

## RELATIONSHIPS BETWEEN COASTAL SOUTH AMERICAN KING AND BLUE-EYED SHAGS<sup>1</sup>

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**Abstract.** The distributions of King and Blue-eyed Shags (*Phalacrocorax albiventer* and *P. atriceps*) were reevaluated, incorporating new data. The differential distributions of the phenotypes do not correlate significantly with austral summer water temperatures. In areas where the forms occur together, hybridization is frequent and plumage-based disassortative mating occurs. At localities of overlap, King and Blue-eyed Shags are virtually identical in skeletal size and shape. Heterozygosity is very similar for both forms over all populations and at Puerto Deseado, but not for the Monte León and Ushuaia populations. Genetic distances between the two forms are very low. King and Blue-eyed Shags should be considered conspecific color morphs of a single widespread species, *Phalacrocorax atriceps*.

**Key words:** *Phalacrocorax albiventer*; *Phalacrocorax atriceps*; allozymes; multivariate morphometrics; distribution; hybridization.

### INTRODUCTION

King and Blue-eyed Shags (*Phalacrocorax* [*Notocarbo*] *albiventer* and *P.* [*N.*] *atriceps*) are both widespread, in several mostly allopatric subspecies, on subantarctic islands, the Antarctic Peninsula, and southern South America. Forms having white cheeks and white dorsal patches have been considered subspecies of the Blue-eyed Shag, and those having black cheeks and lacking dorsal patches, subspecies of the King Shag. King and Blue-eyed Shags had been considered largely allopatric in South America (Murphy 1936), or as sympatric breeders (Behn et al. 1955), in either case being treated as distinct species. However, Reynolds (1934, 1935) and Jouanin (1951) disputed this treatment.

Subsequently, Devillers and Terschuren (1978) found that the distributions of King and Blue-eyed Shags overlap extensively in southern South America, that ecological segregation between the forms was not apparent, and that a high frequency of mixed pairs and apparent hybrids occurred in the areas of overlap. They therefore considered the King Shag a color morph of mainland Blue-eyed Shags, for which *P. atriceps* is the senior name. This treatment is supported by similarity between the forms in courtship behavior

(Siegel-Causey 1986), molt patterns (Rasmussen 1988a, 1988b), feather keratins (Brush and Witt 1983), and qualitative osteology (Siegel-Causey 1988; P. S. Humphrey, pers. comm.; Rasmussen, pers. observ.). However, several unresolved problems remain: (1) Hybrids between King and Blue-eyed Shags have not been documented by specimens. (2) Juvenal-plumaged Blue-eyed Shags strongly resemble adult and juvenile King Shags (Rasmussen 1986a), causing confusion in identification (even involving the type specimen of the Blue-eyed Shag), probably affecting estimates of the frequency of intermediates, and causing spurious distributional data. (3) Identification of hybrids is complicated by individual variation, posture, and observer angle, and photographs are unreliable for documentation of hybrids between King and Blue-eyed Shags. (4) The Falkland Islands population was considered a distinct subspecies largely on the basis of its monomorphism. (5) Devillers and Terschuren did not visit, or examine specimens from, lakes in Tierra del Fuego, but they interpreted Reynolds (1934) to indicate that King and Blue-eyed Shags hybridize there—however, these lakes host exclusively a taxonomically distinct white-cheeked form whose relationships are peripheral to the question of specific relationships of the coastal forms (Rasmussen and Humphrey MS). (6) Devillers and Terschuren's revision did not deal with size-related variation, and regarded all mainland South American Blue-eyed Shags as

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belonging to the same subspecies. (7) The existence of differential water temperature, salinity level, and turbulence preferences hypothesized between the forms by Brown et al. (1975) and Jehl and Rumboll (1976) remained untested.

Despite their conspicuousness, abundance, and wide ranges, the distributions of King and Blue-eyed Shags in South America are not well known. Devillers and Terschuren (1978) provided the best and most current published information on the distributions of these shags, but they and most earlier investigators did not differentiate between juvenile and adult shags, thus leaving many records of "King Shags" open to question. I reanalyzed available data on shag distributions in South America and summarized new information obtained during field work in southern Argentina and Chile. I then tested for correlation of the relative abundance of King Shags with decreasing water temperature. Through analyses of skeletal size and shape, allozyme frequency data, and incidence of hybridization, I tested the hypothesis that King and Blue-eyed Shags are differentiated from one another at localities of cooccurrence and thus should be considered distinct, sympatric species.

## METHODS

### DISTRIBUTIONAL ANALYSIS

In reanalyzing the distributions of King and Blue-eyed Shags, I considered published sight records of Blue-eyed Shags from southern South America to be valid except when it was unclear that the author had differentiated between the two forms, or when there was some other reason to doubt the validity of the sightings. Because of the potential for confusion between King Shags and juvenile Blue-eyed Shags (Rasmussen 1986a), I did not include records of King Shags from the few localities for which I could not verify the identification by specimens or photographs. I did not attempt to interpret old records of *P. cirrhatus* or *P. carunculatus*, or those of Blaauw (1912a, 1912b, 1921), Reynolds (1932, 1934, 1935), Olog (1950), Earnshaw (1971), Tortonesi (1976), or Venegas (1976), all authors who did not always differentiate between the two forms. I incorporated distributional observations made by P. S. Humphrey and myself from 1985–1990, as well as new records communicated to us by other qualified observers.

To test for correlation between distributions of King and Blue-eyed Shags and surface water temperatures, I regressed single diurnal austral summer (December–February) surface water temperatures for each locality (taken on the Pacific coast by crew members of the "Jason" and on the Atlantic coast by the author) against ratios of the two forms at each of 39 localities (21 localities in Chile, 12 in Argentina, and 6 in Tierra del Fuego).

### DETERMINATION OF HYBRIDIZATION

Ninety-six museum study skins and 140 freshly collected King and Blue-eyed Shags from the South American continent and Falkland Islands were examined for evidence of hybridization. In addition, 57 study skins from Macquarie Island, South Georgia, and Antarctica were examined. Adults were considered pure King Shags if the cheeks were extensively black with the demarcation line curving down away from the eye, and white feathers were lacking in the middle of the back. Adults with extensively white cheeks, demarcation lines curving up towards the eye, and with or without white feathers in the center of the back were considered pure Blue-eyed Shags. Juveniles were distinguished using the criteria in Rasmussen (1986a). Birds intermediate between the two pure forms were presumed to be hybrids if from localities where both forms are known; if from areas of allopatry they were considered atypical specimens.

Observations were made on frequencies of mixed pairs at breeding colonies at Isla Chata, near Puerto Deseado, and at Monte León, on 24 February 1985 and 2 March 1986, respectively. Pairs of adult shags were considered to be mated birds if they stood on a nest together and allopreened each other.

### SKELETAL SPECIMENS AND STATISTICAL ANALYSIS

Skeletal specimens used in this study are enumerated by sex, age, and locality in Table 1. Freshly killed shags were weighed to the nearest 50 g with a Pesola scale, and were reweighed when only muscle and skeleton remained. Culmen, tarsus, tail, wing (arc) lengths, and length and width of gonads were measured to the nearest mm.

Skeletal measures used in all multivariate analyses in this study were width and height of

TABLE 1. Numbers of skeletal and tissue specimens of King and Blue-eyed Shags used in this study, by sex and age class at each locality.

Locality	Skeletons								Tissues		
	King				Blue-eyed				King	Hybrid	Blue-eyed
	Sex		Age		Sex		Age				
	Male	Female	Adult	Juvenile <sup>1</sup>	Male	Female	Adult	Juvenile <sup>1</sup>			
Falkland Islands <sup>2</sup>	2	1	3	0	0	0	0	0	3	0	0
Región X, Chile	0	0	0	0	12	10	22	0	0	0	20
Puerto Melo	16	13	29	0	0	0	0	0	10	0	0
Puerto Descado <sup>3</sup>	8	13	21	0	4	43	41	6	21	0	24
Monte León <sup>4</sup>	5	6	10	1	0	16	1	15	8	2	16
Ushuaia	13	27	40	0	2	4	6	0	24	0	2
Totals	44	60	103	1	18	73	70	21	66	2	62

<sup>1</sup> Recently fledged juveniles only, with no wear of remiges.<sup>2</sup> Not used in statistical analyses.<sup>3</sup> Not including one adult male presumed to be a hybrid.<sup>4</sup> Not including (except as tissues) one juvenile female and one adult female presumed to be hybrids.

the cranium; width of the interorbital; lengths of the frontal and rear of the skull; height and width of the lacrimal (prefrontal); length, width, and height of the culmen; length of the quadrate; widths of the sternum and between the acetabula; length of the sacrum; greatest width between the preacetabular ilia; widths between the antitrochanters and between the termini of the ischia; lengths of the furcula, scapula, coracoid, and coracoid articular surface; width of the head of the humerus; lengths of the humerus, ulna, carpometacarpus, digit 2 phalanx 1 of the manus, femur, tibiotarsus, and digit 4 phalanx 1 of the pes. Detailed descriptions of measures are available from the author.

Analyses were done with the BMDP statistical package (Dixon 1985) on an IBM mainframe computer at the University of Kansas Academic Computing Center. Untransformed data were used in univariate statistical analysis. Data for multivariate analysis were natural log-transformed, and as many as three (10%) of the 29 total measures per damaged or incomplete skeleton were estimated with a missing data program. In principal component analysis, for which I used variance-covariance matrices, I tested for correlated variables, significant eigenvalues (eigenvalues with 95% confidence limits entirely greater than the mean eigenvalue), and regions of sphericity. One- and two-way analyses of variance were done on factor scores obtained by principal component analyses between selected groups to test for statistical differences. For results of all discriminant function and canonical analyses, scores on canonical variables were standardized

by multiplying by the pooled within-group standard deviations.

Freshwater shags from lagos Yehuin, Fagnano, Nahuel Huapi, and Vintter were excluded from this analysis and their relationships will be treated elsewhere. Presumed hybrids were also excluded from analyses except where noted otherwise.

In all statistical analyses of skeletal data, the sexes were analyzed separately because King and Blue-eyed Shags are highly sexually dimorphic (Rasmussen 1986b). Small sample sizes for males precluded their use in most multivariate analyses. To determine whether unsexed skeletons of known locality could be sexed for use in further analyses, I used discriminant function analyses between sexes at each locality, with unsexed birds as unknowns, such that unsexed birds were not used in calculation of the discriminant functions but were classified by them. Unsexed birds with posterior probabilities of group membership of 1.0 and with Mahalanobis' *D* values clearly fitting one sex exclusively were therefore assigned to that sex and used in further analyses. One hundred percent of the specimens were correctly sexed for each locality except Región X, for which only 90% were correctly sexed. All Mahalanobis' *D* values between sexes were highly significant. From results obtained I concluded that one unsexed bird from Región X was unequivocally male, and six from other localities were females (two from Puerto Melo, three from Monte León, and one from Ushuaia). These seven originally unsexed specimens were then treated as sexed in further analyses; the remaining five specimens

could not be sexed confidently and so were excluded.

#### ELECTROPHORETIC ANALYSES

Tissue samples from 130 Blue-eyed and King Shags were collected at coastal localities from 1984 to 1987 (Table 1). Liver, pectoral muscle, and heart muscle were collected, frozen in liquid nitrogen within three hours of collection, and transported by air on dry ice at liquid nitrogen temperature, and thereafter stored in an ultra-cold freezer. Starch-gel electrophoresis was performed according to the methods of Selander et al. (1971), Corbin et al. (1974), Barrowclough and Corbin (1978), and Yang and Patton (1981).

Loci that were not polymorphic in at least two individuals from the Falkland Islands, four from Puerto Melo, two from Puerto Deseado, two from Monte León, four from Lago Yehuin, four from Ushuaia, and four from Región X were considered monomorphic. All polymorphic loci were examined for each individual, and for most polymorphic loci each individual was run twice and double-checked. Loci apparently homologous with those detailed by Harris and Hopkinson (1978) were assigned the recommended names (e.g., GOT-S, GOT-M); otherwise, the most anodally migrating (fastest) locus was denoted "1," the next "2," etc. The most anodally migrating allele at a locus was denoted "a," the next "b," etc. If bands appeared to represent ADH, MDH, LDH, SDH, or EST instead of the specific target enzyme, another slice of the same gel was counterstained for the suspected enzyme for verification.

BIOSYS-1 (Swofford and Selander 1989) was used to analyze King and Blue-eyed Shag allozyme data to obtain observed and calculated heterozygosities, percent polymorphic loci, mean numbers of alleles per locus, Nei's (1978) genetic distances modified for small sample sizes, Rogers' (1972) genetic distances, and deviations of loci from Hardy-Weinberg equilibria.

## RESULTS

### DIFFERENTIAL DISTRIBUTIONS

New data on the distribution of King and Blue-eyed Shags are incorporated in Figure 1. Specifically, there is no evidence that King Shags have ever occurred in Lago Yehuin, where the population is composed entirely of Blue-eyed Shags (Fig. 1), although a probable hybrid Blue-eyed

× Rock Shag was collected there (Rasmussen and Humphrey, in prep.). P. S. Humphrey (pers. comm.) recently documented a breeding population of Blue-eyed Shags at Lago Vintter, Chubut (Rasmussen et al. MS); one Blue-eyed Shag was observed in 1983 at Lago Fontana, Chubut (P. S. Humphrey, pers. comm.); a small group of Blue-eyed Shags was seen 15 January 1989 in the Río Chimehuín at the mouth of the Río Curruhué, Neuquén (Gpqc. Cachito, pers. comm. to P. S. Humphrey); and one Blue-eyed Shag was seen in Lago Futulafquen, Chubut (O. Benávidz, pers. comm.). Blue-eyed Shags occur in very small numbers in King Shag colonies in Ushuaia Bay. I know of no specimen, photograph, or other compelling evidence that the King Shag occurs along the central Chilean coast north of Magallanes Province. Devillers and Terschuren's (1978) observations of the proportions of King vs. Blue-eyed Shags at Puerto Deseado and nearby Isla Chata, Bahía Oso Marino, were verified by our observations in 1985 and 1986. No previous information was available on the proportions of the two forms in the colony at Monte León; in 1986 P. S. Humphrey and I found it to comprise 75% Blue-eyed and 25% King Shags.

### ASSOCIATION BETWEEN DISTRIBUTIONS AND WATER TEMPERATURE

Summer surface water temperatures at localities measured varied from 10–17°C. The incidence of Blue-eyed relative to King Shags on the Chilean coast from the Beagle Channel to Isla Mocha was highly correlated with increasing water temperature ( $n = 21$  localities,  $r = 0.60$ ,  $P < 0.01$ ). However, there was no correlation on the Argentine coast from Isla de los Estados to Península Valdés ( $n = 12$  localities,  $r = 0.08$ ,  $P > 0.05$ ) between the proportions of Blue-eyed Shags and water temperature, nor was there a correlation when all Chilean, Argentine, and Fuegian localities were analyzed together ( $n = 39$  localities,  $r = 0.01$ ,  $P > 0.05$ ).

### EVIDENCE OF HYBRIDIZATION

Several fully adult specimens from areas of allopatry showed at least as much intermediacy in cheek pattern as the birds considered intermediate by Devillers and Terschuren (1978). One Antarctic Shag (USNM [National Museum of Natural History] 548038; Fig. 2c) collected at De Gerlache Straits, Antarctica—about 1,000 km

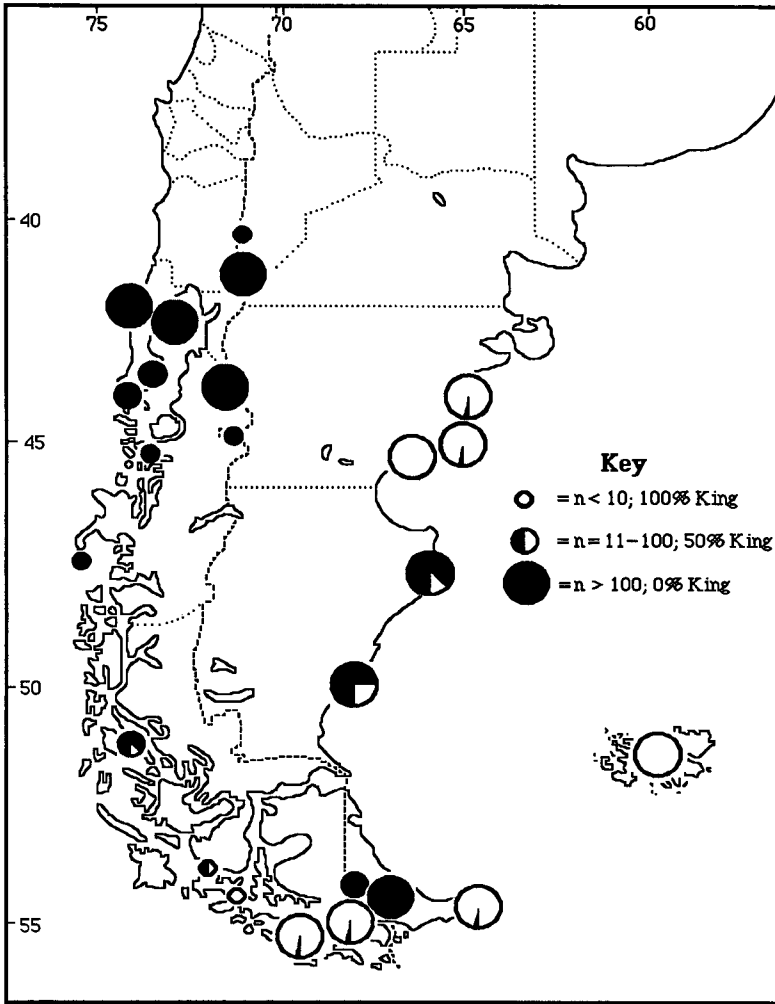


FIGURE 1. Proportions of King and Blue-eyed Shags reported from South American localities in the austral summer by observers familiar with the juvenal plumage of Blue-eyed Shags, or verified by specimens or photographs. At each site, size of circle indicates sample size, and proportion of white to black equals proportion of King to Blue-eyed Shags.

from the nearest known population of King Shags—had 25 black feathers in the white area of one cheek and one black feather in the other cheek. Other atypical specimens that would probably have been treated as intermediates by Devillers and Terschuren (1978) have been collected at Lago Nahuel Huapi, Neuquén, Argentina (MACN [Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”] 37866, similar in pattern to Fig. 2a); Shag Rocks, South Atlantic Ocean (USNM 536649; Fig. 2b); Chonos Islands, Chile (AMNH [American Museum of Natural History] 730166; Fig. 2a); and Macquarie Island

(AMNH 730172; Fig. 2d; AMNH 730170 and AMNH 730171, not illustrated). A *P. atriceps georgianus* with an irregular demarcation line is shown in a close-up photograph (Perrins and Middleton 1985). These examples demonstrate that not all individuals with intermediate or atypical cheek lines are probable hybrids.

Evidence of hybridization between King and Blue-eyed Shags was obtained through field observations of presumed pairs allopreening and standing together on nest rims. At Isla Chata, Santa Cruz Province, in a colony of approximately 800 shags, of which about 85% were Blue-

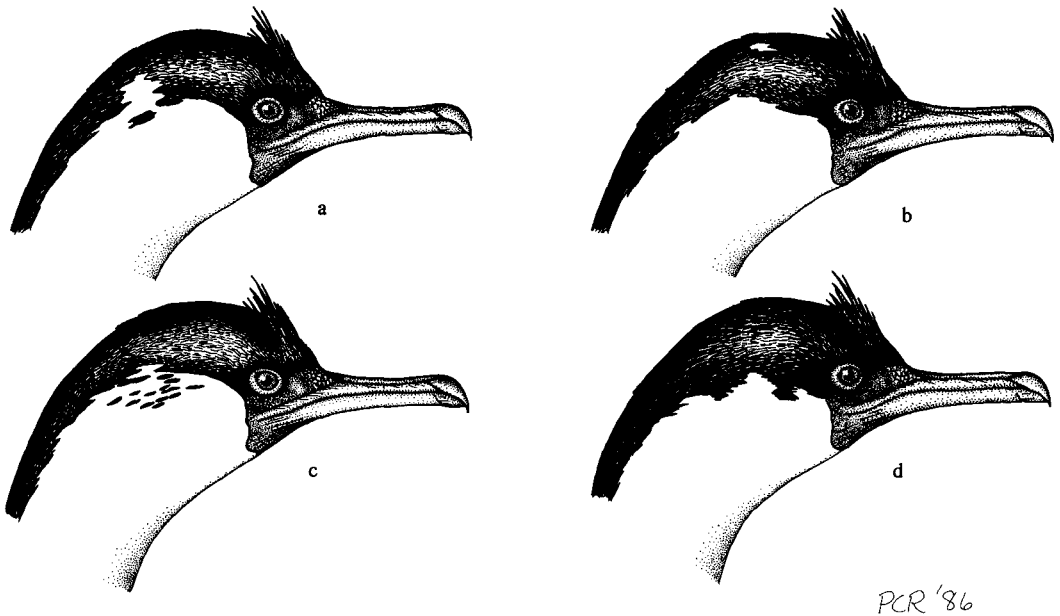


FIGURE 2. Atypical cheek and head feathering in adult specimens of King and Blue-eyed Shags from areas of allopatry: a) AMNH 730166, Chonos Islands, Chile; b) USNM 536649, Shag Rocks, South Atlantic Ocean; c) USNM 548038, Antarctica; and d) AMNH 730172, Macquarie Island.

eyed Shags and 15% were King Shags, I observed 24 obvious pairs in the part of the colony nearest me. Fourteen of these were mixed pairs of adult birds of clearly allocatable form, and only ten pairs were of like form, two of these like pairs being between King Shags. King Shags were significantly more often represented in pairs than expected based on their frequency within the colony ( $\chi^2 = 45.6$ ,  $df = 1$ ,  $P < 0.001$ ), but the number of Blue-eyed Shags represented in pairs did not differ significantly from expected ( $\chi^2 = 0.11$ ,  $df = 1$ ,  $P > 0.05$ ). The frequency of mixed pairs was significantly greater than expected if mating were at random ( $\chi^2 = 19.12$ ,  $P < 0.001$ ). At Monte León, in a colony of some 900 shags of which about 75% were Blue-eyed Shags and 25% King Shags, I observed 28 obvious pairs in the nearest part of the colony. Of these, 17 were mixed pairs, but only 11 pairs were between like forms, four of these between King Shags. King Shags were represented in pairs significantly more often than expected based on their frequency within the colony ( $\chi^2 = 28.0$ ,  $df = 1$ ,  $P < 0.001$ ), but the number of Blue-eyed Shags represented in pairs did not differ significantly from expected ( $\chi^2 = 0.43$ ,  $df = 1$ ,  $P > 0.05$ ). The frequency of mixed pairs was again significantly greater than if mating were at random ( $\chi^2 = 11.77$ ,  $P < 0.001$ ).

At both of these localities I also observed one presumed hybrid paired with a Blue-eyed Shag.

An adult male shag from Puerto Deseado (KUMNH [University of Kansas Museum of Natural History] 82167) and two females collected at Monte León, an adult (KUMNH 82218) and a juvenile (KUMNH 82223), were intermediate in cheek pattern and therefore probable hybrids between King and Blue-eyed Shags. The juvenile's dark cheek feathering was more extensive than in typical juvenile Blue-eyed Shags, but less extensive than in typical juvenile King Shags. The adults had intermediate demarcation lines that curved neither up toward the eyes nor down away from them. None of the three intermediates had any trace of a white dorsal patch, the only other plumage character that, when present, reliably distinguishes King from Blue-eyed Shags. All other specimens examined from areas of cooccurrence were clearly attributable to one form or the other.

#### STATISTICAL ANALYSES

King and Blue-eyed Shags both have relatively wide ranges in southern South America, and preliminary statistical analyses demonstrated the existence of geographic variation and sexual dimorphism. To avoid these confounding effects I

compared the two forms statistically by locality and sex.

*Comparisons of means between species.* Very few adults were represented in the Monte León sample, and variation in body weight among juvenile female Blue-eyed Shags from this site was extremely large (range = 1,350–2,400 g, SD = 314), suggesting that some of these juveniles, although they were fledged and flighted when collected, were still under parental care and had not yet reached adult size. Thus, results using specimens from this locality were considered less reliable than from other localities.

Means for most external and skeletal measurements for female King and Blue-eyed Shags from each of the three localities of cooccurrence (sample sizes of males were too small to permit analyses) were almost identical for both forms (Table 2). Only five measurements differed significantly between forms at a locality, and these only slightly: lacrimal height, culmen length, sacral length, scapula length, and coracoid length. All significant differences were relatively small, only sacral length being significant to the  $P < 0.01$  level; the majority of variables did not differ between forms. Much greater differences were found between localities, for which 23 measures differed; no interaction effects were present.

*Multivariate comparisons between King and Blue-eyed Shags.* In a principal component analysis using only female King and Blue-eyed Shags from Puerto Deseado (the groups with the largest samples), principal components I–IV (PC-I to -IV) were significant (Table 3), but PC-III and -IV constituted a region of sphericity and were not interpreted. The first four factors explained 65% of the total variance. There was no significant difference between forms on PC-I (Fig. 3), a shape axis (Table 3) for interorbital width, lacrimal width, sacral length, and ischial terminus width; of these, lacrimal width explained by far the greatest amount of variance. PC-II was a general size axis on which lacrimal height and width and interacetabular width were uncorrelated, whereas ischial terminus width was negatively correlated with size. Scores for King Shags averaged significantly higher than those for Blue-eyed Shags on PC-II, being positive values in all but one case; this shows that King Shags were larger in size than were Blue-eyed Shags. The fact that PC-I was a shape axis rather than a size axis demonstrates the similarity between female King and Blue-eyed Shags from Puerto Deseado.

A backstepping discriminant function analysis between female Blue-eyed ( $n = 37$ ) and King ( $n = 12$ ) Shags from Puerto Deseado distinguished only 75.0% of the Blue-eyed and 70.3% of the King Shags, for a total correctly identified of only 71.4%. The final discriminant model used seven variables (of the 30 available); the Wilks' lambda was very high ( $\lambda = 0.56$ ) and the eigenvalue was relatively low (0.80), although the  $F$ -statistic was statistically significant ( $F = 4.67$ ;  $df = 7, 41$ ;  $P < 0.001$ ). The Mahalanobis'  $D$  between King and Blue-eyed Shags was 2.03 ( $P > 0.05$ ). CV-I was a contrast between furcula length (standardized coefficient = 1.10) and tarsometatarsus length (-0.83). The other variables in the model were lacrimal height (0.61), culmen length (-0.55), interacetabular width (-0.55), sacral length (0.70), and preacetabular length (0.48). The high Wilks' lambda and low eigenvalue showed that the discriminant function was weak, and the non-significant Mahalanobis'  $D$  showed that female King and Blue-eyed Shags from Puerto Deseado are extremely similar in skeletal size and proportions. Scores for female King and Blue-eyed Shags overlapped almost entirely on CV-I (Fig. 4).

When female Blue-eyed Shags from Región X were used as unknowns in a discriminant function analysis between female King and Blue-eyed Shags from Puerto Deseado (Fig. 4), the Mahalanobis'  $D$  between Blue-eyed Shags from Región X and Puerto Deseado was 0.03 ( $P > 0.05$ ), whereas between Blue-eyed Shags from Región X and King Shags from Puerto Deseado it was 2.03 ( $P > 0.05$ ). Seven of the ten Blue-eyed Shags from Chile were identified correctly as Blue-eyed Shags and three incorrectly as "King Shags."

In a principal component analysis of females from Puerto Deseado, Monte León, and Ushuaia, about 80% of the variance was explained by the first three factors (Table 3). The effect of locality as tested by two-way analysis of variance was significant for scores on PC-I and -II but not those on PC-III. Scores of the two forms did not differ significantly for any of the first three factors, nor were there significant interaction effects, showing that forms did not differ significantly more at one locality than at others. In most cases, at each locality and for each factor the mean principal component scores were similar for both forms, and the range for the smaller sample was contained in the range for the larger (Fig. 5). Exceptions to this were PC-II for Puerto Dese-

TABLE 2. Univariate statistics for female King and Blue-eyed Shags from three localities of overlap. Values given as "mean  $\pm$  standard deviation (*n*)." Significance levels from two-way analyses of variance; first level for each variable is significance for species, second for locality, and third for interaction effects.

Variable (significance)	Pto. Deseado King	Pto. Deseado Blue-eyed	Mte. León King	Mte. León Blue-eyed	Ushuaia King	Ushuaia Blue-eyed
Total mass, g (ns,***,ns)	2,095 $\pm$ 153 (13)	2,065 $\pm$ 118 (41)	2,117 $\pm$ 360 (6)	2,023 $\pm$ 312 (15)	2,345 $\pm$ 202 (25)	2,443 $\pm$ 142 (4)
Muscle/skel mass, g (ns,***,ns)	1,155 $\pm$ 77 (12)	1,164 $\pm$ 65 (21)	1,210 $\pm$ 185 (6)	1,139 $\pm$ 139 (15)	1,263 $\pm$ 85 (16)	1,355 $\pm$ 35 (2)
External culmen I (ns,***,ns)	54.25 $\pm$ 1.60 (12)	54.86 $\pm$ 2.15 (21)	57.00 $\pm$ 2.45 (4)	54.93 $\pm$ 3.20 (14)	60.64 $\pm$ 2.56 (14)	60.50 $\pm$ 2.12 (2)
Wing I (ns,ns,ns)	62.42 $\pm$ 1.68 (12)	61.09 $\pm$ 2.51 (21)	63.00 $\pm$ 2.94 (4)	62.07 $\pm$ 4.68 (14)	62.07 $\pm$ 3.45 (15)	65.00 $\pm$ 0.00 (2)
Wing arc I (ns,ns,ns)	284.00 $\pm$ 4.71 (11)	284.19 $\pm$ 5.33 (21)	289.25 $\pm$ 11.87 (4)	290.93 $\pm$ 10.31 (14)	285.33 $\pm$ 27.93 (15)	294.50 $\pm$ 0.71 (2)
Tail I (ns,***,ns)	117.83 $\pm$ 6.03 (12)	121.57 $\pm$ 8.90 (21)	126.50 $\pm$ 7.14 (4)	132.21 $\pm$ 10.47 (14)	117.80 $\pm$ 6.63 (15)	119.50 $\pm$ 10.61 (2)
Cranial w (ns,ns,ns)	35.82 $\pm$ 0.56 (12)	35.64 $\pm$ 0.73 (36)	36.12 $\pm$ 1.65 (6)	35.37 $\pm$ 0.99 (14)	36.49 $\pm$ 0.80 (27)	36.23 $\pm$ 1.15 (3)
Cranial h (ns,ns,ns)	25.28 $\pm$ 0.45 (12)	24.96 $\pm$ 0.69 (36)	25.37 $\pm$ 0.88 (6)	25.04 $\pm$ 0.77 (14)	25.41 $\pm$ 0.68 (27)	24.97 $\pm$ 1.10 (3)
Interorbital w (ns,*,ns)	15.61 $\pm$ 0.92 (12)	15.20 $\pm$ 1.06 (36)	15.45 $\pm$ 0.54 (6)	15.01 $\pm$ 0.86 (14)	16.26 $\pm$ 1.37 (27)	16.43 $\pm$ 0.75 (3)
Frontal I (ns,***,ns)	26.43 $\pm$ 0.89 (12)	25.93 $\pm$ 0.82 (36)	26.13 $\pm$ 0.79 (6)	25.45 $\pm$ 1.36 (14)	27.53 $\pm$ 1.07 (23)	27.50 $\pm$ 1.25 (3)
Rear skull I (ns,*,ns)	38.53 $\pm$ 0.85 (12)	37.79 $\pm$ 1.03 (36)	38.77 $\pm$ 1.26 (6)	37.60 $\pm$ 1.29 (15)	39.04 $\pm$ 0.92 (23)	39.60 $\pm$ 0.30 (3)
Lacrimal w (ns,*,ns)	13.62 $\pm$ 0.72 (12)	13.20 $\pm$ 0.51 (37)	13.30 $\pm$ 0.70 (6)	13.01 $\pm$ 0.52 (15)	14.18 $\pm$ 0.71 (23)	13.63 $\pm$ 0.29 (3)
Culmen I (*,*,ns)	2.87 $\pm$ 0.36 (12)	2.96 $\pm$ 0.41 (37)	3.37 $\pm$ 0.50 (6)	3.12 $\pm$ 0.57 (15)	3.23 $\pm$ 0.47 (23)	3.40 $\pm$ 0.44 (3)
Culmen I (*,***,ns)	63.50 $\pm$ 1.82 (12)	62.93 $\pm$ 2.11 (34)	64.33 $\pm$ 0.73 (6)	61.69 $\pm$ 2.72 (14)	68.56 $\pm$ 2.80 (26)	67.10 $\pm$ 1.66 (3)
Culmen w (ns,ns,ns)	11.48 $\pm$ 0.58 (11)	11.24 $\pm$ 0.65 (37)	11.05 $\pm$ 1.40 (6)	11.17 $\pm$ 0.69 (15)	11.93 $\pm$ 0.65 (23)	11.63 $\pm$ 0.15 (3)
Culmen h (ns,ns,ns)	9.44 $\pm$ 0.45 (12)	9.12 $\pm$ 0.58 (37)	9.25 $\pm$ 0.67 (6)	9.17 $\pm$ 0.45 (15)	9.55 $\pm$ 0.59 (23)	9.67 $\pm$ 0.57 (3)
Quadrate I (ns,ns,ns)	16.02 $\pm$ 0.45 (12)	15.88 $\pm$ 0.32 (39)	16.35 $\pm$ 0.85 (6)	16.13 $\pm$ 0.66 (15)	16.31 $\pm$ 0.51 (27)	16.10 $\pm$ 0.44 (3)
Sternal w (ns,*,ns)	66.08 $\pm$ 2.54 (13)	65.92 $\pm$ 2.45 (43)	67.03 $\pm$ 2.89 (6)	65.15 $\pm$ 3.51 (13)	69.96 $\pm$ 3.05 (27)	68.05 $\pm$ 2.48 (4)
Interacetabular w (ns,ns,ns)	16.54 $\pm$ 0.65 (13)	16.60 $\pm$ 0.80 (42)	16.95 $\pm$ 0.85 (6)	16.74 $\pm$ 0.93 (14)	17.33 $\pm$ 0.92 (27)	16.95 $\pm$ 1.08 (4)
Sacral I (**,*,ns)	119.22 $\pm$ 2.19 (12)	117.66 $\pm$ 3.45 (43)	122.30 $\pm$ 4.23 (6)	116.29 $\pm$ 4.38 (14)	122.52 $\pm$ 5.20 (27)	121.30 $\pm$ 3.94 (4)
Iliac wing w (ns,*,ns)	38.95 $\pm$ 2.22 (13)	38.36 $\pm$ 1.64 (43)	38.50 $\pm$ 2.16 (6)	39.03 $\pm$ 1.99 (15)	40.59 $\pm$ 2.10 (27)	40.35 $\pm$ 2.09 (4)
Antitrochanter w (ns,***,ns)	35.08 $\pm$ 1.38 (13)	34.56 $\pm$ 0.86 (43)	35.77 $\pm$ 0.99 (6)	34.55 $\pm$ 1.33 (14)	36.21 $\pm$ 1.26 (27)	36.40 $\pm$ 1.11 (4)
Ischial terminus w (ns,ns,ns)	40.18 $\pm$ 1.79 (13)	39.46 $\pm$ 2.18 (43)	38.90 $\pm$ 2.46 (6)	38.42 $\pm$ 2.09 (14)	40.75 $\pm$ 2.15 (27)	40.05 $\pm$ 2.62 (4)
Furcula I (ns,***,ns)	62.07 $\pm$ 1.79 (13)	60.52 $\pm$ 1.50 (43)	61.67 $\pm$ 2.87 (6)	60.95 $\pm$ 2.79 (12)	64.08 $\pm$ 2.49 (27)	62.93 $\pm$ 1.72 (3)
Scapula I (*,***,ns)	82.11 $\pm$ 2.10 (13)	80.93 $\pm$ 2.21 (43)	82.78 $\pm$ 3.49 (6)	79.09 $\pm$ 3.65 (15)	85.24 $\pm$ 2.74 (27)	85.24 $\pm$ 2.12 (4)
Coracoid I (*,***,ns)	61.50 $\pm$ 1.48 (13)	60.73 $\pm$ 1.30 (43)	63.10 $\pm$ 3.12 (6)	61.13 $\pm$ 3.00 (15)	63.90 $\pm$ 2.46 (27)	63.25 $\pm$ 1.92 (4)
Coracoid articular I (ns,***,ns)	20.30 $\pm$ 0.68 (13)	20.18 $\pm$ 0.90 (43)	20.57 $\pm$ 0.97 (6)	20.48 $\pm$ 1.02 (15)	21.32 $\pm$ 1.29 (27)	21.77 $\pm$ 1.05 (4)
Humerus head w (ns,ns,ns)	22.26 $\pm$ 0.78 (13)	22.53 $\pm$ 1.29 (43)	22.35 $\pm$ 0.90 (6)	21.72 $\pm$ 0.76 (15)	22.70 $\pm$ 0.96 (27)	22.82 $\pm$ 0.53 (4)
Humerus I (ns,*,ns)	140.12 $\pm$ 2.81 (13)	139.73 $\pm$ 2.98 (42)	143.52 $\pm$ 5.34 (6)	140.65 $\pm$ 6.68 (15)	142.76 $\pm$ 3.87 (26)	143.97 $\pm$ 4.02 (4)
Ulna I (ns,ns,ns)	150.60 $\pm$ 2.58 (12)	149.24 $\pm$ 3.65 (38)	153.60 $\pm$ 5.85 (6)	150.99 $\pm$ 7.49 (14)	152.28 $\pm$ 4.34 (27)	151.70 $\pm$ 4.82 (3)
Carpometacarpus I (ns,ns,ns)	64.04 $\pm$ 1.73 (12)	63.46 $\pm$ 1.62 (38)	64.60 $\pm$ 2.57 (6)	63.15 $\pm$ 3.00 (15)	65.00 $\pm$ 1.94 (26)	63.73 $\pm$ 2.49 (3)
Manus digit 2 phalanx I (ns,ns,ns)	23.87 $\pm$ 0.69 (12)	23.98 $\pm$ 0.90 (39)	24.18 $\pm$ 0.29 (6)	23.89 $\pm$ 1.34 (15)	24.69 $\pm$ 0.88 (27)	24.63 $\pm$ 1.55 (3)
Femur I (ns,***,ns)	55.40 $\pm$ 1.11 (13)	55.56 $\pm$ 1.38 (43)	57.18 $\pm$ 2.07 (6)	55.89 $\pm$ 3.08 (15)	58.07 $\pm$ 2.17 (27)	58.22 $\pm$ 1.47 (4)
Tibiotarsus I (ns,***,ns)	107.25 $\pm$ 1.36 (13)	107.05 $\pm$ 2.62 (43)	109.93 $\pm$ 5.30 (6)	107.49 $\pm$ 5.11 (15)	111.17 $\pm$ 3.73 (27)	112.17 $\pm$ 3.75 (4)
Tarsometatarsus I (ns,*,ns)	61.68 $\pm$ 1.18 (12)	61.62 $\pm$ 1.52 (39)	63.22 $\pm$ 2.16 (6)	61.11 $\pm$ 2.73 (15)	63.92 $\pm$ 2.23 (27)	62.93 $\pm$ 2.48 (3)
Pes digit 4 phalanx I (ns,***,ns)	25.52 $\pm$ 0.44 (12)	25.53 $\pm$ 0.80 (39)	26.10 $\pm$ 1.21 (6)	25.54 $\pm$ 1.38 (15)	26.65 $\pm$ 0.95 (27)	26.97 $\pm$ 0.93 (3)

ns =  $P > 0.05$ , \* =  $P \leq 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .



TABLE 3. Factor loadings, significance, and summary statistics on PC-I and -II for female King ( $n = 12$ ) and Blue-eyed ( $n = 37$ ) Shags from Puerto Deseado, and PC-I to -III for King and Blue-eyed Shags from Puerto Deseado, Monte León ( $n = 6$  King and 14 Blue-eyed Shags, respectively), and Ushuaia ( $n = 27, 3$ ). Significant positive (+) and negative (-) factor loadings for correlation coefficients for Puerto Deseado only ( $df = 48, P < 0.05$ ) and three localities ( $df = 96, P < 0.05$ ) are indicated.

Variable	Puerto Deseado only		Three localities		
	PC-I	PC-II	PC-I	PC-II	PC-III
Cranial width	-0.232	0.356+	0.565+	0.365+	-0.040
Cranial height	-0.022	0.409+	0.503+	0.248+	-0.594-
Interorbital w	0.296+	0.434+	0.598+	0.051	-0.035
Frontal length	0.020	0.318+	0.597+	0.292+	-0.163
Rear skull l	0.034	0.698+	0.653+	0.321+	0.007
Lacrimal h	0.150	0.228	0.493+	0.302+	-0.496-
Lacrimal w	0.993+	-0.060	0.750+	-0.661-	0.005
Culmen l	0.180	0.578+	0.733+	0.320+	-0.120
Culmen w	-0.011	0.364+	0.421+	0.303+	-0.371-
Culmen h	-0.189	0.538+	0.433+	0.340+	-0.117
Quadrate l	-0.102	0.578+	0.571+	0.298+	0.381+
Sternal w	-0.065	0.571+	0.664+	0.389+	0.085
Interacetabular w	0.005	0.229	0.512+	0.235+	-0.023
Sacral l	0.333+	0.435+	0.721+	0.197+	0.029
Iliac wing w	-0.157	0.434+	0.506+	0.377+	0.030
Antitrochanter w	0.062	0.537+	0.680+	0.313+	0.064
Ischial terminus w	0.425+	-0.370	0.428+	0.214+	0.190
Furcula l	0.004	0.741+	0.782+	0.407+	0.040
Scapula l	-0.180	0.758+	0.648+	0.520+	0.126
Coracoid l	0.023	0.824+	0.760+	0.435+	0.261
Coracoid articular l	0.132	0.534+	0.685+	0.280+	0.093
Humerus head w	0.065	0.561+	0.510+	0.279+	0.179
Humerus l	0.195	0.618+	0.655+	0.368+	0.416
Ulna l	0.213	0.651+	0.663+	0.225+	0.412
Carpometacarpus l	0.099	0.741+	0.666+	0.415+	0.427
Manus digit 2 phalanx l	0.168	0.549+	0.541+	0.316+	0.350
Femur l	0.040	0.491+	0.722+	0.352+	0.324
Tibiotarsus l	0.141	0.643+	0.745+	0.374+	0.277
Tarsometatarsus l	-0.042	0.691+	0.712+	0.438+	0.328
Pes digit 4 phalanx l	0.046	0.439+	0.622+	0.371+	0.385
Summary					
Eigenvalue	0.020	0.010	0.025	0.010	0.003
% variance explained	32.80	17.08	51.63	21.28	6.87
ANOVA					
Locality <i>F</i>	—	—	5.80**	8.01***	0.14 ns
Species <i>F</i>	0.27 ns	6.62*	0.19 ns	3.22 ns	0.45 ns
Interaction <i>F</i>	—	—	1.02 ns	0.45 ns	0.46 ns

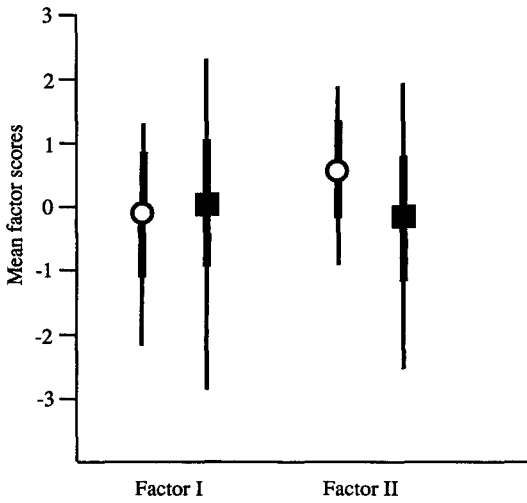
ns =  $P > 0.05$ , \* =  $P \leq 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

ado, which as noted above was significantly different, and PC-III for Monte León, for which the range of the smaller sample was greater than for the larger sample. On PC-II King Shags had slightly larger scores than Blue-eyed Shags at each locality, although the differences were not significant. PC-I and -III showed no consistent pattern in relative mean scores of King and Blue-eyed Shags. PC-I was a strong general size axis (Table 3), and PC-II contrasted all variables (except the uncorrelated interorbital width) with lacrimal width, which was strongly negatively

correlated with size. PC-III contrasted limb elements with cranial height, lacrimal height, and culmen width. Discriminant function analyses were not done between female King and Blue-eyed Shags from Monte León and Ushuaia because of the small sample of King Shags from the former locality and Blue-eyed Shags from the latter.

#### COMPARISONS OF ALLOZYMES

Nine loci were variable in this analysis: EST-1, EST-D, GOT-S, G-6-PD, PEP-B (LGG), PEP-C



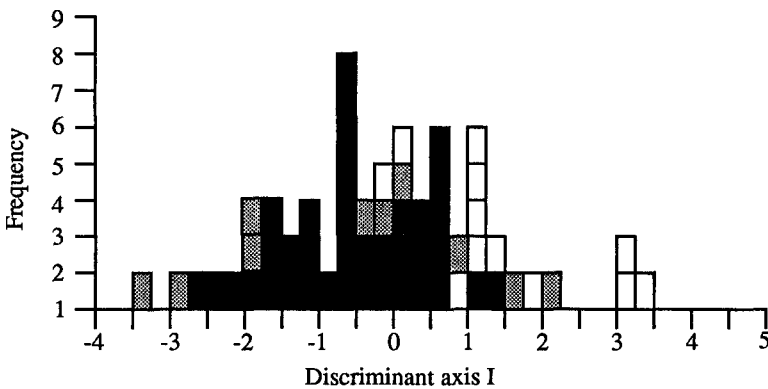
○ = Puerto Deseado female King Shags, *n* = 12  
 ■ = Puerto Deseado female Blue-eyed Shags, *n* = 37

FIGURE 3. Means, standard deviations, and ranges for scores on PC-I and -II for female King and Blue-eyed Shags from Puerto Deseado.

(LA-2), PEP-D (PP), PEP-E (LA-1), and 6-PGD. PGM-2 and -3 and CK-1 were also polymorphic but were not used because of post-translational modification, evidenced by larger numbers of bands in tissues which had undergone thawing

more often. The following 29 loci were monomorphic for both King and Blue-eyed Shags (the number of individuals examined for each locus is given in parentheses after the locus name): ACON-M (*n* = 79); ADH (135); ADK (78); AKP (25); ALD-1 (52); ALD-2 (36); EAP (101); F-1,6-DP (56); FUM-1 (92); FUM-2 (92); GDH (133); GOT-M (148);  $\alpha$ GPDH-1 (72);  $\alpha$ GPDH-2 (48); GPI (71); ICD-1 (22); ICD-2(22); LAP-1 (115); LDH-1 (130); LDH-2 (60); MDH-1 (102); MDH-2 (147); MPI (22); NP (81); PGM-1 (134); PK-1 (64); SDH-A (85); SOD-A (81); SOD-B (73).

Allele frequencies for each form at each locality of cooccurrence and for all populations combined are given in Table 4. One uncommon allele was found only in the Blue-eyed Shag (EST-1c) and four uncommon alleles were found only in the King Shag (EST-1d; G-6PDa, c; PEP-Da). No alleles fixed in one form were absent from the other. Levels of heterozygosity were approximately equal in King and Blue-eyed Shags at Puerto Deseado and across all populations combined (Table 5), but were much higher for Blue-eyed Shags at both Monte León and Ushuaia than for King Shags from those localities. The percentage of polymorphic loci was low in King Shags from Monte León and Blue-eyed Shags from Ushuaia, perhaps reflecting the small sample sizes from these localities.



□ = female Puerto Deseado King Shags  
 ■ = female Puerto Deseado Blue-eyed Shags  
 ▨ = female Región X Blue-eyed Shags

FIGURE 4. Scores on CV-I for female King and Blue-eyed Shags from Puerto Deseado, with females from Chile treated as unknowns.

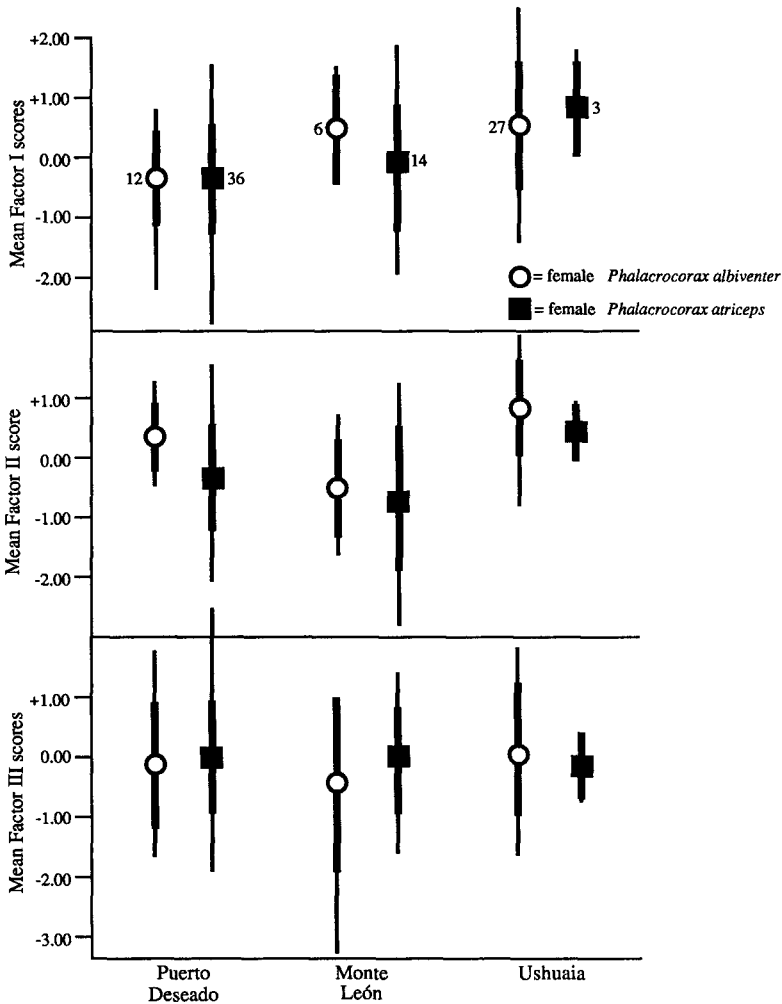


FIGURE 5. Means, standard deviations, and ranges of scores on PC-I, -II, and -III for female King and Blue-eyed Shags at three localities of cooccurrence.

Genetic distances between King and Blue-eyed Shags at Puerto Deseado and Monte León were extremely small; at Puerto Deseado, Nei's D was 0.000; at Monte León, 0.001; and with all localities pooled, 0.000. At Puerto Deseado, Rogers' D was 0.007; at Monte León, 0.016; and with all localities pooled, 0.006. There was, however, slight genetic differentiation between the forms at Ushuaia, where Nei's D was 0.007 and Rogers' D was 0.06.

Hardy-Weinberg predictions for allele frequency distribution were met for EST-D, GOT-S, PEP-D, and 6-PGD (Table 6). EST-1 and, to a lesser degree, PEP-E deviated strongly from Hardy-Weinberg equilibrium. All loci con-

formed to Hardy-Weinberg predictions in both forms at Monte León and in Blue-eyed Shags at Ushuaia.

## DISCUSSION

In every South American region in which the King Shag breeds, the Blue-eyed Shag has also now been documented to occur, with the exceptions of Isla de los Estados and the Falkland Islands. Recently, the Blue-eyed Shag has been documented in Chubut Province (de la Peña 1980), the Beagle Channel (Humphrey et al. 1970), and the east coast of Isla Grande de Tierra del Fuego (Clark 1984). This might represent recent range extension by the Blue-eyed Shag, but

TABLE 4. Allele frequencies for Blue-eyed and King Shags.

Locus	Allele	Puerto Deseado		Monte León			Ushuaia		All	
		Blue-eyed	King	Blue-eyed	King	Hybrid	Blue-eyed	King	Blue-eyed	King
EST-1	a	0.020	0.025	0	0	0	0	0	0.008	0.023
	b	0.960	0.975	1.0	1.0	1.0	1.0	0.957	0.984	0.961
	c	0.020	0	0	0	0	0	0	0.008	0
	d	0	0	0	0	0	0	0.043	0	0.016
EST-D	a	0.180	0.175	0.187	0	0.500	0.250	0.125	0.167	0.185
	b	0.820	0.825	0.813	1.0	0.500	0.750	0.875	0.833	0.815
GOT-S	a	0	0.025	0.063	0	0	0	0	0.056	0.008
	b	1.0	0.975	0.937	1.0	1.0	1.0	1.0	0.944	0.992
G-6-PD	a	0	0.025	0	0	0	0	0.020	0	0.016
	b	1.0	0.950	1.0	1.0	1.0	1.0	0.958	1.0	0.961
	c	0	0.025	0	0	0	0	0.021	0	0.023
PEP-B	a	0.040	0.075	0.125	0.063	0.500	0	0	0.056	0.031
	b	0.960	0.925	0.875	0.937	0.500	1.0	1.0	0.944	0.969
PEP-C	a	1.0	0.950	1.0	0.937	1.0	0.250	0.875	0.937	0.923
	b	0	0.050	0	0.063	0	0.750	0.125	0.063	0.077
PEP-D	a	0	0	0	0	0	0	0	0	0.005
	b	0.980	1.0	1.0	0.937	1.0	1.0	0.958	0.968	0.969
	c	0.020	0	0	0.063	0	0	0.042	0.032	0.023
PEP-E	a	0.940	1.0	0.844	1.0	1.0	0.750	0.937	0.913	0.977
	b	0.060	0	0.156	0	0	0.250	0.063	0.087	0.023
6-PGD	a	0.980	1.0	1.0	1.0	1.0	1.0	0.979	0.992	0.992
	b	0.020	0	0	0	0	0	0.021	0.008	0.008

more likely it is due to the increased numbers of skilled observers in the past 20 years. Despite the recent increases in knowledge, the distributions and relative abundances of King and Blue-eyed Shags in southern South America remain poorly known.

Most of the regions where the Blue-eyed Shag is now abundant were completely glaciated repeatedly during the Pleistocene, the only exceptions being coastal Santa Cruz Province, Argentina and from the northwest corner of Chiloé Island to Mocha Island, Chile (Mercer 1976, Porter et al. 1984). Conversely, most of the areas of present abundance of the King Shag were con-

tinuously free of ice, except for western Isla Grande de Tierra del Fuego (southern Magallanes Province, Chile). In most of their formerly glaciated range, shags typically nest on cliffs, whereas in the unglaciated areas, colonies are on relatively flat surfaces (Rasmussen 1989).

At every locality of cooccurrence from which a large sample is available, one form or the other is numerically predominant by a wide margin (Fig. 1). This suggests that the distributions of the two forms are not static at the present time, possibly because of recency of contact, selection for rare morphs, dominance of one genotype, or environmental conditions selecting against one

TABLE 5. Direct-count ( $\hat{H}_o$ ) and calculated ( $\hat{H}_c$ ) heterozygosities and accompanying standard errors (SE), percent polymorphic loci ( $\hat{P}$ ) using the 0.99 criterion for consideration of a locus as polymorphic, average number of alleles per polymorphic locus for King and Blue-eyed Shags from three localities of overlap and from all localities pooled.

Statistic	Puerto Deseado		Monte León		Ushuaia		All localities	
	King	Blue-eyed	King	Blue-eyed	King	Blue-eyed	King	Blue-eyed
$\hat{H}_o$	0.014	0.014	0.010	0.025	0.020	0.039	0.019	0.021
SE ( $\hat{H}_o$ )	0.007	0.008	0.006	0.012	0.010	0.022	0.009	0.009
$\hat{H}_c$	0.019	0.017	0.010	0.025	0.023	0.039	0.021	0.023
SE ( $\hat{H}_c$ )	0.009	0.009	0.009	0.013	0.009	0.022	0.009	0.009
$\hat{P}$	15.79	15.81	7.89	10.53	18.42	7.89	18.42	18.42
Alleles/poly. locus	2.17	2.00	2.00	2.00	2.00	2.00	2.13	2.13
Alleles/locus	1.18	1.18	1.08	1.11	1.21	1.08	1.32	1.24
SE (alleles/locus)	0.07	0.07	0.04	0.05	0.08	0.04	0.10	0.08

morph. As noted by Devillers and Terschuren (1978), discrepancies in published reports (e.g., Holgersen 1945, Brown et al. 1975, Watson and Angle in Humphrey et al. 1970, Harper in Humphrey et al. 1970) suggest that shag distributions are currently dynamic, although these differences might instead reflect observer error. The first three hypotheses are supported by the high numbers of mixed pairs at breeding colonies. Despite the widespread hybridization, identifiable intermediates comprise only a small fraction of the individuals at any mixed colony, and this suggests that the hybrid zones have been formed very recently, or that there is genetic masking of phenotypes, such as incomplete dominance.

The hypothesis that, in South America, King Shags occur in colder water than Blue-eyed Shags (Brown et al. 1975) is falsified by the lack of correlation between summer water temperatures and the relative distributions of the forms. Behn et al. (1955) noted that, over their entire ranges, the Blue-eyed Shag is primarily distributed in cold water and in islands south of the Antarctic Convergence, and that the King Shag occurs mainly north of the Antarctic Convergence. Since that time the ranges of both have become much better known, and Behn et al.'s (1955) scheme does not accurately summarize the distributions of the two forms. Jehl (in Jehl and Rumboll 1976) noted that it appeared that the Blue-eyed Shag was the predominant form in areas of more turbulent water than the King Shag, but no quantitative data are available to show whether such a relationship actually exists.

Hybridization between King and Blue-eyed Shags was reported by Devillers and Terschuren (1978) but had not been documented by specimens prior to the present study. Devillers and Terschuren published photographs that they believed to be of birds intermediate in cheek pattern. However, inspection of photographs is unreliable in estimating proportions of intermediate specimens in a population because of the changing appearance of a bird due to its posture or the angle of the camera. Data from areas of allopatry, where the potential for hybridization and introgression is minimal, show that individual variation of adults within a form is greater than has previously been recognized. This strongly suggests that not all "intermediate" adults found in areas of cooccurrence are hybrids, but may in actuality only represent simple individual variation. This problem cannot be resolved until the progeny of marked mixed pairs are followed

through to their first basic or subadult plumage, because the cheek patterns of juveniles are dissimilar to those of adults (Rasmussen 1986a).

Devillers and Terschuren's (1978) observation that hybridization is frequent is supported by field data and specimens collected in this study. Siegel-Causey (1986) noted that courtship behaviors do not differ between King and Blue-eyed Shags, and that birds courted others of either form. Despite the plumage-based disassortative mating in mixed colonies, intermediates are difficult to distinguish; almost all adults are easily identified to form. This suggests that hybrids are superficially similar to one or the other parental type in cheek phenotype, and in areas of high rates of hybridization, it rules out the possibility of a single gene controlling cheek pattern with heterozygotes showing intermediate phenotypes—otherwise one would expect a high proportion of intermediates relative to parental phenotypes. At both Isla Chata and Monte León, Blue-eyed Shag phenotypes outnumber King Shag phenotypes by about 3:1; this suggests dominance by genes for expression of the white-cheeked morph, but the presence of a few undisputed intermediates shows that dominance must not be total.

King Shags are known to hybridize occasionally with the Guanay, *Phalacrocorax bougainvillii* (Devillers and Terschuren 1978; Malacalza 1984; B. Mayer, *in litt.*, photographs inspected by author), and a probable hybrid Blue-eyed × Rock Shag specimen was collected at Lago Yehuín in 1986 (Rasmussen and Humphrey, *in prep.*). In addition, the more closely related Kerguelen Shag (*P. verrucosus*) apparently hybridizes with island forms of both King and Blue-eyed Shags (Weimerskirch et al. 1989). Hybridization has very rarely been documented in the Phalacrocoracidae, but this may be partly due to the difficulty of detection of hybridization among the mostly black cormorants and shags.

Female King and Blue-eyed Shags from each of three localities do not differ significantly in size or shape. They are more similar to each other at each locality than to members of their own form at other localities. Alternative hypotheses possibly explaining this are: (1) the same environmental factors have acted on both forms at each locality, causing them to evolve in the same direction; (2) gene flow between the rare and common forms at each locality has led secondarily to their uniformity in size and shape; or (3) the two forms are morphs of the same species

that differ only in plumage characters and have never been separated geographically. If the first hypothesis were true, the forms might be specifically distinct, but if the second hypothesis is true, the forms are not distinct species under the biological species concept, because high levels of interbreeding are required to result in the demonstrated homogeneity between the forms. If the third hypothesis is true, the morphs were incipient species. The second and third hypotheses are both supported by the widespread occurrence of hybridization.

Conclusions on levels of divergence between forms based on allozyme frequencies are often largely congruent with those based on multivariate morphometric data sets (Marten and Johnson 1986, Corbin et al. 1988), although just as often genetic and morphometric data provide markedly different answers on divergence between taxa (Zink 1982, 1986, 1988; Karl et al. 1987; St. Louis and Barlow 1987). In the case of King and Blue-eyed Shags, allozymic and morphometric data sets provide congruent results, showing that the two forms are very similar at localities of overlap. If subspecies are defined as being allopatric or having only a narrow zone of contact during the breeding season, King and Blue-eyed Shags should not be treated as two subspecies of a single species, because their breeding ranges overlap in over 50% of their South American ranges. All available morphometric, allozymic, molt, and behavioral data support Devillers and Terschuren's (1978) treatment of King and Blue-eyed Shags as conspecific morphs of a single species, *Phalacrocorax atriceps*.

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