 0.91 (14)
	F	35.61 ± 0.75 (10)	36.24 ± 1.35 (11)	35.68 ± 0.69 (48)	35.50 ± 1.13 (25)	35.70 (1)	35.57 ± 0.56 (8)	36.50 ± 0.88 (27)
Cranial h (**, ***, **)	M	25.42 ± 0.68 (12)	25.46 ± 0.92 (15)	26.38 ± 0.56 (13)	26.08 ± 0.78 (5)	25.00 ± 0.28 (2)	25.49 ± 0.46 (7)	26.36 ± 0.87 (14)
	F	25.00 ± 0.54 (10)	25.42 ± 0.72 (12)	25.04 ± 0.65 (48)	25.17 ± 0.75 (25)	25.70 (1)	24.67 ± 0.60 (8)	25.38 ± 0.76 (27)
Interorbital w (***, ***, ns)	M	15.38 ± 1.15 (12)	17.15 ± 1.40 (15)	17.46 ± 1.04 (13)	16.60 ± 1.02 (4)	18.35 ± 1.77 (2)	13.97 ± 0.68 (7)	17.99 ± 1.52 (14)
	F	14.31 ± 0.94 (10)	16.12 ± 1.10 (12)	15.30 ± 1.03 (48)	15.12 ± 0.71 (25)	17.00 (1)	12.59 ± 1.11 (8)	16.38 ± 1.36 (27)
Frontal 1 (***, ***, ns)	M	28.01 ± 0.63 (12)	27.16 ± 1.23 (15)	26.76 ± 0.85 (10)	27.56 ± 1.23 (5)	27.05 ± 0.07 (2)	26.66 ± 1.12 (7)	29.23 ± 0.66 (14)
	F	26.60 ± 0.75 (10)	26.62 ± 0.78 (12)	26.05 ± 0.86 (48)	25.81 ± 1.25 (25)	25.60 (1)	25.60 ± 0.79 (8)	27.55 ± 1.05 (27)
Rear skull 1 (***, ***, ns)	M	39.50 ± 0.88 (12)	39.78 ± 1.10 (15)	40.63 ± 0.65 (10)	39.10 ± 1.60 (5)	38.85 ± 1.34 (2)	37.90 ± 0.84 (7)	41.59 ± 0.76 (14)
	F	37.66 ± 1.03 (10)	37.98 ± 1.28 (12)	37.97 ± 1.04 (48)	37.86 ± 1.26 (26)	37.40 (1)	36.26 ± 0.43 (8)	39.14 ± 0.89 (27)
Lacrimal h (***, *, ns)	M	13.68 ± 0.45 (12)	13.71 ± 0.60 (15)	13.84 ± 0.64 (10)	13.56 ± 0.95 (5)	13.35 ± 0.35 (2)	12.50 ± 0.57 (7)	14.79 ± 0.70 (14)
	F	13.55 ± 0.54 (10)	13.58 ± 0.90 (12)	13.31 ± 0.59 (49)	13.04 ± 0.57 (26)	13.20 (1)	12.59 ± 0.43 (8)	14.11 ± 0.68 (27)
Lacrimal w (***, *, ns)	M	3.24 ± 0.48 (12)	3.27 ± 0.49 (15)	3.27 ± 0.26 (10)	3.28 ± 0.41 (5)	3.80 ± 0.00 (2)	2.63 ± 0.42 (7)	3.40 ± 0.55 (14)
	F	2.94 ± 0.50 (10)	2.83 ± 0.48 (12)	2.94 ± 0.39 (49)	3.19 ± 0.55 (26)	3.80 (1)	2.06 ± 0.35 (8)	3.30 ± 0.52 (27)
Culmen 1 (***, ***, ns)	M	70.58 ± 3.54 (12)	65.56 ± 2.60 (14)	66.79 ± 2.84 (13)	61.96 ± 3.03 (5)	67.80 ± 3.82 (2)	64.79 ± 2.54 (7)	71.23 ± 2.80 (13)
	F	66.38 ± 2.64 (10)	61.96 ± 3.03 (12)	63.08 ± 2.03 (46)	62.55 ± 2.43 (25)	64.50 (1)	60.35 ± 2.59 (8)	68.46 ± 2.67 (26)
Culmen w (***, ***, ns)	M	12.22 ± 0.56 (12)	11.96 ± 0.71 (15)	12.37 ± 0.46 (10)	12.10 ± 1.09 (5)	11.35 ± 1.20 (2)	11.60 ± 0.43 (7)	13.11 ± 0.64 (14)
	F	11.54 ± 0.63 (10)	11.44 ± 0.82 (12)	11.29 ± 0.64 (48)	11.16 ± 0.82 (26)	11.20 (1)	10.20 ± 0.19 (8)	11.89 ± 0.61 (27)
Culmen h (***, ***, ns)	M	9.52 ± 0.65 (12)	9.97 ± 0.87 (15)	10.24 ± 0.52 (10)	9.70 ± 0.61 (5)	9.70 ± 0.71 (2)	8.56 ± 0.60 (7)	10.64 ± 0.71 (14)
	F	9.25 ± 0.69 (10)	9.71 ± 1.02 (12)	9.20 ± 0.56 (49)	9.23 ± 0.48 (26)	8.60 (1)	7.74 ± 0.37 (8)	9.61 ± 0.62 (27)
Quadrate 1 (***, ***, *)	M	16.89 ± 0.41 (12)	16.84 ± 0.69 (15)	17.59 ± 0.27 (13)	16.94 ± 0.94 (5)	16.15 ± 0.78 (2)	16.21 ± 0.29 (7)	17.57 ± 0.58 (14)
	F	15.71 ± 0.58 (8)	15.96 ± 0.71 (12)	15.91 ± 0.35 (51)	16.23 ± 0.70 (26)	15.30 (1)	15.00 ± 0.33 (8)	16.29 ± 0.56 (27)
Sternal w (***, ***, ns)	M	68.85 ± 2.86 (12)	68.87 ± 2.16 (15)	69.35 ± 2.17 (13)	66.68 ± 4.14 (5)	68.80 ± 5.66 (2)	65.86 ± 2.40 (7)	74.44 ± 3.54 (15)
	F	64.62 ± 3.48 (10)	64.61 ± 2.69 (13)	65.96 ± 2.45 (56)	66.11 ± 3.17 (23)	66.30 (1)	63.36 ± 1.36 (8)	69.71 ± 3.07 (28)
Interacetabular w (***, ***, *)	M	17.12 ± 0.96 (12)	17.30 ± 0.86 (15)	18.09 ± 0.51 (13)	16.74 ± 0.52 (5)	16.75 ± 0.49 (2)	16.97 ± 1.31 (7)	18.21 ± 0.93 (15)
	F	15.95 ± 0.60 (10)	16.81 ± 0.72 (13)	16.59 ± 0.77 (55)	16.75 ± 0.85 (25)	16.40 (1)	15.99 ± 0.50 (8)	17.32 ± 0.95 (28)
Sacral 1 (***, ***, ns)	M	121.24 ± 3.77 (12)	123.87 ± 3.99 (16)	129.87 ± 5.72 (12)	122.90 ± 6.66 (5)	124.90 ± 2.12 (2)	123.91 ± 4.08 (7)	131.61 ± 3.99 (15)
	F	113.62 ± 4.78 (10)	116.40 ± 4.94 (13)	118.00 ± 3.27 (55)	118.08 ± 4.69 (25)	114.90 (1)	114.70 ± 3.40 (8)	122.64 ± 4.67 (28)
Iliac wing w (***, **, ns)	M	39.25 ± 1.73 (12)	40.03 ± 1.69 (15)	40.72 ± 1.58 (13)	39.12 ± 1.74 (5)	39.30 ± 1.13 (2)	35.63 ± 0.78 (7)	42.11 ± 2.09 (15)
	F	37.89 ± 1.73 (10)	37.51 ± 1.94 (13)	38.50 ± 1.79 (56)	38.72 ± 1.98 (26)	37.70 (1)	36.25 ± 1.18 (8)	40.39 ± 2.02 (28)
Antitrochanter w (***, ***, ns)	M	35.72 ± 1.26 (12)	36.61 ± 1.42 (15)	37.51 ± 1.26 (13)	35.90 ± 1.02 (5)	34.95 ± 1.91 (2)	35.44 ± 1.04 (7)	38.13 ± 1.12 (15)
	F	34.23 ± 1.17 (10)	34.78 ± 1.88 (13)	34.68 ± 1.01 (56)	34.91 ± 1.29 (25)	32.40 (1)	33.39 ± 1.05 (8)	36.32 ± 1.19 (28)

APPENDIX. Continued.

Variable (significance)[b]	Sex	Región X	Puerto Melo	Puerto Deseado	Monte León	Falkland Islands	Lago Yehuin	Ushuaia
Ischial terminus w (***, ns, ns)	M	38.15 ± 1.05 (12)	38.10 ± 1.83 (15)	39.87 ± 1.61 (12)	40.28 ± 2.50 (5)	39.30 ± 0.57 (2)	39.51 ± 2.06 (7)	41.11 ± 2.79 (15)
	F	36.71 ± 2.42 (10)	39.05 ± 1.74 (13)	39.63 ± 2.18 (56)	38.52 ± 2.07 (24)	41.10 (1)	39.16 ± 1.36 (8)	40.81 ± 2.33 (28)
Furculum l (***, ***, ns)	M	63.39 ± 1.99 (12)	63.51 ± 2.69 (16)	66.31 ± 2.10 (13)	63.52 ± 3.08 (5)	64.50 ± 4.24 (2)	62.59 ± 1.12 (7)	68.47 ± 1.34 (15)
	F	60.03 ± 1.14 (10)	60.00 ± 2.40 (13)	60.88 ± 1.69 (56)	60.98 ± 2.53 (22)	62.10 (1)	58.71 ± 1.62 (8)	64.13 ± 2.51 (27)
Scapula l (***, ***, ns)	M	85.11 ± 3.32 (12)	85.07 ± 1.96 (15)	87.76 ± 2.60 (13)	80.86 ± 10.86 (5)	86.15 ± 6.29 (2)	81.39 ± 2.05 (7)	90.91 ± 2.41 (15)
	F	78.63 ± 3.10 (10)	80.28 ± 3.78 (13)	81.21 ± 2.22 (56)	79.91 ± 3.65 (26)	82.20 (1)	77.15 ± 1.45 (8)	85.34 ± 2.77 (28)
Coracoid l (***, ***, ns)	M	62.73 ± 2.77 (12)	63.36 ± 1.92 (16)	65.74 ± 2.06 (13)	63.48 ± 2.03 (5)	64.70 ± 2.40 (2)	62.29 ± 1.25 (7)	67.66 ± 1.51 (15)
	F	59.74 ± 1.43 (10)	60.22 ± 2.56 (13)	60.90 ± 1.37 (56)	61.63 ± 2.91 (26)	60.80 (1)	59.07 ± 1.09 (8)	63.85 ± 2.38 (28)
Coracoid articular l (***, ***, ns)	M	20.53 ± 0.68 (12)	20.47 ± 0.81 (16)	21.81 ± 0.85 (13)	21.26 ± 0.55 (5)	21.70 ± 0.14 (2)	19.86 ± 0.87 (7)	21.75 ± 0.86 (15)
	F	19.37 ± 0.75 (10)	19.61 ± 1.20 (13)	20.21 ± 0.85 (56)	20.47 ± 0.93 (26)	21.10 (1)	19.11 ± 0.85 (8)	21.39 ± 1.30 (29)
Humerus head w (***, ***, ns)	M	22.73 ± 0.78 (12)	22.33 ± 1.08 (16)	23.20 ± 1.06 (13)	22.56 ± 0.75 (5)	21.95 ± 0.64 (2)	22.51 ± 0.47 (7)	23.67 ± 0.76 (15)
	F	21.35 ± 0.78 (10)	21.18 ± 1.07 (13)	22.47 ± 1.19 (56)	21.83 ± 0.82 (26)	21.40 (1)	20.91 ± 0.64 (8)	22.80 ± 0.95 (28)
Humerus l (***, ***, ns)	M	142.57 ± 3.28 (12)	143.86 ± 4.11 (16)	149.33 ± 3.37 (13)	146.84 ± 3.17 (5)	144.75 ± 6.58 (2)	139.99 ± 4.81 (7)	150.09 ± 3.61 (15)
	F	134.32 ± 3.45 (10)	137.66 ± 4.33 (13)	139.82 ± 2.92 (55)	141.68 ± 6.21 (26)	131.90 (1)	134.49 ± 2.93 (8)	143.08 ± 3.95 (27)
Ulna l (***, ***, *)	M	152.92 ± 4.46 (12)	152.85 ± 4.32 (15)	160.49 ± 3.81 (12)	154.78 ± 6.04 (5)	155.85 ± 5.02 (2)	149.13 ± 5.04 (7)	161.42 ± 2.77 (14)
	F	143.94 ± 4.14 (10)	146.71 ± 6.22 (12)	149.57 ± 3.45 (50)	151.90 ± 6.73 (25)	140.80 (1)	144.55 ± 3.28 (8)	152.40 ± 4.53 (27)
Carpometacarpus l (***, ***, ns)	M	64.53 ± 1.64 (12)	64.30 ± 2.32 (15)	67.65 ± 1.87 (13)	65.54 ± 0.94 (5)	63.90 ± 0.42 (2)	62.64 ± 1.99 (7)	67.86 ± 1.52 (14)
	F	61.30 ± 1.72 (10)	61.99 ± 2.69 (12)	63.60 ± 1.65 (50)	63.65 ± 2.71 (26)	60.00 (1)	60.80 ± 1.37 (8)	64.79 ± 1.98 (26)
Manus D2P1 (***, ***, ns)	M	24.73 ± 1.01 (12)	24.55 ± 0.87 (15)	25.63 ± 0.87 (13)	24.38 ± 0.37 (5)	24.35 ± 0.35 (2)	23.10 ± 0.93 (7)	25.39 ± 0.94 (14)
	F	23.38 ± 0.93 (10)	23.62 ± 0.89 (12)	23.95 ± 0.85 (51)	23.93 ± 1.05 (26)	21.30 (1)	22.46 ± 0.50 (8)	24.64 ± 0.91 (27)
Femur l (***, ***, ns)	M	57.42 ± 1.19 (12)	57.00 ± 1.39 (16)	60.01 ± 1.51 (13)	59.02 ± 2.02 (5)	60.35 ± 3.32 (2)	56.76 ± 1.64 (7)	61.71 ± 2.05 (15)
	F	54.39 ± 1.88 (10)	54.85 ± 1.51 (13)	55.52 ± 1.32 (56)	56.37 ± 3.03 (26)	57.10 (1)	54.07 ± 1.37 (8)	58.08 ± 2.07 (28)
Tibiotarsus l (***, ***, ns)	M	109.85 ± 2.61 (12)	111.44 ± 3.44 (16)	115.66 ± 2.38 (12)	113.92 ± 2.22 (5)	116.55 ± 4.45 (2)	110.00 ± 3.03 (7)	118.20 ± 4.73 (15)
	F	103.40 ± 2.73 (10)	105.55 ± 3.55 (13)	107.09 ± 2.37 (56)	108.33 ± 4.89 (26)	108.50 (1)	105.74 ± 2.27 (8)	111.37 ± 3.96 (28)
Tarsometatarsus l (***, ***, ns)	M	62.72 ± 1.31 (12)	63.24 ± 2.26 (15)	64.79 ± 1.57 (13)	63.44 ± 1.45 (5)	66.10 ± 1.98 (2)	61.81 ± 1.93 (7)	66.81 ± 1.82 (14)
	F	58.92 ± 1.57 (10)	60.18 ± 2.33 (12)	61.63 ± 1.44 (51)	61.49 ± 2.75 (26)	60.90 (1)	59.42 ± 1.80 (8)	63.77 ± 2.28 (27)
Pes D4P1 (***, ***, ns)	M	26.33 ± 0.73 (12)	26.47 ± 0.97 (15)	26.85 ± 1.06 (13)	25.88 ± 0.30 (5)	27.00 ± 0.99 (2)	24.99 ± 1.23 (7)	28.37 ± 0.85 (14)
	F	24.90 ± 1.33 (10)	24.78 ± 0.98 (12)	25.53 ± 0.73 (51)	25.63 ± 1.23 (26)	25.10 (1)	24.34 ± 0.65 (8)	26.50 ± 0.95 (27)

[a] l = length; h = height; w = width; D2P1 = digit 2 phalanx 1; D4P1 = digit 4 phalanx 1.
[b] Significance levels from two-way ANOVAs (except for external measures which are from one-way ANOVAs); first set for each variable is significance of locality, second for sex, and third for interaction effects: ns, $P > 0.05$; *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.