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MORPHOLOGICAL AND VOCAL VARIATION AMONG SUBSPECIES OF THE BLACK-FACED SHEATHBILL[1]

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Abstract. The Black-faced Sheathbill (*Chionis minor*) is a sedentary and polytypic species. Four allopatric subspecies are known, each breeding on one archipelago in the Southern Indian Ocean. To evaluate the degree of isolation of these four subspecies, morphometrics and vocalizations of adult birds of Iles Kerguelen and Crozet were compared with those of the other localities (Prince Edward and Heard Islands). Two groups were distinguished (Prince Edward-Crozet and Kerguelen-Heard) on geographic and morphological criteria. In the eastern group (Kerguelen-Heard), corresponding to higher latitudes, sheathbills were larger and heavier, following Bergmann's Rule. The sheathbills from Iles Kerguelen also had a lower-pitched voice than those from Iles Crozet, consistent with their larger body size. Moreover, the birds from the southernmost locality (Heard Island) had a shorter culmen, consistent with Allen's Rule, but longer tarsi and deeper sheaths. Within the western group (Prince Edward-Crozet), and at Iles Kerguelen, there also was variability on a microgeographical scale. Differences

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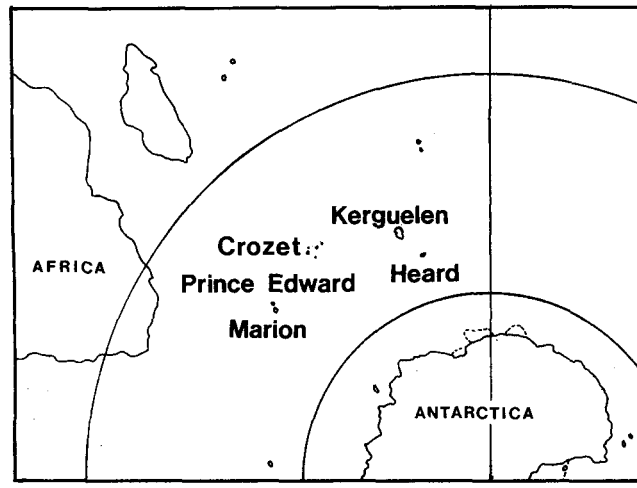

FIGURE 1. Breeding range of the Black-faced Sheathbill in the Southern Indian Ocean. Island names indicated in bold.

between subspecies of Black-faced Sheathbill therefore could be due not only to environmental correlates of latitude, but also to possible genetic drift. The four subspecies are allopatric and do not differ in their breeding schedule or in their general behavior and diet, suggesting that differentiation may be recent and mainly due to geographical isolation.

Key words: speciation, reproductive isolation, morphometrics, vocalizations, Chionis minor, *Black-faced Sheathbill.*

The biological species concept (Mayr 1970) considers species as groups of natural populations capable of interbreeding and separated from other similar groups by mechanisms of reproductive isolation, such as geographical, morphometrical, coloration, behavioral, and phenological. However, variability within the range of a given species also can occur. Thus, geographical variations in body size and coloration are well documented in seabirds, particularly in Procellariiforms or in the White-tailed Tropicbird *Phaethon lepturus* (del Hoyo et al. 1992). Geographical reproductive isolation also seems to play a major role in the Black-faced Sheathbill *Chionis minor.* Four subspecies usually are recognized from body size, leg coloration and caruncles, each subspecies breeding on a remote archipelago in the Southern Indian Ocean (Marchant and Higgins 1993): *C. m. marionensis* at Prince Edward Islands, *C. m. crozettensis* at Iles Crozet, *C. m. minor* at Iles Kerguelen, and *C. m. nasicornis* at Heard Island (Fig. 1). Black-faced Sheathbills are sedentary and have never been recorded on the nearest continent or more than a few kilometers offshore, because of their poor flying abilities (Verheyden and Jouventin 1991).

This paper provides new and more accurate information about biometry of *Chionis minor* than previously available. New insight into the speciation of *Chionis minor* and the role of reproductive isolation may be achieved by combining morphological and ethological studies.

METHODS

Field work was conducted at Iles Kerguelen (48°27′–50°S, 68°37′–70°35′E) in late December 1992, and at Ile de la Possession in the eastern part of the Crozet archipelago (45°50′–46°30′S, 50°–53°21′E) in November 1994. Adult Black-faced Sheathbills were caught using a shepherd's hook. We identified them as adults because they were ringed, and known to have bred in the past or to be at least 3 years old, which is the minimum age of first breeding (Burger 1980a, Jouventin et al. 1996). Measurements (wing length, tarsus length, culmen length, culmen width, and sheath depth) were taken for each individual, following Burger (1980b). Black-faced Sheathbills are sexually dimorphic with males larger than females (Burger 1980b). Therefore, birds were sexed from size and bill shape index (i), the latter defined as follows (Warham 1972, Burger 1980b):

$$i = \text{culmen length} \times \text{culmen width} \times \text{sheath depth} \times 0.1$$

Morphometrics of birds from Iles Kerguelen were compared with those from Prince Edward Islands (data from Marion Island, A. E. Burger, pers. comm.) and Ile de la Possession, using univariate statistics (Kruskal-Wallis H-tests and multiple comparison pairwise z-tests; Scherrer 1984). We obtained the length of the appendages relative to individual body size by dividing tarsus and culmen length by wing length (see Aldrich and James 1991). However, wing length varies in the course of the year due to molt or abrasion of the outer primaries. We measured wing length during the austral spring and assumed that the abrasion stage of the outer primaries was similar in both Iles Crozet and Kerguelen, which allowed us to compare these two localities only. Multivariate analyses were conducted using the

SAS statistical package (SAS Institute 1988); variables were not transformed. A principal component analysis on correlation matrix between the variables used (Digby and Kempton 1987) was conducted, using the PRINCOMP procedure. Discriminant analyses also were performed by running a stepwise analysis in order to determine the two most discriminant parameters (STEPDISC procedure), before subsequent use in the discriminant function analysis (nonparametric method of the DISCRIM procedure using uniform kernel and *a posteriori* cross-validation techniques for estimating error rates in classification).

Data from skins of birds from Heard Island and Iles Kerguelen were compared separately because of the small sample size and the way the skins had been prepared; mean measurements from skins are found in Marchant and Higgins (1993), the raw data were provided by D. James (pers. comm). The measurements taken from skins were not suitable for a multivariate analysis because they differed from those from live birds (see Results). So, we used them only as complementary information.

Visual observations of bare parts coloration and caruncles were performed at close range on a larger sample of adult individuals ($n = 55$), and were easy to obtain because Black-faced Sheathbills are very tame.

Calls ("Bob-calls," see Burger 1980a) of Black-faced Sheathbills from Iles Crozet and Iles Kerguelen were recorded with a Sennheiser-MD 421 microphone and a Uher-4000C tape recorder. Frequency parameters, including modal (MOD), lowest (LOF) and highest (HIF) values of the fundamental frequency, were analyzed after a fast Fourier transformation with an Amiga micro-computer (sampling rate 6,512 Hz; step size 256 points, see Richard 1991). For all tests, probabilities ≤ 0.05 were considered significant, and means are given $\pm$ SD.

RESULTS

BIOMETRY

Univariate statistics. For each locality, measurements are given in Table 1. For live birds, differences between Iles Kerguelen, Prince Edward Islands, and Iles Crozet were significant for tarsus length and bill measurements (Kruskal-Wallis H-test, all $P < 0.001$, see Table 1), and values tended to be highest at Iles Kerguelen, and lowest at Prince Edward Islands. However, most measurements did not differ significantly between Prince Edward Islands and Iles Crozet. Iles Kerguelen females tended to be larger than Iles Crozet and Prince Edward Islands males for culmen length and sheath depth, but these differences were not significant (multiple comparison pairwise z-test, all $P > 0.05$). Iles Crozet sheathbills tended to have the widest and the shortest culmens. Iles Kerguelen males had significantly longer wings than Iles Kerguelen females and Iles Crozet individuals (Kruskal-Wallis H-test, $H_3 = 55.0$, $P < 0.001$, multiple comparison pairwise z-test, all $P < 0.05$); wing length did not differ significantly between Kerguelen females and Iles Crozet males and females (multiple comparison pairwise z-test, all $P > 0.05$). Relative to body size, culmen length did not vary significantly between Iles Crozet and Kerguelen (Mann-Whitney U-test, $z = 0.48$, $P > 0.05$), whereas tarsi were significantly longer on Iles Crozet (Mann-Whitney U-test, $z = 3.69$, $P < 0.001$, see Table 1).

For Iles Kerguelen birds, measurements from skins were significantly smaller than those obtained from live birds (Mann-Whitney U-test, all $P < 0.001$), except for culmen length and sheath depth (sheath depth was significantly higher for skins in females: Mann-Whitney U-test, $z = 2.39$, $P < 0.02$). Kerguelen specimens had a longer culmen than those from Heard Island (at least for males, Mann-Whitney U-test, $U = 14.5$, $n_1 = 9$, $n_2 = 10$, $P < 0.01$). Conversely, the latter tended to have longer tarsi and deeper sheaths than the former, although differences were not significant, probably due to small sample size.

Multivariate analyses. Both principal component and discriminant analyses revealed different population groups. Within each population, there tended to be several differences, but these differences were much less marked than those between populations. The individuals from Prince Edward Islands and Iles Crozet were closer to each other than they were to those from Iles Kerguelen. Principal component analysis used tarsus, culmen length and sheath depth, and Axis 1 and Axis 2 explained 77.0% and 13.5% of the variance, respectively. The two most discriminant parameters were sheath depth and culmen width, if we considered the birds from Prince Edward Islands, Iles Crozet and Iles Kerguelen simultaneously. Seventy-two percent of the individuals subjected to a discriminant analysis based on sex and locality were correctly classified into their *a priori* groups. If we considered localities only, 78.5% of individuals were correctly classified. When data from sheathbills of Iles Crozet and Prince Edward Islands were grouped and compared to those from Iles Kerguelen, the discriminant analysis performed on the two most discriminant parameters without considering sex revealed that only 8.5% of individuals were misclassified.

EXTERNAL FEATURES AND BARE PARTS COLORATION

As at Heard Island (see photographs in Downes et al. 1959), but not at Prince Edward Islands (photographs in Burger 1979, and drawings in Burger 1980a and 1980b) and Iles Crozet, adult Black-faced Sheathbills from Iles Kerguelen seem to have a rounded head, due to the absence of a conspicuous head crest (Fig. 2), and small and not very swollen caruncles. Moreover, the caruncles at the base of the bill of *minor* are present at the sides of the upper mandible only, whereas birds of Iles Crozet and Prince Edward Islands also have prominent caruncles on the forehead at the base of the culmen and, at least for those from Iles Crozet, at the base of the lower mandible and on the chin (Marchant and Higgins 1993; this study). The orbital ring has the same color whatever the locality. At Ile de la Possession, birds have pinkish gray legs, whereas those from Iles Kerguelen have pink legs. Legs also are pink at Heard Island, but they are sometimes black at Prince Edward Islands (Table 1). There was no seasonal variation in bare parts coloration at Iles Crozet and Kerguelen. At Prince Edward Islands, the orbital ring "appeared to be brighter [. . .] in some birds" (Burger 1980b) during the breeding season.

TABLE 1. Measurements (mm; mean ± SD) and coloration of bare parts of adult Black-faced Sheathbills in different localities. Material and references: (1) live birds, this study, (2) live birds, Burger (pers. comm.), (3) skins, mean values in Marchant and Higgins (1993), raw data from D. James (pers. comm.). All sex differences significant ($P < 0.01$) except for sheath depth in the museum specimens from Heard Is.

	n	Iles Kerguelen (1)	*n*	Prince Edward Is. (2)	*n*	Iles Crozet. (1)	*n*	Iles Kerguelen (3)	*n*	Heard Is. (3)
Wing										
males	30	245.8 ± 4.9	24	218.0 ± 5.9	7	221.0 ± 2.6	9	234.2 ± 4.5	9	233.6 ± 6.1
females	29	234.0 ± 4.4	28	207.3 ± 5.2	6	211.3 ± 4.0	6	222.7 ± 2.9	9	220.2 ± 5.4
Tarsus										
males	31	48.4 ± 1.7	45	46.7 ± 1.6	7	45.9 ± 1.6	9	44.6 ± 1.4	10	45.0 ± 1.4
females	29	45.5 ± 1.5	39	44.1 ± 1.1	6	43.3 ± 1.6	6	41.8 ± 2.8	9	42.5 ± 0.7
Culmen length										
males	30	33.7 ± 1.0	45	32.0 ± 0.9	7	29.9 ± 0.6	9	33.7 ± 0.9	10	32.4 ± 1.1
females	29	31.1 ± 0.9	38	30.0 ± 0.9	6	28.4 ± 0.7	6	31.0 ± 0.9	9	29.7 ± 1.3
Sheath depth										
males	30	20.9 ± 1.1	34	16.8 ± 0.8	7	16.9 ± 0.6	7	21.3 ± 1.5	3	22.1 ± 2.6
females	29	17.9 ± 1.0	26	14.5 ± 0.7	6	15.8 ± 0.7	6	18.9 ± 0.7	5	20.2 ± 2.3
Culmen width										
males	30	9.4 ± 0.7	43	9.4 ± 0.4	7	10.9 ± 0.4		—		—
females	29	8.6 ± 0.4	36	8.8 ± 0.5	6	9.7 ± 0.4		—		—
Bill shape index										
males	30	660.2 ± 68.9	33	515.1 ± 41.6	7	552.0 ± 34.9		—		—
females	29	480.5 ± 47.3	26	390.8 ± 30.8	6	437.7 ± 33.1		—		—
Tarsus/wing										
both sexes	58	0.185 ± 0.043	13	0.205 ± 0.007		—		—		—
Culmen/wing										
both sexes	59	0.130 ± 0.006	13	0.135 ± 0.005		—		—		—
Bare parts coloration										
legs	flesh-pink		81.3% pale pink 18.7% dark pink or black		pinkish gray		flesh-pink to white-pink		flesh-pink to pinkish white	
orbital ring	pink		"usually bright pink"		pinkish mauve		pink		pink or flesh-pink	

VOCALIZATIONS

Sonograms are shown in Figure 3. Iles Kerguelen individuals had a significantly lower-pitched voice than those from Iles Crozet: the MOD, LOF and HIF values of the fundamental frequency of Bob-calls were significantly lower in the Kerguelen sheathbills than in their Crozet conspecifics (Mann-Whitney *U*-test, all $P < 0.001$). The differences were so large that no overlap occurred between the two populations (Table 2 and Fig. 4).

DISCUSSION

Our analyses have confirmed the distinction by Peters (in Marchant and Higgins 1993) of two main groups of Black-faced Sheathbills: *marionensis-crozettensis* in the Western Indian Ocean (Fig. 1) and *minor-nasicornis* in the Eastern Indian Ocean; the specimens from Heard Island were not significantly different from those from Iles Kerguelen. Individuals belonging to the *minor-nasicornis* group live at higher latitudes (48°27′ to 50°S for Iles Kerguelen and 53°05′S for Heard Island vs. 45°50′ to 46°30′S for Iles Crozet and 46°54′S for Prince Edward Islands) and have a larger body size than those from the *marionensis-crozettensis* group; this agrees with Bergmann's Rule: body size and mass tend to increase in the coldest parts of a species' range, which generally are at highest latitudes and/or altitude. Moreover, the sheathbills from Iles Kerguelen have proportionally shorter tarsi than those from Iles Crozet, consistent with Allen's Rule: appendages and extremities tend to be shorter in the coldest parts of a species' range. Within the *minor-nasicornis* group, individuals from Heard Island have the shortest culmens (and perhaps the shortest wings if the abrasion stage of the outer primaries is similar to that of the specimens from Iles Kerguelen), also consistent with Allen's Rule. By contrast, their sheaths seem the most prominent, the nonsignificance of the difference being possibly due to our small sample size. But on the whole, the differences in morphometrics suggest an adaptive response to higher latitudes and a colder climate, especially at Heard Island where the mean annual temperature is 1.2°C (Woehler 1991) vs. 4.5°C at Kerguelen (Weimerskirch et al. 1989). Within the *marionensis-crozettensis* group, morphometric differences cannot be explained by Allen's Rule, because latitudes (see above) and mean annual temperatures (5.3°C at Prince Edward Islands [Derenne et al. 1976] vs. 4.8°C at Iles Crozet [Bost et al. 1992]) are similar in both localities. Bare parts, caruncle size, head shape, and coloration of legs

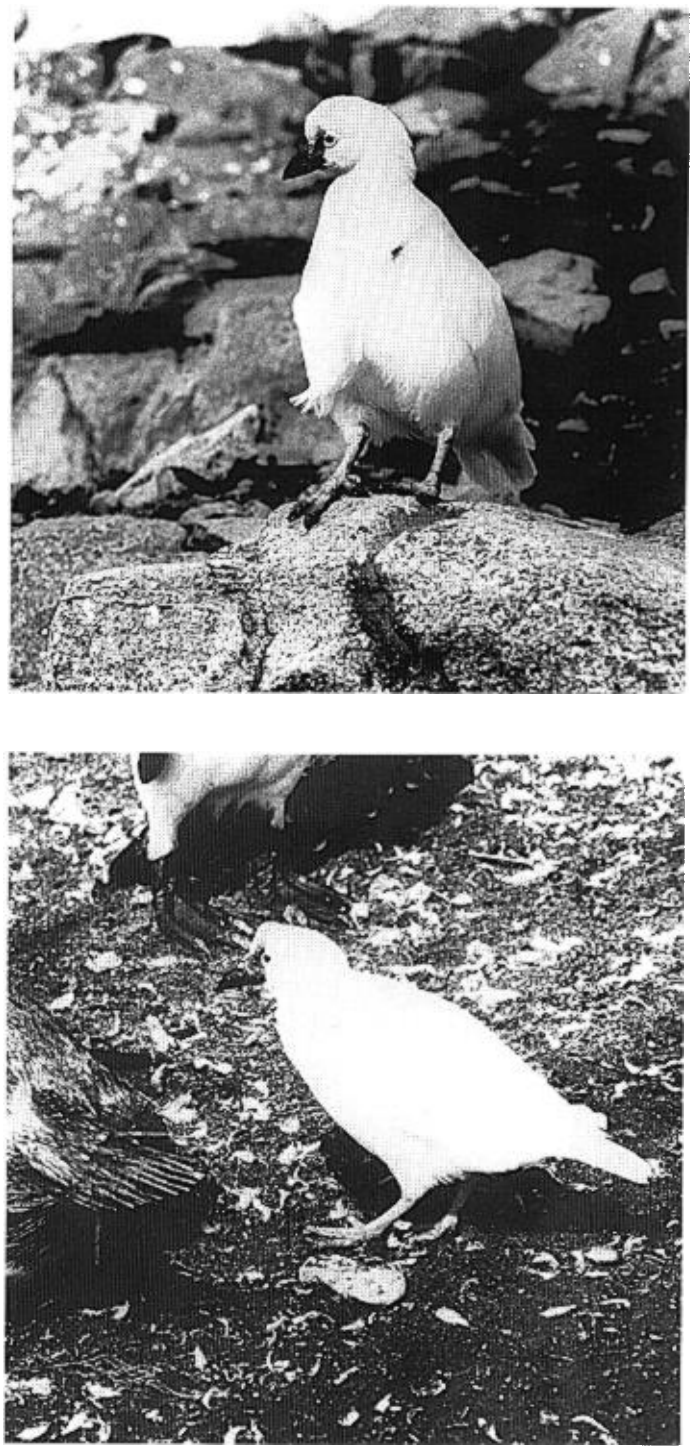

FIGURE 2. Adult Black-faced Sheathbills. Top: *C. m. minor*. Bottom: *C. m. crozettensis* standing behind a King Penguin (*Aptenodytes patagonicus*).

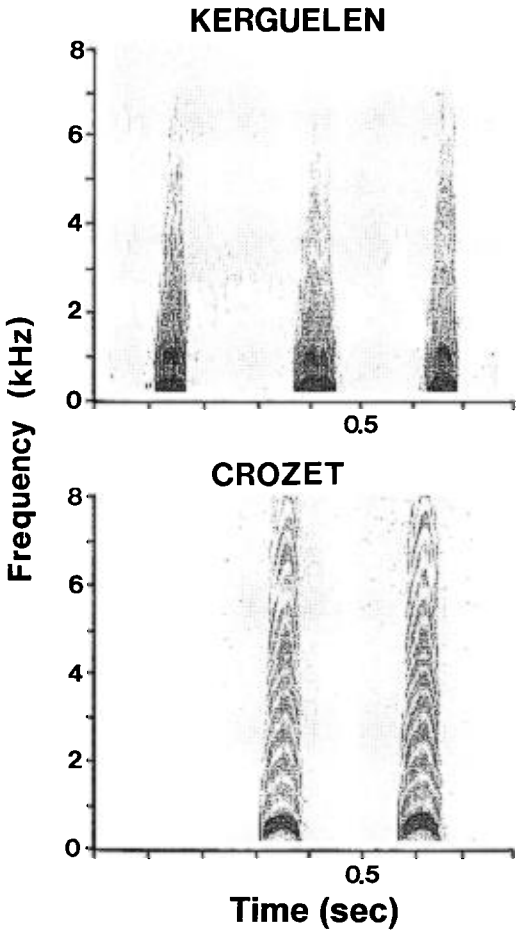

FIGURE 3. Sonograms showing Bob-calls of *Chionis minor minor* from Iles Kerguelen (top) and *C. m. crozettensis* from Iles Crozet (bottom).

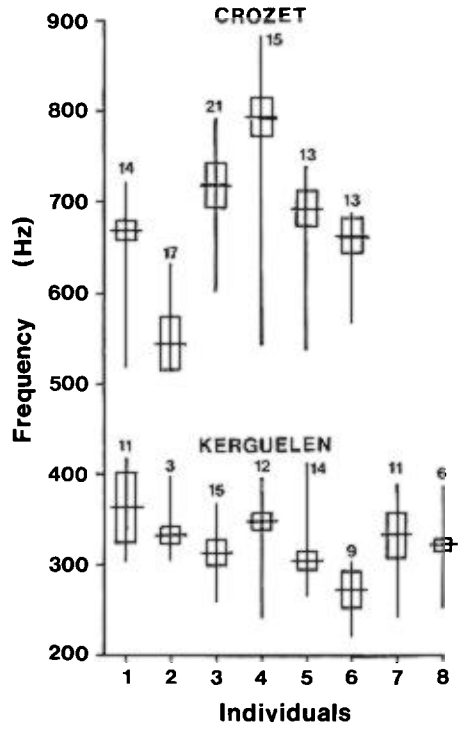

FIGURE 4. Mean values of the modal, lowest and highest components of the fundamental frequency of Bob-calls recorded from Iles Crozet (n = 6) and Kerguelen (n = 8). Vertical bars: range; boxes: SD; figures above plots = number of calls per individual.

also differ between the two main groups (Table 1). But contrary to caruncle size and head shape, leg coloration also varies on a microgeographical scale. This variability is found at Prince Edward Islands (Table 1), but also at Iles Crozet. In this locality, legs are grayish pink in 100% of adult sheathbills from Ile de la Possession in the eastern part of the archipelago vs. 4.8% of adults from Iles des Pingouins in the western part of the archipelago (unpubl. data).

Our results suggest that the differences observed within the *Chionis minor* species are due to geographical isolation: Prince Edward Islands and Iles Crozet are 1,000 km apart, the distance between Iles Crozet and Kerguelen is 1,500 km, and between Iles Kerguelen and Heard Island is about 520 km (Fig. 1). Furthermore, geographical isolation seems to have occurred not only between the four populations of Black-faced Sheathbills which are all allopatric and sedentary (Marchant and Higgins 1993), but also between populations of the same subspecies: movements have never been recorded between Marion and Prince Edward Islands, only about 20 km apart (Burger 1979), nor between the western and the eastern part of the Crozet archipelago, 170 km apart (P. Jouventin, pers. observ.). Because Black-faced Sheathbills are poorly suited for long-distance flights (Verheyden and Jouventin 1991), it is likely that they colonized the archipelagos of the Southern Indian Ocean with the help of the strong pre-

TABLE 2. Mean modal (MOD), lowest (LOF) and highest (HIF) values of the fundamental frequency of the Bob-calls recorded from Kerguelen and Crozet Black-faced Sheathbills.

Locality	MOD (Hz)	LOF (Hz)	HIF (Hz)
Iles Kerguelen (n = 8)	322.8 ± 28.3	258.7 ± 28.9	381.5 ± 36.7
Iles Crozet (n = 6)	679.7 ± 83.4	545.4 ± 31.5	739.9 ± 87.5

vailing westerly winds. Colonization probably occurred from the West to the East, perhaps starting from Patagonia, South Georgia or the Antarctic Peninsula, where the Pale-faced Sheathbill *Chionis alba* lives (Jones 1963). However, it is impossible to know accurately where the differentiation process between *C. alba* and *C. minor* started, as the fossil remains of the ancestor of sheathbills have not yet been discovered (Lowe 1916).

Evolution of Black-faced Sheathbills in the Southern Indian Ocean could have proceeded as follows. In the most southern and coldest localities (Kerguelen, and more especially Heard Islands), a greater body size evolved, following Bergmann's Rule. At the same time, the head crest disappeared, the caruncles became less prominent and the culmens at Heard Island shorter, in agreement with Allen's Rule. The voice, at least at Iles Kerguelen, became lower-pitched than in the northern part of the breeding range (particularly at Iles Crozet), consistent with larger body size as suggested by previous studies (Guillotin and Jouventin 1980, Wallschläger 1980).

Other climatic factors such as humidity, and trophic factors also have been invoked to account for morphological differences between bird populations (Aldrich and James 1991, Moen 1991). Thus, it was necessary to take into account wet-bulb temperature, evaporative power of the air and foraging constraints to explain the variations in the American Robin *Turdus migratorius*, a partially migratory species, the different populations of which breed in different habitats and under very contrasting conditions (Aldrich and James 1991). Yet, the climate of the subantarctic archipelagos in the Southern Indian Ocean is cold-temperate and oceanic. Moreover, these archipelagos are very small land masses dispersed among large ocean areas. The largest of them is Kerguelen (7,200 km^2, almost as large as Corsica); Heard, Prince Edward and Crozet Islands, each covering less than 500 km^2. Temperatures and precipitation at these localities do not vary very much in the course of the year, due to the presence of the ocean which acts as a buffer. Whatever the locality, Black-faced Sheathbills live on the coast where the buffer effect of the ocean is maximized. They also have a wide dietary spectrum, being opportunistic foragers (Marchant and Higgins 1993, Jouventin et al. 1996). Consequently, we can consider mean annual temperature and latitude as the only environmental parameters that vary significantly throughout the range of this sedentary species. Hence, some of the differences observed among the different subspecies of *Chionis minor* (head pattern variations, culmen length, and wing length) probably represent a response to latitude and temperature, whereas the discrepancy with Allen's Rule concerning the long tarsi and deep sheath of Heard Island sheathbills compared to those from Iles Kerguelen suggests that other morphometrics (tarsus length and sheath depth at Heard Island), and leg coloration might be the consequence of genetic drift or a founder event.

There also can be variability within the same locality. Thus, the influence of particular ecological conditions at Iles Kerguelen on body size and mass also has been shown for two seabird species (Bost et al. 1992). For Black-faced Sheathbills, which are terrestrial (Verheyden 1988), the presence of an extensive intertidal zone at Iles Kerguelen gives additional opportunities for feeding and maintaining territories on shores free of penguin and cormorant colonies. However, the intertidal zone is almost absent from other localities (Jouventin et al. 1996). Thus, the greater number of habitats at Iles Kerguelen can explain the level of heterozygosity in the sheathbill population, which is three times higher at Iles Kerguelen than at Iles Crozet (Viot et al. 1993). Population size (3,000–5,000 pairs at Iles Kerguelen vs. 2,000–3,000 pairs at Iles Crozet, Jouventin et al. 1988) might also be another factor of intrapopulational variability. Therefore, genetic variability at Iles Crozet may be insufficient to explain differences between islands. Coloration of legs in sheathbills from Ile de la Possession might be explained by a founder event; this island was probably colonized from the western part of the Crozet archipelago.

However, Black-faced Sheathbills breed at similar dates (Jouventin et al. 1996) and seem to perform the same agonistic and pair displays irrespective of breeding locality (for Prince Edward Islands see Burger 1980a; for Iles Crozet and Kerguelen, C. Verheyden and J. Bried, pers. observ.), suggesting that the speciation process is recent (0.4 to 1 million years ago between Crozet and Kerguelen subspecies, according to Viot et al. 1993). This latter hypothesis also is supported by the known ages of the islands: about 45 million years for Kerguelen and Heard Islands, 10 million years for the eastern part of the Crozet archipelago, less than 500,000 years for the western part (Giret 1987), and about 300,000 years for Prince Edward Islands (McDougall 1971).

More data are still needed: morphometrical data from a large sample of live individuals are lacking for Heard Island. A genetic study, including electrophoretic and mitochondrial DNA analysis, would allow a comparison with similar data collected at Iles Crozet and Kerguelen (Viot et al. 1993), and provide information about within-group differentiation and geographical isolation processes. But other mechanisms of reproductive isolation, such as vocalizations and visual signals (head patterns and bare parts), are useful in avian systematics (e.g., Lanyon 1969, Jouventin 1982, Pierotti 1987). Acoustic and visual species-specific recognition could be investigated to determine the extent of behavioral differences between the subspecies of the Black-faced Sheathbill, perhaps by recording calls from Heard and Prince Edward Islands and conducting playback experiments, and by performing experimental modifications of caruncle size, head crest and leg coloration.

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