



DISTRIBUTION AND RELATIONSHIPS OF SOUTH AMERICAN SKUAS

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INTRODUCTION

The skuas of the *Stercorarius skua* superspecies, or genus «*Catharacta*» (Fig. 1), comprise a group of races or closely related species widespread in the southern oceans and on Antarctica, with one representative isolated in the North Atlantic. The key to their intricate relationships clearly lies in the South American quadrant where all four of the strongly characterized southern forms, here listed binomially, occur within at most 1800 km of each other (Fig. 2). The Chilean Skua, *S. chilensis*, breeds south to the Cape Horn archipelago (Reynolds, 1935), 770 km north of the South Shetlands where both McCormick's Skua, *S. maccormicki*, and the Brown Skua, *S. lonnbergi*, nest (e.g. Watson, 1975). A thousand kilometres—and the Antarctic convergence—separate the Falkland Islands, stronghold of the Falkland Skua, *S. antarcticus*, from the South Shetlands, while South Georgia, where *lonnbergi* occurs alone, is 1350 km from the Falklands. The literature is mute or confusing regarding the respective limits of the ranges of *antarcticus* and *chilensis*.

The Falkland Skua has been generally thought to breed only in that archipelago (Murphy, 1936; Hellmayr and Conover, 1948; Olrog, 1963; Meyer de Schauensee, 1966) but Boswall and Prytherch (1972), Boswall (1973), and Jehl and Rumboll (1976) drew attention to the nesting of *antarcticus*-like birds at Punta Tombo, Chubut. The northern limit of the breeding range of the Chilean Skua has been placed at the mouth of the Río Santa Cruz (Hellmayr and Conover, 1948) or in Chubut (Meyer de Schauensee, 1966, 1970; Olrog, 1963), but from unspecified information, or evidence that Murphy (1936) had judged unsatisfactory. There was a need for a clarification of the ranges of the two forms on the Patagonian coast and this was one of the principal goals of an expedition to Patagonia, the Falkland Islands and the Magellanic area, which I undertook during the austral summer of 1975-1976 under the auspices of the Leopold III Foundation for the Exploration and Conservation of Nature, and in the company of Jean A. Terschuren.

← Fig. 1. Chilean Skua, *Stercorarius chilensis*, Canal Moraleda (45° S.), Chile, 26 January 1976 (above).
Falkland Skua, *Stercorarius skua antarcticus*, Carcass Island, West Falklands, 13 December 1975 (below).

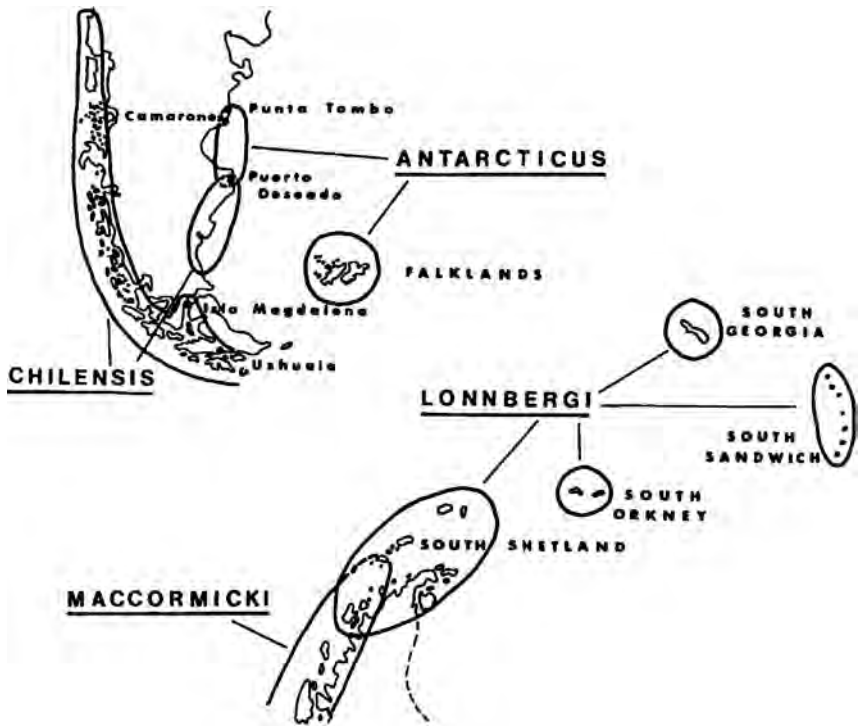


Fig.2. Range of the skuas (*Stercorarius chilensis*, *S. maccormicki*, *S. skua antarcticus* and *S. s. lonnerbergi*) in the South American quadrant.

Particularly, we hoped to find a zone of contact between the two forms, either on the mainland or in the Falklands, where the presence of the Chilean Skua had been mentioned by Wace (1921) and Hamilton (1934, 1937).

METHODS

Falkland Skuas were studied on New Island and Carcass Island, off West Falkland, both of which carry large numbers of breeding birds, between 25 November and 14 December 1975. Smaller groups were scrutinized at Port Stanley and in the Volunteer area of East Falkland on 17-25 November and 20-21 December. A total of 1200 individuals were seen, and detailed plumage descriptions were recorded for the main types, while most others were more briefly characterized by reference to the first. A total of 82 individuals, representing the main trends of variation, were photographed at short distance in colour and black and white, using Kodachrome 64, High Speed Ektachrome,

Agfa CT 18, Ilford FP 4 and Kodak Plus-X film, with a Pentax SP camera and mainly a Novoflex 400 mm telephoto lens. Several hundred breeding Chilean Skuas were seen on Magdalena Island, Strait of Magellan (Fig. 2), on 21 and 22 January 1976, but their shy behaviour permitted only limited morphological observations. Detailed plumage analyses were recorded of birds away from, but probably in the vicinity of, breeding areas at Ushuaia, southern Tierra del Fuego (31 December 1975 and 1 January 1976), and in the Chilean Fjords between Punta Arenas and the Golfo de Corcovado (23-26 January 1976). A total of 150 adult and immature Chilean Skuas were seen closely, detailed notes of their plumage recorded, and colour photographs of 15 of them secured. Twelve fledglings were examined in the hand on Magdalena Island. Along the Patagonian coast, skuas were found at Punta Tombo (13-14 November), Camarones (15 November) and Puerto Deseado (9-13 January), and treated like the Falkland populations, with detailed notes made for all individuals that could be approached closely (106), and colour photographs secured for 30 individuals.

Skua specimens were examined in the British Museum (BM), the Muséum national d'Histoire naturelle (MNHN), the American Museum of Natural History (AMNH), the Museo Argentino de Ciencias Naturales «Bernardino Rivadavia», Buenos Aires (MACN), the Dominion Museum, Wellington, the War Memorial Museum, Auckland, the Canterbury Museum, Christchurch, the National Museum, Melbourne, the Australian Museum, Sidney, the Universitets Zoologiske Museum, Copenhagen, the San Diego Natural History Museum (in 1971), the California Academy of Sciences, the Institut royal des Sciences naturelles de Belgique, the collection of the University of Aberdeen, the Royal Scottish Museum (RSM), and the Zoologisches Museum, Berlin. In particular, photographs and field notes from the South American expedition were compared with the BM collection. Altogether, 68 *chilensis*, 76 *antarcticus*, and one apparent intermediate were seen, as well as 653 skuas of other forms (241 *lonnbergi*, 32 *hamiltoni*, 163 *skua*, 239 *maccormicki*).

FALKLAND SKUA

Although it was the first of the southern skuas to be described (Lesson, 1831 : 616), the Falkland Skua has not been very much studied. Specimens are relatively rare in collections and photographs infrequent, so that even knowledge of its appearance is somewhat confused. Thus, Watson writes as recently as 1975, «small and dark», though the latter is hardly typical. Contrary to the Brown Skua (Stonehouse, 1956; Burton, 1968a, 1968b), the Great Skua, *S. skua* (Perdeck, 1960; Andersson, 1976), McCormick's Skua (Spellerberg, 1971) and the Chilean Skua (Moynihan, 1962), its behaviour has not been specifically studied.



Fig. 3. Adult Falkland Skua, *S. s. antarcticus*, West Falklands, 10 December 1975.

SIZE AND APPEARANCE

The Falkland Skua is usually described as small, Murphy (1936) precisising that it is «the smallest of all known forms of the [superspecies]». Although the statement is strictly correct, based on linear measurements of bill and wing length, it is misleading. The Falkland Skua is a very massive bird (Fig. 3), heavier, more sturdy and larger looking than the longer-winged *chilensis* (pers. obs.), and probably than *maccormicki* (Bennett, 1922). It has a large, angular head and a prominent supra-orbital ridge which gives the eye a deep-set appearance. The bill is short, but very high, blunt and powerful. The tarsus is long (Murphy, 1936), so that the bird stands high, and has a peculiar, long-legged, short-bodied, heavy appearance (Fig. 3). The range of size variation, as seen for instance in «clubs» (Tinbergen, 1953; Perdeck, 1960) or pondside assemblies, does not seem very great (Fig. 4). Among pairs, however, one individual, presumably the female, is usually conspicuously larger than the other. This was also noted for *S. lonnbergi* by Falla (1937), and for *S. skua* by Perdeck (1960), but apparently not by Moynihan (1962) for *S. chilensis*, or Spellerberg (1971) for *S. maccormicki*. Measurements and proportions, derived from the BM series, are shown in Table 1.

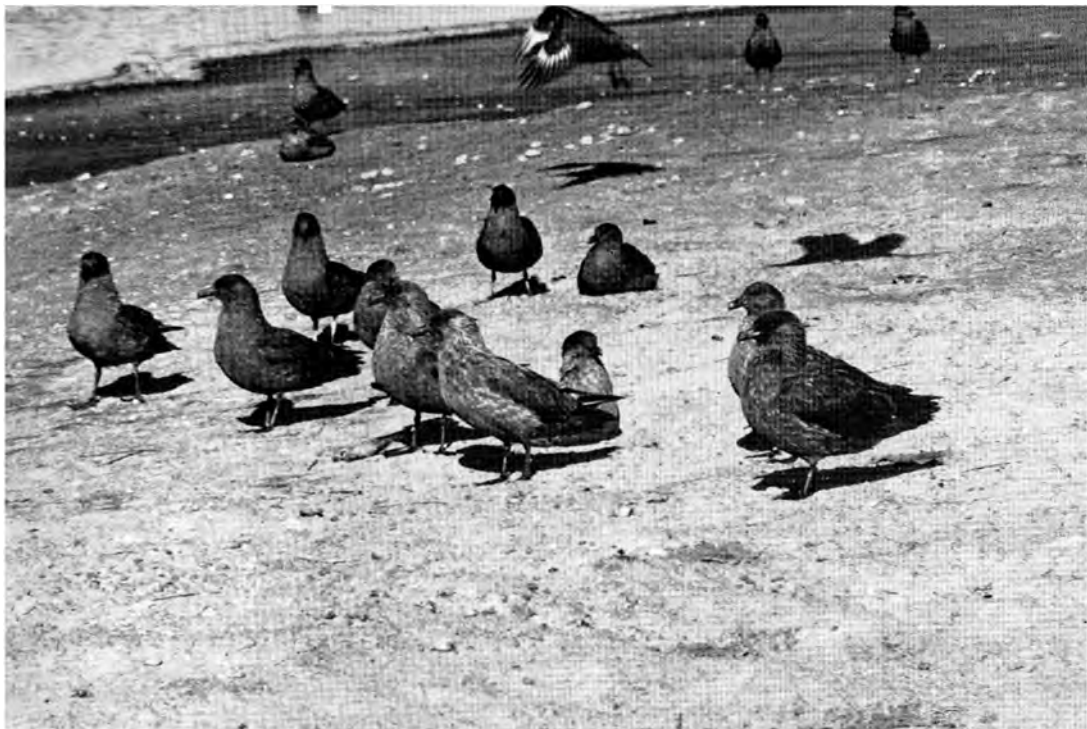


Fig. 4. Group of Falkland Skuas, New Island, West Falklands, 2 December 1975.

ADULT PLUMAGE

The overall appearance of breeding adults is strikingly variable, from very dark and uniform to very light and mottled (Fig. 5). However, no break in the series is visible and the intermediate types are more numerous than the extremes (see Table 2), so that no «morphs» are recognizable.

The ground colour of the plumage is a very dark brown to blackish, a little darker usually on the back and about the head than on the underparts, and darker still, almost black, on upper wing coverts, wing linings, upper surface of flight feathers and tail. The tone is a little lighter, browner, even more vinaceous, less blackish, in lighter birds than in darker ones, but most of the variation is induced by the amount of pale relief.

The pale relief takes exclusively the form of light shaft streaks, or oblong shaft spots, sometimes flaring into a funnel-shaped light tip (Fig. 6). It is pale buff, straw-coloured, golden, whitish or white, rarely rufous, and then generally mixed with another hue.



Fig. 5. Pair of Falkland Skuas, representing light and dark individuals, Carcass Island, 10 December 1975.

On the darkest birds, the relief is confined to sharp shaft streaks on the back and scapulars (Fig. 7), light streaking on the auriculars and sides of the nape, sharp or more diffuse, sparse, central spots on feathers of the underparts, particularly the chest, and expanded light tips to the flank feathers. Almost always, a part of the auriculars, just below and behind the eye, is the lightest area on the bird, the light streaks coalescing into a patch (Fig. 7). Also, the flanks nearly always carry a few big light feather tips, contrasting with the rest of the underparts. Conversely, the tertials, wing coverts, particularly greater and median, and the forehead, supra-orbital ridge, lores, and base of mandible are the last to be invaded by the pale relief, remaining solidly dark, even in quite light birds (Fig. 6). Primaries and secondaries, tail and underwings are always, or almost always unmarked.

The lighter the bird is, the greater is the area involved in pale relief, the larger the light marks, and the paler their tone. The top of the crown is spotted or streaked (Fig. 3, 6), the lower cheeks, auriculars and sides of nape have long narrow streaks, often coalescing on the cheeks, and sometimes on the nape, the ensemble often forming a pale ruff [supporting a forward-slanted dark crown (Fig. 6). Rare, extremely light birds have the whole head very pale, except the area around the eye and lores (Fig. 8). The underparts are variously spotted or even vaguely barred by the whitish centres of small feathers, while big triangular feather tips make a very light flank band (Fig. 3, 6). The



Fig. 6. Adult Falkland Skua, New Island, 7 December 1975.

back and scapulars are sparingly or profusely streaked, and flared tips can be present in addition, sometimes of a different hue from the shaft streaks. This pattern frequently invades the lesser coverts and a varying number of median and greater coverts, often some and not others in a row.

On many, but not all, individuals the shaft streaks of the cheeks and nape are formed by hardened barbs and have a shiny, golden, metallic appearance. These tips are often fused into a reflecting shield on the auriculars (Fig. 3, 6, 7, 8), but apparently never on the nape, contrary to what is seen in small skuas (jaegers, *Stercorarius* sp.) and McCormick's Skua. However, the streaks are often very profuse on the nape, giving it a sparkling appearance (Fig. 3, 6, 7, 8). Many birds appear capped to a greater or lesser extent (Fig. 6, 9, 10). Even very dark birds often have the forecrown and loreal area the darkest, enhanced by slight pallor on the auriculars. On progressively lighter birds the effect becomes more pronounced, until it is broken again by an excess of relief (Fig. 3, 8). However, there are individuals of any overall shade in which this appearance is not detectable.

The underwing lining is always very black (Fig. 1, see also Fig. 9, 10), contrasting sharply with the silvery-grey greater underwing coverts and undersides of the flight feathers, and the white flashes at the base of the primaries. This pattern is particularly conspicuous during



Fig. 7. Dark adult Falkland Skua, New Island, 4 December 1975.

Long Call performances, which are generally directed sideways at partner or intruder.

Some extreme birds (five seen) have pure white shaft streaks and flared tips, the paleness expanding around the tip of the feather (Fig. 8). One skua seen at New Island on 28 November was essentially pure white, with normally pigmented soft parts and even whiter patches in the wing still visible.

In order to quantify the variations, samples of skuas observed in the field were subjectively allocated to four classes, defined as:

- Very light (LL). — Head, neck, nape, back and scapulars very pale, profusely streaked and blotched. Underparts light; very pale flanks.
- Light (L). — Head, neck and underparts more uniform but still appearing light because of the relief. Back and scapulars conspicuously blotchy, pronounced flank streak.
- Dark (D). — Fairly uniform, darkish appearance, with no conspicuous mottling on neck and sparsely marked flanks. Spotting and streaking of back and scapulars conspicuous.

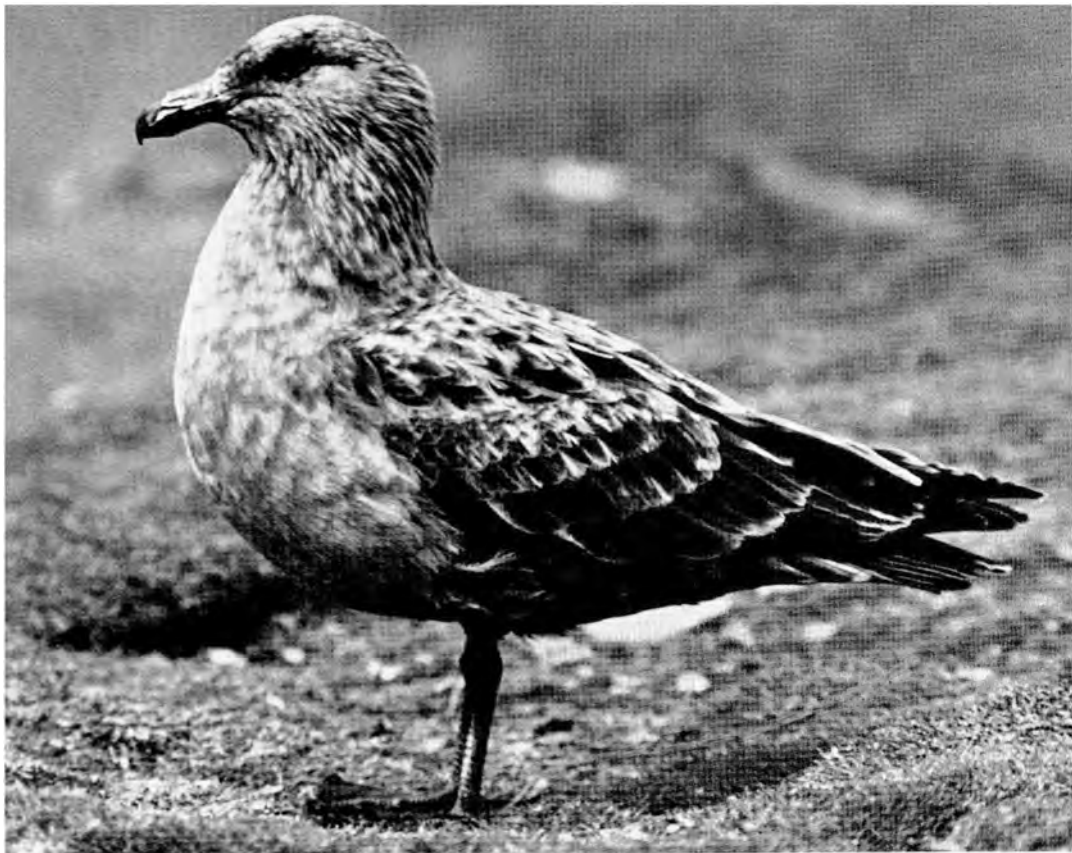


Fig 8. Very light adult Falkland Skua, Carcass Island, 13 December 1975.

— Very Dark (DD). — Uniform, very dark or blackish appearance, with no light areas. Streaking visible only at close range.

Consistency of choice in allocating a skua to a class was checked by photographs. Samples taken at New Island, Carcass Island and Eagle Point indicate the homogeneity of the Falkland population (Table 2). No trend of mating preference could be noted, pairs seemed made indifferently of like or very distinct partners. This impression is borne out by the figures of Table 3, where observed numbers of plumage class combinations in a sample of 38 New Island pairs are compared to the expected numbers of such combinations in the hypothesis of random mating. None of the discrepancies is significant. No correlation between sex and plumage class could be detected, but no really exhaustive investigation of this aspect could be conducted because of the difficulty of keeping track of correctly sexed pairs in densely populated areas, without the help of colour marking.

The birds were starting their breeding cycle at the time of our visit and most were in fairly fresh plumage. Faded feathers are generally lighter in tone than fresh ones and the tips tend to lighten further. The variation in plumage appearance among Falkland birds is not, however, in any way a result of differential wear.

Table 1: Measurements of some South American skuas

| | N | Wing | | | Culmen | | | Tarsus | | |
|-------------------------------------|-------|------|-----|-----|--------|------|------|--------|------|------|
| | | min | max | av | min | max | av | min | max | av |
| <i>S. s. antarcticus</i> | | | | | | | | | | |
| Falklands | 35-36 | 355 | 397 | 379 | 41.2 | 49.5 | 45.6 | 61.5 | 72.9 | 68.6 |
| Punta Tombo | 1 | — | — | 385 | — | — | 45.0 | — | — | 67.2 |
| Punta Tombo | 4* | 370 | 384 | 378 | 48.3 | 50.6 | 49.9 | 65.1 | 68.8 | 67.0 |
| Puerto Deseado | 2 | 375 | 375 | 375 | 45.5 | 48.3 | 46.9 | 66.5 | 66.5 | 66.5 |
| <i>S. chilensis</i> | | | | | | | | | | |
| Fuegia, Chile, Perú | 13 | 372 | 415 | 394 | 46.1 | 49.6 | 47.8 | 67.5 | 71.0 | 69.1 |
| Fuegia, Chile | 2* | 406 | 411 | 409 | 51.5 | 52.2 | 51.9 | 67.0 | 67.9 | 67.5 |
| Falklands, Stanley | 1 | — | — | 410 | — | — | 49.8 | — | — | 69.0 |
| Falklands, Eagle Pt. | 2 | 375 | 377 | 376 | 43.6 | 43.8 | 43.7 | 65.4 | 70.0 | 67.4 |
| Patagonia, Sta. Cruz | 2 | 405 | 417 | 411 | 47.6 | 47.8 | 47.7 | 68.6 | 71.7 | 70.2 |
| Patagonia, Sta. Cruz | 1* | — | — | 405 | — | — | 49.8 | — | — | 70.0 |
| Puerto Deseado | 2 | 373 | 397 | 385 | 47.0 | 47.2 | 47.1 | 67.0 | 69.0 | 68.0 |
| <i>S. s. ant.</i> × <i>S. chil.</i> | | | | | | | | | | |
| Puerto Deseado | 1 | — | — | 389 | — | — | 49.0 | — | — | 68.0 |
| Chubut (winter) | 1* | — | — | 385 | — | — | 51.1 | — | — | 71.0 |

* Measured by Suzanne I. Bond.

Table 2: Variation of *Stercorarius antarcticus* in various Falkland samples.

| | Sample | Plumage class, frequency in % | | | |
|----------------------------|--------|-------------------------------|----|----|----|
| | | LL | L | D | DD |
| Volunteer Pt., E. Falkland | 18 | 27 | 50 | 17 | 6 |
| New I, territorial pairs | 98 | 27 | 48 | 14 | 11 |
| New I, «club» group | 75 | 8 | 59 | 16 | 17 |
| New I, total | 195 | 19 | 51 | 16 | 14 |
| Carcass I, N.-W. colony | 445 | 15 | 60 | 17 | 8 |
| Carcass I, S.-E. area | 132 | 8 | 56 | 24 | 12 |
| Carcass I, total | 577 | 14 | 58 | 19 | 9 |



Fig 9. Pair of Falkland Skuas Long-Calling, Carcass Island, 10 December 1975.

Table 3: Observed and expected numbers of mating combinations for 38 pairs on New Island.

| Mating combination | Class distance | Number observed | Expected number for random mating |
|--------------------|----------------|-----------------|-----------------------------------|
| 1: LL × LL | 0 | 3 | 2.4 |
| 2: L × L | 0 | 13 | 11.5 |
| 3: D × D | 0 | 0 | 0.5 |
| 4: DD × DD | 0 | 1 | 0.3 |
| 5: LL × L | 1 | 9 | 10.5 |
| 6: L × D | 1 | 6 | 4.6 |
| 7: D × DD | 1 | 1 | 0.8 |
| 8: LL × D | 2 | 1 | 2.0 |
| 9: L × DD | 2 | 1 | 3.8 |
| 10: LL × DD | 3 | 2 | 1.7 |
| 1-2-3-4 combined | 0 | 17 | 14.6 |
| 5-6-7 combined | 1 | 16 | 15.8 |
| 8-9 combined | 2 | 2 | 5.9 |
| 10 | 3 | 2 | 1.7 |

SOFT PARTS

The iris is dark brown, the bill black, the tarsus black, frequently with rings of white, unpigmented skin.

JUVENILE AND IMMATURE PLUMAGES

We did not see any bird in juvenile dress but this stage is fairly well documented by six specimens in BM, five collected by Halmiton on Carcass Island, on 1 March 1932. One (BM 1940-12-6-28) of these has a uniformly dark back, scapulars and wing coverts; the others have U-shaped terminal edges to the back and scapular feathers, greyish buff in one, strongly reddish in three, very strongly cinnamon and very extensive in one; their wing coverts carry similar marks, irregularly distributed, very developed in two specimens. The upper tail coverts are uniformly dark in all specimens except the reddest one, which has diffuse reddish tips to many coverts. The colour of the underparts varies from a shade similar to a normal dark adult in the uniform-backed specimen, and only slightly more reddish in another one, through two that match dull *chilensis*, one that matches average *chilensis*, to one that is as bright cinnamon as the brightest adult *chilensis*. On all, the head is brown and uncapped and the chin and throat are brown, the colour grading progressively to reddish below the throat. The underwing coverts are entirely dark brown in the most uniform individual, dark brown with reddish feathers near the edge of the wing and near the scapulars in the four other individuals for which the colour can be judged. An MNHN specimen from West Falkland (1884-1056) matches the most uniform BM specimen, but is very slightly darker below. The reddish juvenile plumage of *antarcticus* was noted by Mathews (1913).

Immature stages of skuas, after the juvenile plumage, are difficult to ascertain because of the pelagic life of young birds (Eklund, 1961; Thomson, 1966; Watson, 1975) and their long delayed return to colonies. However, we occasionally saw, in the Falklands, and on the coast of Patagonia, non-territorial birds with visibly weaker, shorter bills, that had the appearance of immatures. Such individuals were generally very dark and uniform and had little or no streaking on the nape. Also, a large club of non-breeders on New Island, probably formed largely of older immatures, contained a high proportion of rather dark and uniform plumaged birds (Fig. 4). It seems likely that, as in *lonnbergi* (Falla, 1937), immature stages are darker, more uniform, than the adult plumage. Out of the 1200 individuals examined, three had profuse reddish (in two) or ochre (in one) streaking about the head and nape, superficially resembling *S. skua* of the northern hemisphere. None was a breeder, two were at the Stanley slaughterhouse, the third was part of a club. These probably represent immature types. In general, the «red factor» (Lowe and Kinnear, 1930) is uncommon and may correspond to a degree of immaturity. A few spots or drops of red in the plumage are not unusual, but for this colour to become at all prominent is very rare and was seen in only 8 of 1200 individuals examined.

BEHAVIOUR

The hostile and sexual behaviour of all large skuas is very much alike (Moynihan, 1962; Spellerberg, 1971), and one would not expect *antarcticus* to differ greatly from its close relatives. The most obvious ritualised display is the Long Call performance, delivered on the ground or in flight. On the ground, the wings are usually held up during its delivery, the neck arched (Fig. 9); in flight, the Long Call is delivered by birds gliding on V-held wings, with neck bent upwards and forwards as described by Moynihan (1963) for *S. chilensis*. Long-Calling birds on the ground usually hold themselves parallel to each other (Fig. 9), thus displaying to its fullest extent the underwing pattern of very dark coverts contrasting with silvery flight feathers and showy white patches at the base of the primaries. Perdeck (1960) noted the same orientation in *S. skua* but wondered whether it might be due to wind. This is definitely not so with *antarcticus*, as we noted birds standing parallel in a variety of orientations with respect to the wind, standing parallel in sheltered, windless spots, and staying parallel while shifting their common position during a single sequence of Long Calls.

The posture assumed during the Long Call is similar in overall appearance to that reported for all other skuas of the *Catharacta* group (Perdeck, 1960; Moynihan, 1962; Burton, 1968b; Spellerberg, 1971). A more detailed consideration of the relative position of body parts in the posture (Fig. 10), however, reveals very close similarity with *skua*, and probably *chilensis*, and greater divergence from *maccormicki* (Fig. 11). In *antarcticus* the body is always tilted upwards; the neck bent down with respect to the line of the body from a small amount (Fig. 1) to more than 45° (Fig. 10, above), occasionally to 90° (Fig. 10, below); the head is held in line with the neck, or often slightly above the line of the neck (Fig. 1), sometimes a little below, perhaps occasionally bent down to 90° ; the tail is held in general cocked above the line of the body. These relative positions are summarized in Fig. 12. Postures with neck and head almost in line with the body or slightly bent down correspond to the «Oblique» of Perdeck (1960). They are the most frequent and often used alone. Positions with the neck bent down to extreme angles correspond to the «Bend» of Perdeck (1960; but not of Spellerberg, 1971), but are rather rarely assumed by *antarcticus*, generally after an «Oblique» from which the «Bend» is assumed by a slow, smooth transition. The physical appearance of the postures assumed by *antarcticus* is identical in detail to that of corresponding positions of *skua* (photographs in Perdeck, 1960); however, we never saw *antarcticus* bend the neck or head as far down as *skua* sometimes does (cf. Perdeck's plate IV, Fig. 1). Moynihan's drawings of *chilensis* are more difficult to analyse than photographs, but seem to represent very similar postures.

The display of *maccormicki*, though similar at first glance, differs quite clearly in detail: the neck is raised at an angle nearing 90° above the line of the body, the head in turn held close to perpendicular to the



Fig 10. Long-Call postures of Falkland Skuas, Carcass Island, 10 December 1975.





Fig. 11. McCormick's Skua, *S. maccormicki*, Long-Calling, Terre Adélie, January 1968 (Photo P. Isenmann).

line of the neck; the body is generally more strongly tilted (Fig. 11, 12; Spellerberg, 1971; and photographs by Paul Isenmann). Published photographs of the display of *lonnbergi* (Stonehouse, 1956; Bonner, 1964; Burton, 1968a, 1968b) show an «Oblique» posture very similar to that of *antarcticus* and *skua*, with the body a little more erect, but mostly with the neck more contracted, drawn in, less extended. A drawing by Burton (1968b) suggests that *maccormicki*-like postures may also be assumed by *lonnbergi*, but the point should be clarified.

Other postures noted included «uprights» (Perdeck, 1960), generally with head horizontal, «gape» (Burton, 1968b), and «bill-down» (Moynihan, 1962). We never saw grass pulling or pecking at the ground.

Pairs are usually fairly far apart, although loose colonies form. At New Island, where the terrain is very rugged and broken, pairs are mostly evenly spaced at distances of 50 m or more over large areas of high concentration, with many isolated pairs and small groups scattered

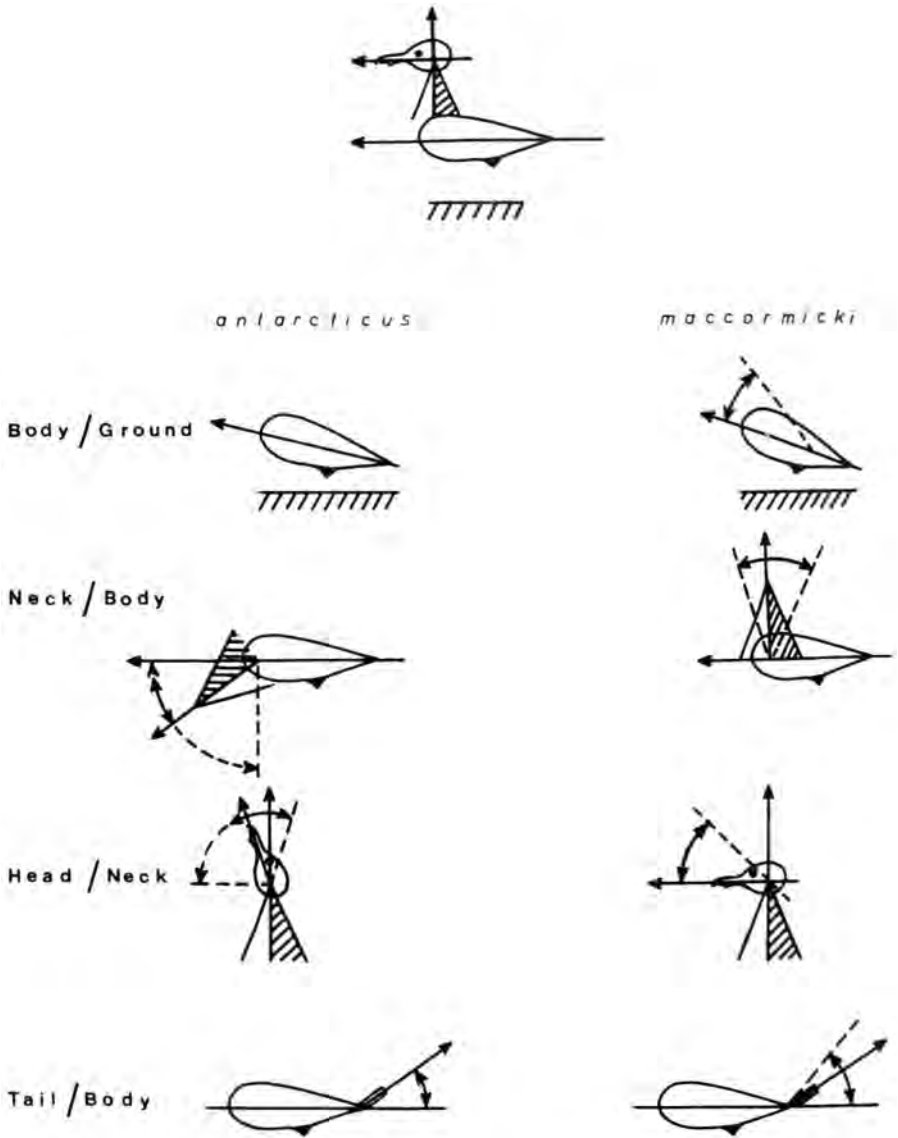


Fig. 12. Analysis of the Long Call postures of *Stercorarius s. antarcticus* and comparison with *S. maccormicki*.

elsewhere. Locally, stronger concentrations occur. At Carcass Island, a large part of the population is concentrated in one extensive loose colony over flat, relatively unbroken ground. Here, nests are often as close as 10 or 20 m apart, but there is still no impression of a dense colony, as provided, for instance, by gulls.

The adults are strongly territorial, driving away other skuas and gulls, and fiercely attacking human intruders. Our experience with them was during the prelaying and incubation period, as the first egg was found on New Island on 28 November and most nests found contained complete clutches of two eggs by the time we left Carcass Island on 15 December. During the entire period, the birds were very aggressive, most pairs swooping repeatedly whenever their territory was crossed, the attacks becoming more frenzied as one approached the nest. Occasionally a bird even hit, either with wing or leg. Low-pitched notes (Long Call Notes or Alarm Long Call Notes of Moynihan, 1962) are often uttered near the point of closest approach to the target or as the bird soars off, and gakkering often accompanies the swoop. In general, the smaller member of the pair, presumed to be the male, seemed more aggressive. Some pairs threaten on the ground near the nest, with raised wings and Long Calling, instead of swooping; the bird then usually places itself sideways to the intruder. Occasional pairs, very rare, show remarkable passivity.

Nest scrapes are placed in a variety of situations, including Diddle-dee (*Empetrum rubrum*) heath, short grass meadows, Tussac (*Poa flabellata*)-covered flats, long grass patches.

A few skuas always attend the colonies of Gentoo Penguins, *Pygoscelis papua*, and the mixed colonies of Emperor Shags, *Phalacrocorax atriceps albiventer* (for use of trinomial, see Devillers and Terschuren, 1978), and Rockhopper Penguins, *Eudyptes crestatus*, and we saw predation on both eggs and chicks of those species. This, however, is unlikely to be a major source of food for the predator, as very few nests can be robbed in undisturbed colonies; the abundant spills of food brought to the chicks are probably the main attraction for the skuas. On New Island, the litter of wings and carcasses of Thin-billed Prions, *Pachyptila belcheri*, near skua nests leaves no doubt that the immense colony of this species pays a tribute to the skuas. Large numbers of skuas are generally flying far out at sea during the day, and it seems probable that offshore activities contribute to an important degree to the diet of the species.

EGGS

The normal clutch is made of two eggs, but with Ian Strange, on Ship Island, off New Island on 6 December, we found a clutch of four eggs, two, and particularly one, of which were small. The ground colour is variable, in shades of olive and brown; all the eggs we saw were heavily and sharply blotched with profuse dark markings.

POPULATION

The New Island population, difficult to census because many small groups and isolated pairs occupy remote parts of the cliff tops, was evaluated at 300-350 pairs, an extrapolation based on 220 pairs actually counted. Carcass Island is a bit smaller than New Island, 1500 ha vs. 2000 ha and easier to cover entirely. A similar total, 300 pairs, was censused. These two concentrations are among the largest in the Falklands (Strange and Napier, pers. com.) but several other big «colonies» exist, as at Dunbar Island, Pebble Island, Cape Dolphin (Woods, 1975, BM), and pairs or small groups occupy other areas, such as the vicinity of the shaggeries of Eagle Point, where we had seven pairs, although the species is almost absent from many places. It is thus impossible to estimate the total population of the archipelago with any degree of certainty, but a guess of 3000-5000 pairs is perhaps not unreasonable. This, essentially, would be the total population of *S. antarcticus*.

CHILEAN SKUA

The hostile behaviour of the Chilean Skua has been the object of a detailed study by Moynihan (1962), but otherwise this form has not drawn any more attention than the preceding. I am aware of only one published photograph that may represent it (Campbell, 1974: 91), and the descriptions available are based on few specimens, probably in large part immatures. Its breeding range lies almost entirely within the maze of islands, fjords and canals that lie south and west of Tierra del Fuego and the southern Andes. This is one of the least populated areas on earth, and one of difficult access, which partly explains the scanty knowledge of this striking species.

SIZE AND APPEARANCE

The Chilean Skua appears slenderer, less bulky, less massive, than the Falkland Skua. In direct comparison, the wings seem longer, proportionately narrower. The tarsus is proportionately shorter. The bill, longer, thinner and weaker, gives it a different physiognomy. Measurements and proportions of specimens of the two forms are compared in Table 1 (most of the *chilensis* specimens measured are immatures).

ADULT PLUMAGE

The bright cinnamon underparts of *chilensis* are usually emphasized. This character is certainly evident in many individuals, but we were surprised to find Chilean Skuas much more variable and duller than we had expected after examination of series of specimens. It seems that the latter are composed of an uncharacteristic proportion of very

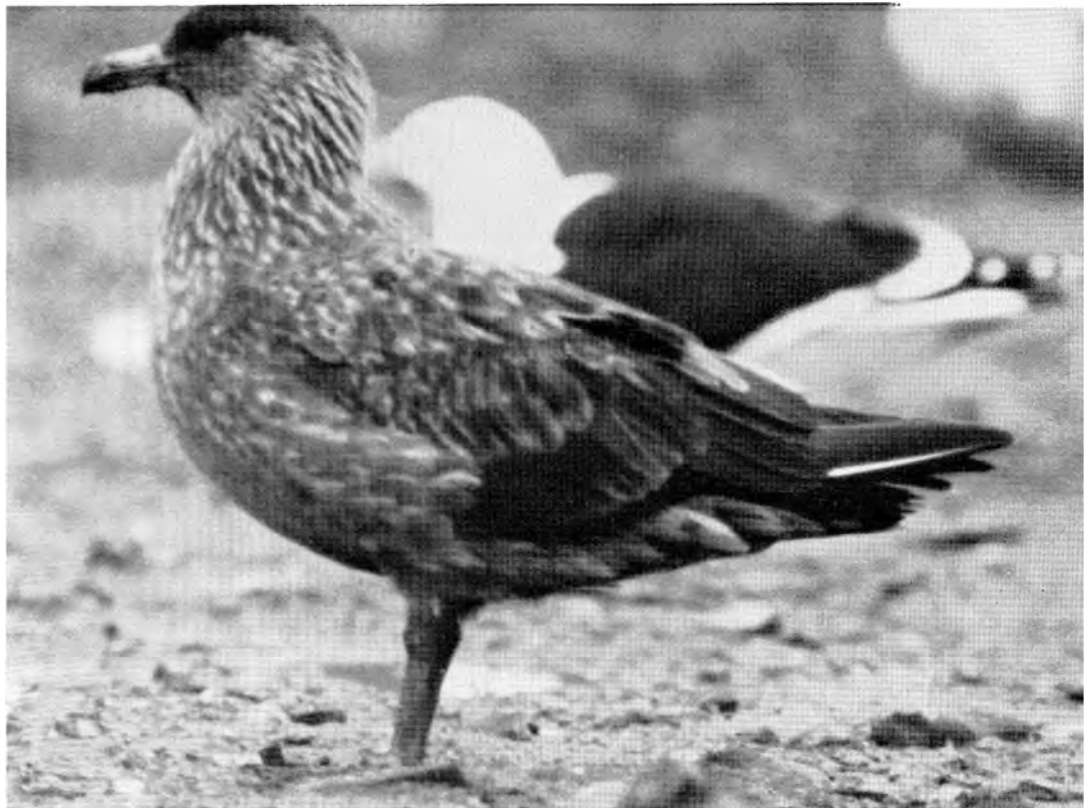


Fig. 13. Chilean Skua, *S. chilensis*, at the Ushuaia rubbish tip, 1 January 1976.

bright individuals, perhaps because they have attracted the collector, and particularly of immatures, probably because of collection of migrants in relatively low latitudes. Thus, of 15 *S. chilensis* from the South American continent in BM, 11 are immatures (9 collected at low latitudes in Chile, Peru and Brazil), 2 probable immatures and only 2 unquestionable adults. Our observations of *chilensis* did not start until 31 December, by which time the breeding cycle was well along, so that a considerable amount of fading could have taken place. However, since very bright individuals were seen, and did not seem less or more worn than others, and since variability included areas that are little exposed to the light such as the underwing, the range of variation is likely not to have been much affected by the fading process.

All individuals have a dark brown or blackish cap (Fig. 13), encompassing the forehead and the entire occiput, generally ending just below the eye, but sometimes including the lores and feathering at the base of the maxilla and, occasionally, the feathering at the base of the mandible. Because it extends farther on the nape and generally not as far down at the base of the bill, this cap looks less slanted forward than on *antarcticus* and resembles very much that of the small northern skuas or jaegers. Often the forehead is paler than the rest of the crown (Fig. 14) and there is sometimes light spotting on the top of the head.



Fig. 14. Chilean Skua, Canal Moraleda, Chile, 26 January 1976. Note strongly capped appearance.



Fig. 15. Chilean Skuas, Canal Moraleda, 26 January 1976.

The cheeks, the sides of the neck, the flanks, the back, and the scapulars form in general a dark area varying from blackish or dark brown to grey brown or even grey, but always lighter than the cap (Fig. 13). This area expands as a broad collar across the front of the neck or upper breast (Fig. 1), and is variously relieved by whitish straw or golden streaks on cheeks and nape, by straw or pale rufous mottling on the chest collar, by pale rufous streaking on the flanks, and by light grey feather edges, perhaps due to wear, on back and scapulars. The streaks generally coalesce into light surfaces on the auriculars and back of the cheeks and often also on the nape, sometimes even on the mandibular region, thus strongly underlining and enhancing the cap, and the nape sparkles with golden metallic hardened feather tips (Fig. 14). The back and scapular pattern (Fig. 13, 15) is very different from that of *antarcticus*, the profusion of shaft streaks being largely replaced by a uniform area or by brown feathers with grey edges and subterminal mottling or barring quite similar to that of immature gulls, *Larus* sp. (confirmed by BM and AMNH specimens). Rufous shaft streaks are also present in some individuals (fully adult?). Some very black-backed individuals, perhaps immatures, have the dark area much reduced, to nape, back, scapulars, sides of chest and patches on flanks, the light (cinnamon) area of the underparts then expanding to cheeks, chest and most of the flanks.



Fig. 16. Chilean Skua, Canal Sarmiento, 52° S., Chile, 24 January 1976.

The wing coverts are a little darker than the back, in general, and darken progressively from lesser to greater, to almost match the very dark secondaries and primaries (Fig. 13, 15). Lesser and median, and sometimes greater, coverts can be edged broadly with pale grey brown, like the back feathers. The centers of the coverts, flight feathers and tail feathers are as dark as the crown. The upper tail coverts are either all dark or largely spotted with light tones (Fig. 15), grey or rufous, the latter generally in very bright cinnamon birds.

There is always an area of uniform light colour on the underparts, including at least the chin and the area around the bend of the throat, and, below the pectoral band, the abdomen and most of the undertail coverts (Fig. 1). The colour of this region is usually cinnamon, sometimes bright rufous, but can be no more than dull pale reddish, buff or even, in rare individuals, pale grey with no redness whatsoever. The light colour often invades parts of the cheeks (Fig. 16) and is of variable extent on the sides of the neck, and, mixed with brown, in the pectoral band and the flanks. The reddest, and most conspicuously uniform area is invariably at the bend of the throat. Occasionally, in birds with very light upperparts, part of the red area grades to pure white, especially at the bend of the throat, and on the abdomen.

The lesser and median underwing coverts are of the same colour as the underparts and usually rather bright cinnamon (Fig. 1). Often, a number of feathers have brown centers, or brown bars, arranged in parallel rows. The axillars are often browner than the coverts, sometimes only red-tipped and red-edged. The greater underwing coverts are pale silvery like the underside of the primaries, often with dark centers. Almost all birds have at least red bands under the wings, the brightest individuals also have the greatest amount of that colour under the wing. Birds with whitish, discoloured areas on the underparts also have a lot of white underwing coverts.

No geographical trend was detected in the variation of *S. chilensis*. Both extremely bright and extremely dull individuals, as well as all intermediates, were noted among breeders at Magdalena Island, at Ushuaia, along the entire length of the Chilean fjords from Punta Arenas to the Golfo de Corcovado (as well as among 9-12 fall migrants, worn adults or subadults, seen in Pisco Bay, Perú, on a later visit, 16-19 May 1978).

SOFT PARTS

The iris is brown, the legs black, as in other skuas, but the bill was—at least at the time of our observations—always light blue, except for the tip which appeared dark (Fig. 13). Photographs confirm the light colour of the bill. Light bills with dark tips are mentioned on specimen labels quoted by Humphrey *et al.* (1970).

JUVENAL PLUMAGE

Although Mathews (1913) had noted that juvenile Chilean Skuas were more deeply coloured than adults, Murphy (1936) characterized «youthful examples» as having «less solid cinnamon coloration on the feathers than adults», and I had been able to recognize only two juveniles among the collections examined, birds that showed on the upperparts the light subterminal bars typical of other young skuas. We were thus surprised on Isla Magdalena to discover that fledglings were in fact brighter than adults, and often had unmarked upperparts (Fig. 17). We handled about 12 young that were sufficiently feathered to judge their pattern. All had bright cinnamon underparts, very dark, deep red in some, with generally less admixture of brown on cheeks, breast, flanks, and underwing coverts than adults, the pectoral collar not always apparent. The upperparts were black to very dark brown, uniform in about half the individuals (Fig. 17, below), decorated with varying amounts of narrow cinnamon subterminal bars in the others (Fig. 17, above). All were strongly «capped», but lacked pale streaking on cheeks and nape. The bills were blue with a black tip. Juvenile *chilensis* appear to always differ from juvenile *antarcticus* by their cinnamon chin and throat, and much redder underwing coverts.

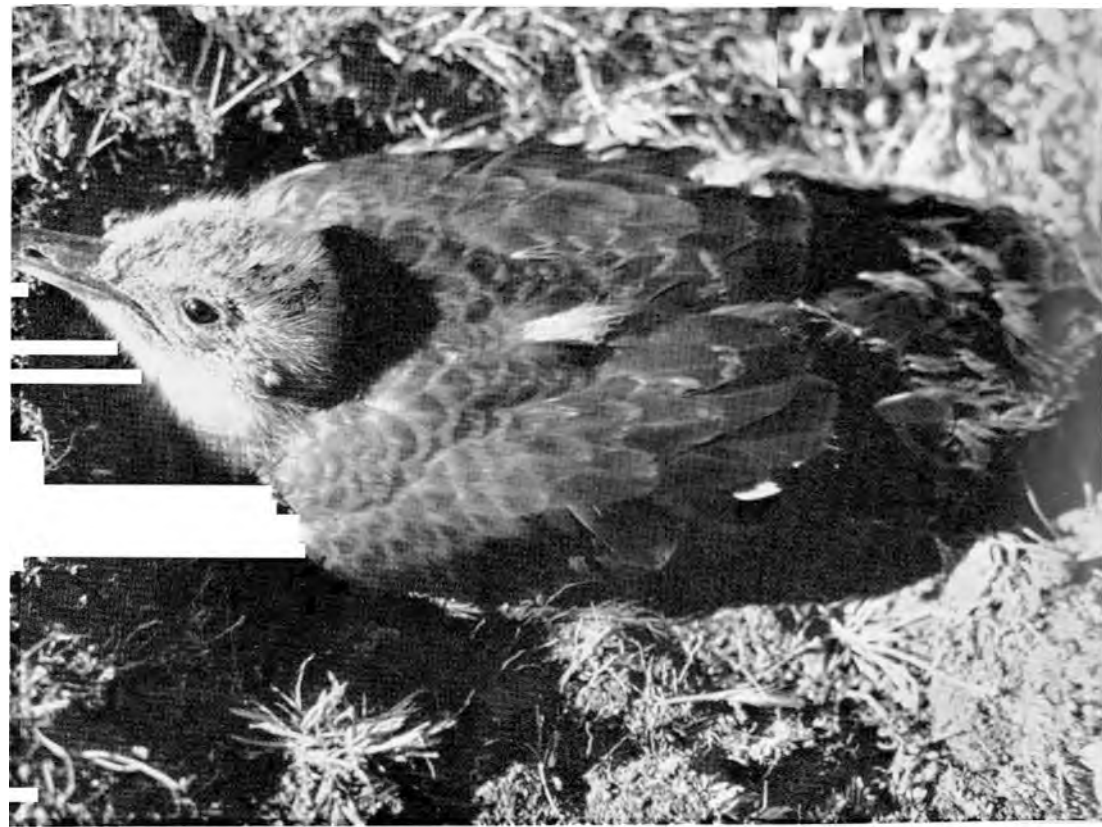


Fig. 17. Two juvenile Chilean Skuas, Magdalena Island, Strait of Magellan, 21-22 January 1976.

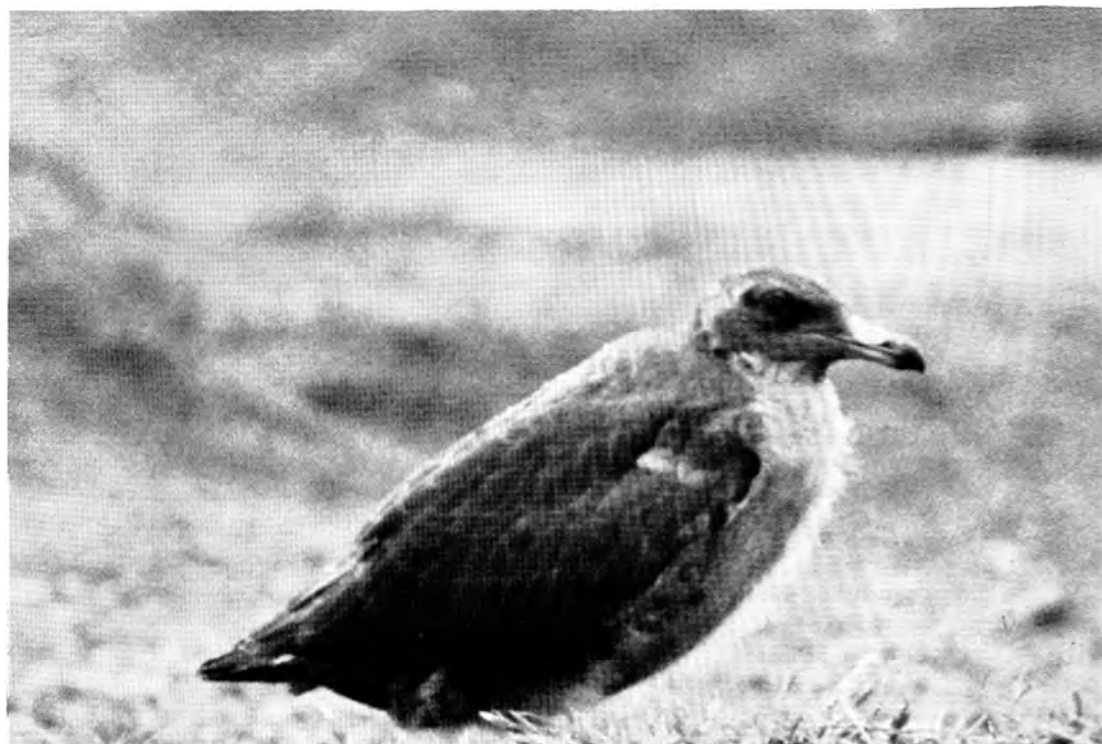




Fig. 18. Downy Chilean Skua, Magdalena Island, 21 January 1976.

Immature stages are not positively known, but are probably characterized by lack of streaking on the nape and presence of rufous flames on the back, and may show a progressive reduction of brightness, the development of a brown breast band, of brown clouding on the flanks and of light feather edges on the back.

BEHAVIOUR

The 200 or so pairs on Magdalena Island had chicks at the time of our visit, ranging from very small downy ones (Fig. 18) to almost flying ones. Falkland Skuas are apparently particularly fierce at that stage of the cycle (Strange, pers. com.). On the contrary, these Chilean Skuas showed very little aggression towards us, taking off at great distances, flying high and letting their chicks be approached or handled without any interference. Only one pair stooped a few times and not very low. This lack of aggressiveness of the Chilean Skua has already been noted by Reynolds (1935) and Moynihan (1962). It contrasts sharply with the bold behaviour of *S. antarcticus*, *S. lonnbergi* (Murphy, 1936; Falla, 1937), *S. skua* (Perdeck, 1960; pers. obs.), *S. maccormicki* (Spellerberg, 1971).

Also specific to this form may be a habit of breeding in very tight colonies, reminiscent of those of gulls (Reynolds, 1935; Moynihan, 1962) although loose colonies can also be formed (Reynolds, 1935) as is the case on Magdalena.

The Long-Call performance is similar to that of *S. antarcticus*, as much as I can judge from Moynihan's description and our limited experience with *S. chilensis*, but we found the voice quite different, higher-pitched and more nasal.

EGGS

A number of cold eggs in nest scrapes were about the island; all had a pale, washed-out appearance, with faint, diffuse markings, strikingly different from those of *antarcticus* we saw. The same character could be noted in eggs that had been collected fresh in the Cape Horn region, kindly shown to us by Oliver Bridges, who also tells us (pers. com.) that the condition is typical for this form. Some eggs of *antarcticus* are, however, similarly described (Murphy, 1936).

THE CHILEAN SKUA IN THE FALKLANDS

Wace (1921) was the first to report *S. chilensis* in the Falkland Islands, as a rare visitor, «perhaps commoner in the western part of the archipelago». He offered no supporting data. Hamilton (1934, 1937) saw three birds at Eagle Point, East Falkland, on 26 November 1930, and collected two of them (BM 1932: 7-2-33, 1932: 7-2-34). One of these, he thought paired with a Falkland Skua. On 29 October 1936, he collected another individual at Stanley, East Falkland (BM 1949: 7-8-142). These records were discounted by Murphy (1936) and ignored by Cawkell (in Cawkell and Hamilton, 1961) and Woods (1975), but the specimens are perfectly typical *chilensis* in every character of the plumage. Their measurements and proportions are included in Table 1. The Stanley bird has typical *chilensis* proportions, the Eagle Point birds are rather short-winged and heavy-billed, though still within or close to the range of continental *chilensis* variation.

We saw a typical *S. chilensis*, in adult plumage, at Carcass Island on 9 December. It was associating with a small group of non-breeding or off-nest *antarcticus* loafing in an intertidal area and was not located again on the island despite intensive search for the next five days. We saw no other *chilensis* during our stay in the Falklands, and found only typical *antarcticus* at Eagle Point, visited on 22 and 23 November. These few records indicate more than accidental occurrence, as the species can easily be overlooked. Resident ornithologists, except Hamilton, have not been watching for it (Strange, pers. com.). It is even possible that *S. chilensis* breeds somewhere in the archipelago, which is vast and relatively little explored.

We saw only one individual that showed characters suggestive of a hybrid origin; it was a probable immature, member of a club at New Island, with a brown cap, the chin and one cheek cinnamon, variegated brown and cinnamon underparts, but blackish underwing linings, and the back profusely streaked with gold, cinnamon and whitish. Four other individuals, with some red about the cheeks and underparts, and a very few light brownish or cinnamon edges to the underwing coverts may also have shown *chilensis* influence but were very probably within the limits of variation of *antarcticus*. No other bird showed any amount of red or brown in underwing linings.

THE SKUAS OF THE COAST OF CHUBUT

We estimated 40-45 breeding pairs of skuas at Punta Tombo (44° S) on 13 and 14 November and about 10 at Camarones, 100 km farther south on 15 November. A large colony apparently exists on an island of Bahía Bustamante, another 100 km to the south. At Punta Tombo we censused 36 territorial pairs on the peninsula, while E. Shaw, who accompanied us, found another five to six near the base of the peninsula. Boswall and Prytherch (1972) had counted 21 pairs and evaluated 25 in 1971 so that a slight increase could have taken place. The skuas were strongly territorial, extremely aggressive and probably about to lay. At least two pairs already had one egg. This two-week advance of Punta Tombo over the Falklands is characteristic of the entire seabird community. At Camarones, birds seemed at the same stage as at Tombo, with some incubating; the islet on which they nest was not reached, so the presence of eggs could not be checked.

The skuas at both Punta Tombo and Camarones appeared similar to those of Falklands (Fig. 19). No individual was seen or photographed that could not be matched by a Falkland individual. The measurements of the few specimens available from Chubut are within the variation of a Falkland sample (Table 1).

The range of plumage variation from light to dark birds is also similar but no extremely light individuals were seen at Punta Tombo or Camarones and dark birds appeared more prevalent. Table 4 shows the results of an arbitrary sorting of territorial individuals of Punta Tombo and Camarones into five classes. These are the same as later used in Falklands, except for the distinction of one additional category (FL) towards the darker end of the «L» class. A Carcass Island sample, distributed into the same five classes, is used for reference. The comparison between birds from the two regions is not too inaccurate as both evaluations were done at a fairly short interval of time and photographs of sample birds could be compared. It confirms a higher proportion of dark, uniform plumaged individuals in the continental population, and a paucity of birds with strong pale relief. Joseph R. Jehl, Jr. (*in litt.*) obtained similar results at Punta Tombo on 20-21 November 1973. He classified a sample of 30 skuas into four



Fig. 19. Falkland Skua, *S. s. antarcticus*, Punta Tombo, Chubut, Argentina, 14 November 1975.

Table 4: Variation of *S. antarcticus* in samples from mainland Patagonia, compared to a Falkland sample. Territorial birds only.

| Locality | Sample size | Plumage class, frequency in % | | | | |
|----------------------|-------------|-------------------------------|----|-----|-----|----|
| | | LL | L | FL | D | DD |
| Carcass I, Falklands | 402 | 15 | 36 | 23 | 18 | 7 |
| Pta Tombo, Patagonia | 59 | 2 | 10 | 37* | 34* | 17 |
| Camarones, Patagonia | 17 | 0 | 12 | 58 | 18 | 12 |

* There is some uncertainty regarding the allocation of 23 birds (39%) to one or the other of these classes.

categories, «pale», «tan», «medium» and «chocolate» and found respectively 2, 13, 11 and 4 birds in each category (2, 12, 10, 0 when non-breeding birds are excluded).

In details of plumage, continental birds tend perhaps to be a little more often speckled with fine straw-coloured shaft streaks, dots, or drops, both on the upperparts and below, than Falkland individuals of similar hues. However, photographs of Punta Tombo and Camarones individuals could all be matched by Falkland specimens in the BM collection, and several birds described at Punta Tombo were exactly like individuals seen later in Falklands.

THE SKUAS OF THE COAST OF SANTA CRUZ

Between Cabo Tres Puntas, at the southern end of the Golfo San Jorge, and the Río Santa Cruz, a series of islets and headlands harbour seabird colonies that constitute a possible source of food for skuas. At the mouth of the Río Santa Cruz, Chilean Skuas were collected in November 1882 (Oustalet, 1891); two specimens preserved in MNHN are typical in plumage. Another individual, a female in breeding condition, was collected by J.R. Jehl, Jr. (*in litt.*) on 16 November 1973. Measurements and proportions of the three specimens are included in Table 1. Five skuas from Puerto Deseado are in the MACN, Buenos Aires, collection. By coloration, two of them are typical dark *S. antarcticus*, indistinguishable from Falkland individuals, two are relatively dull, but apparently normal *chilensis*, while the fifth is clearly intermediate, generally resembling *antarcticus*, but with numerous red edgings to underwing and vent feathers. The two *antarcticus* have heavy bills, the two *chilensis* slenderer ones. Their measurements and proportions are shown in Table 1. Skuas were reported at Puerto Deseado in 1961 by Zapata (1967) and his description indicates at least some *chilensis* characters.

During a visit to Puerto Deseado, 9 to 13 January, we saw daily five to ten skuas entering the estuary of the Río Deseado and visiting the bird colonies that populate its islands. They could never be approached closely enough for critical examination though some birds resembled *chilensis* and others *antarcticus*. On 10 January we were able to study and photograph ten skuas which attended the Deseado rubbish tip and the nearby slaughter house. Of these, one, a very heavy, dark, sparsely streaked bird, with a completely black bill (Fig. 20 below) was a normal *antarcticus* indistinguishable from a very dark Punta Tombo individual. It had completely blackish underwing linings. A second bird was very much like a fairly dark Falkland Skua in every respect except perhaps the presence of irregular, slightly cinnamon-tinged areas on throat, lower cheeks and belly. At the other extreme, one individual was a very typical adult *chilensis* with a dark cap, grey back, cinnamon underparts, grey-brown pectoral collar, blue, black-tipped bill and bright cinnamon underwing linings. A second, darker bird was equally typical. Three other birds were like Chilean Skuas in possessing a cap, largely cinnamon underwing linings, bicolored bill, uniform dark back, and much cinnamon underneath, but had perhaps too much dark brown mottling on the chest; a fourth individual had the cinnamon



of the underparts and underwing paling to whitish at places, a condition sometimes found in *chilensis*, but also some atypical brown spotting on the chest. One particularly bright *chilensis*, observed at very close range (Fig. 20 above) showed approach to *antarcticus* in a heavy, black bill (with pinkish mandibular rami). One individual was quite intermediate, closer to *chilensis*, but much too brown underneath and with reduced red under the wing. Thus, this small sample was composed of three apparently pure individuals, two *chilensis* and one *antarcticus*, of five *chilensis* showing signs of possible *antarcticus* influence, one slightly aberrant *antarcticus*, and one intermediate individual.

Skuas do not seem to breed on the islands of the estuary but rather on offshore islands. On 12 January, we were able to land on one of these, Chata Island, a small, flat islet of the Pingüino group, separated from the mainland by a 2 km - wide channel (Devillers and Terschuren, 1978). Unfortunately, difficult sea conditions and freshening winds forced us to leave the island unexpectedly soon so that very little time could be devoted to the skuas and no collecting could be done. We found no nests, but pairs were formed, alarming and Long Calling, and we were told (McLeod, pers. com.) that skuas do breed on the island, as well as — in larger numbers — on nearby, larger, Pingüino Island. Chata is exploited for guano and it is possible that the skuas are subjected to regular eggging and did not have eggs or young.

Of about ten pairs that seemed to inhabit the island, most appeared constituted of *chilensis*, or birds resembling *chilensis* at the distance they were seen. Unfortunately, they were difficult to approach, took off at a great distance, flew at a great height and did not stoop. Three of these pairs could be seen reasonably well. One was made of two birds with *chilensis*-like grey-brown upperparts, one cinnamon below, the other greyish, a second one was made of a rather dull, typical *chilensis* and of a bird with a slender, bicoloured bill, but which had perhaps some Falkland characters; a third one comprised a bright, typical *chilensis* and a dull one.

In sharp contrast to the behaviour of these birds, four individuals attacked us vigorously near the south end of the islet. They stooped very low and repeatedly, three of them persisting in their attacks as long as we were in the area. Two of them were certainly paired. All four were completely typical *antarcticus*, very massive, with dark bills, and uniformly blackish underwing linings, without a trace of red; in plumage, two corresponded to the light (L), or rather «fairly light» (FL), and two to the «dark» (D) categories; the obvious pair being FL-D.

In addition to the apparently territorial birds, one single, fairly tame, individual with the uncapped head and underparts of a light *antarcticus*,

← Fig. 20. Skuas among Dominican Gulls, *Larus dominicanus*, at Puerto Deseado, Santa Cruz, Argentina, 10 January 1976; above, *S. chilensis* with dark, heavy bill; below, *S. s. antarcticus*.

the back of a *chilensis*, a cinnamon throat and a bicoloured bill was seen and photographed. Finally, of five birds seen attending the large Imperial Shag (*Phalacrocorax atriceps*) colony that occupies the southern end of the island, one was a typical *chilensis*, one a typical light *antarcticus*, one a light *antarcticus* with some red under the wing, one a light *antarcticus* with pinkish white areas below and a slender bill, and one a very dark *antarcticus* with a bicoloured bill.

On a small islet between Chata and the mainland, on which landing was not possible, a pair of skuas, made of apparently pure *antarcticus* (D and L) threatened and Long Called at the passage of the boat. Two other birds, both dark (D) *antarcticus*, stood on the islet.

South of Puerto Deseado, a number of islets and headlands, some obviously carrying colonies of cormorants, are suitable for skuas. We could not visit them, but spent a day (8 January 1976) at a large Magellanic Penguin (*Spheniscus magellanicus*) colony at Cabo Virgenes, near Río Gallegos, 500 km south of Puerto Deseado. Skuas were absent, only one bird being seen at a considerable distance. Residents of the Virgenes area (John Blake, pers. com.) do not know the species in the area. Similarly, there seems to be no breeding skuas along the north-eastern coast of Tierra del Fuego (Humphrey *et al.*, 1970; Oliver Bridges, pers. com.). We saw two or three individuals at sea off Cabo Domingo, near Río Grande on 3 January 1976, but too distant to be identified. One individual found long dead on the road was a typical *chilensis*, probably subadult. Skuas seen by J.R. Jehl, Jr. at Río Grande in October and November 1973 (Jehl and Rumboll, 1976; Jehl, *in litt.*) were all *S. chilensis*.

THE FALKLAND SKUA IN FUEGIA

In the Fuegian area, skuas are known to breed in the northwestern part of Isla Grande (Moynihan, 1962; Humphrey *et al.*, 1970; Jori *et al.*, 1974), on Magdalena and Contramaestre in the Strait of Magellan (Olrog, 1948; Pisano, 1971; Parmelee and MacDonald, 1975; pers. obs.), on islands of the Beagle Channel near Ushuaia (Olrog, 1948; Humphrey *et al.*, 1970) and in the archipelagic area to the south of Isla Grande (Reynolds, 1935). All information available is that *chilensis* is in general the only form involved. However, Oustalet (1891) reports captures of *antarcticus* at Baie Orange in the Cape Horn archipelago and «Ile Elizabeth» (Isla Isabel) in the Strait of Magellan (specimens no longer extant; Erard, *in litt.*). Moynihan's (1962: 12) passing remark that two «extreme types», one of them «essentially dark brown all over», could be seen in the Lee Bay (Strait of Magellan) colony he studied is difficult to interpret. It is possible that *antarcticus* is a sporadic non-breeding visitor to Tierra del Fuego, but its local breeding in small numbers cannot be entirely ruled out.

SUMMARY OF DATA
AND TAXONOMIC IMPLICATIONS

Pure populations of, respectively, *S. antarcticus* and *S. chilensis* inhabit the Falkland Islands on the one hand, western and southern Tierra del Fuego and archipelagic Chile on the other hand. There is no indication at present that each is more than an occasional straggler within the main range of the other form, and no evidence of important introgression of *chilensis* characters into the Falkland population was detected. No reverse introgression was apparent either within the *chilensis* samples seen, but our investigation of that form was not sufficiently detailed to rule it out.

On the Atlantic coast of Patagonia, skuas breed from at least Punta Tombo in the north to the Río Santa Cruz in the south, points separated by 700 km. In the northern part of this area (Punta Tombo, Camarones) breeds a homogeneous population of birds similar to topotypical Falkland *antarcticus*, while at the southern end (Santa Cruz) only typical *chilensis* has been collected. At Puerto Deseado nests a mixed population, including apparently pure *chilensis* and *antarcticus*, as well as a number of birds showing clear signs of intermediacy.

A full understanding of the contact between the two forms will require detailed investigation of the numerous islets that dot the coast on either side of Puerto Deseado between Comodoro Rivadavia and at least Puerto San Julian. The investigation should include detailed data on mating and parent/juvenile inheritance, as well as limited collecting.

In the meantime, I believe that *chilensis* and *antarcticus* are best treated as distinct species as they long have been (Saunders, 1876, 1896; Mathews, 1913; Ridgway, 1919). The two forms differ in proportions, appearance, behaviour and voice, and rather more in plumage and soft part colouration than is usual among Stercorariidae. There are far greater and more constant differences in every plumage between *S. chilensis* and *S. antarcticus* than there is between *S. parasiticus* and *S. pomarinus*, if one excepts the peculiar shape of the central rectrices in the latter two. Even juvenile specimens of *chilensis* and *antarcticus* are always identifiable on pattern and colour alone, while immature *parasiticus* and *pomarinus* can be strictly identical in plumage. Significantly, the plumage differences involve pattern as well as colour, and in particular, in the possession of gull-like edged or barred feathers on the back and scapulars, *chilensis* is unique within the *S. skua* superspecies. The bicoloured bill and very red plumage are also unique for adult skuas, but they are immature traits in other forms (*maccormicki*, *antarcticus*). More importantly still, one of the characters in which the two forms differ the most, the underwing pattern, made by light-coloured, bright cinnamon underwing coverts in *chilensis*, and by very dark, blackish coverts, contrasting sharply with the remiges in *antarcticus*, affects a signal area, prominently exhibited during display (cf. Fig. 1).

That larids can discriminate between red and black is indirectly suggested by the frequent appearance of those colours, sometimes in combination, on signal elements, such as bill, eyes and eye-rings of gulls (Tinbergen, 1953; Smith, 1966; pers. obs.).

The two forms clearly hybridize, probably extensively, in their zone of contact. However, local, and sometimes massive, hybridization is a rather frequent larid trait, and treating as conspecific all forms that hybridize extensively but locally, such as Western and Glaucous-winged Gulls, *Larus occidentalis* and *glaucescens* (Oregon and Washington, Scott, 1971), Glaucous-winged and Glaucous Gulls, *L. glaucescens* and *L. hyperboreus* (Alaska, Strang, 1977), Glaucous-winged and Herring Gulls, *L. glaucescens* and *L. argentatus* (Alaska; Williamson and Peyton, 1963), Glaucous and Herring Gulls (Iceland, Ingolfsson, 1970), Grey-hooded and Silver Gulls, *L. cirrocephalus* and *L. novaehollandiae* (south-west Africa, Sinclair, 1977) would produce rather unwieldy polytypic species and obscure the phylogenetic relationships of the constituent forms (Devillers, in prep.).

The contact between the skuas is not extremely recent, since hybrid specimens were collected at Puerto Deseado in 1915, and yet no obvious sign of introgression is apparent in the northern populations of Punta Tombo and Camarones, and the differences between the two forms have not been smoothed out even at Puerto Deseado. That 60 years is indeed a respectable amount of time for this kind of phenomenon is clearly shown by the 40 years it took for a high degree of hybridization to involve large Glaucous Gull populations in Iceland (Ingolfsson, 1970). There thus would seem to be at least partial resistance to free gene flow.

Moreover, the very limited data that we have indicate the presence of pure birds of both parental forms in the area of contact, as in Short's (1969) «zones of overlap and hybridization», and, more importantly, suggest a degree of assortative mating and retention of the characteristic behaviour of the parental forms in the contact area. The contact between *lonnbergi* and *maccormicki* on the Antarctic Peninsula which is also old and has not led to obliteration of the differences between the two species in the zone of contact (Gain, 1914; Bennett, 1920, 1922, 1926; Watson, 1975) is nevertheless accompanied by hybridization (Parmelee *et al.*, 1975, 1977).

The affinities of *antarcticus* are partly with the large subantarctic *lonnbergi* of South Georgia and islands to the east. Hamilton (1934) has argued the conspecificity of these two forms. Although *antarcticus* is much smaller than *lonnbergi*, many adults and some juveniles from the Falklands are indistinguishable in plumage from subantarctic birds (Hamilton, 1934; BM specimens). However, *lonnbergi* is never capped and generally has a uniform dark head forming a hood in lighter birds. In structure, *lonnbergi* is rounder-headed than *antarcticus*, with less heavy supra-orbital ridges. Its Long-Call posture is slightly different from that of the Falkland Skua. The smallish, long-billed skua of Tristan da Cunha and Gough, *hamiltoni*, is very similar to *lonnbergi* in adult plumage, though often somewhat capped and much more

streaked with rufous and straw on the back; its juvenile plumage is practically identical to that of *antarcticus* (three specimens in BM and RSM). It has a heavy square head like *antarcticus* (live birds in London Zoo). The northern hemisphere *S. skua* resembles *antarcticus* in head shape, somewhat capped appearance and blackish underwing linings when adult, and in the Long-Call posture. Some juveniles of the two forms are extremely similar (Mathews, 1913; specimens, BM). In adult plumage, *S. skua* shows an extreme development of the streaking expressed in some *antarcticus*, which gives it a very distinct appearance. Some specimens, however, differ very little from some *hamiltoni* (direct comparison in RSM). The treatment of those four allopatric forms is largely a matter of taste, but their close affinity, particularly that of *antarcticus*, *skua* and *hamiltoni* (cf. also Mathews, 1913), is probably best expressed by treating them as races of *S. skua*.

I would thus suggest dividing the group of large skuas, or, skuas in the American sense, into three species: *S. maccormicki*, *S. chilensis*, and *S. skua*, the latter with four allopatric races. *S. maccormicki* is sympatric with *S. s. lonnbergi* on the Antarctic Peninsula and *S. chilensis* overlaps with *S. s. antarcticus* in Patagonia, in both cases with at least limited hybridization.

DISCUSSION

Lowe and Kinnear (1930), Murphy (1936), and Hamilton (1934) emphasized the great individual variation of skuas, suggested that no or almost no plumage characters could be considered diagnostic of one form or another, and in general stressed the chaotic nature of the overall geographic variation, for instance in characters like the «red factor». It is largely that impression that led them to, partly in despair, lump all skuas in one species. However, once specimens of like age are compared, and misidentifications eliminated, the variability proves considerably less random, the adult plumages distinctive, and average tendencies significant (Devillers, 1977). Moreover, if one considers the distribution of skuas in the South American quadrant—ignoring for the moment the Patagonian coast area—an interesting pattern emerges.

In two important characters at least, the geographic variation appears quite orderly if followed from Antarctica to the Fuegian area along the arc of the Antarctic Peninsula, the Scotia Arc and the Falkland archipelago. Light phase Maccormick's Skua populations with their distinctive, contrasted plumage of light and dark uniform areas give way to mixed, then essentially dark phase populations of the species, the latter quite similar to *lonnbergi* but more uniform and never with red in the plumage. Like *maccormicki*, *lonnbergi* is never capped, but small amounts of rufous colour can appear in the plumage of some individuals. This tendency is much more pronounced in *antarcticus*, with which the «red factor» is almost always present in juveniles. A

large proportion of *antarcticus* is indistinctly capped. Finally, both redness and capped appearance reach their full expression in *S. chilensis*. It may be significant that the four foci correspond to those of the four forms, *bransfieldensis*, *georgicus*, *albiventer* and *atriceps*, of the Imperial Cormorant, *Phalacrocorax atriceps* (Devillers and Terschuren, 1978), an important provider species for the skuas.

It seems possible that the speciation of the great skuas entirely took place in South America, an originally clinal species occupying the entire arc, breaking up into four populations which may have been more isolated than today during climatic vicissitudes. We are now witnessing secondary contacts on the Antarctic Peninsula and in Patagonia. Earlier expansions and contacts with hybridization may have been responsible for the dimorphic populations of *maccormicki* on the Antarctic Peninsula, and the variable, capped appearance of the Falkland swarm. The presence of *lonnbergi* on subantarctic islands to the west of South Georgia, from Kerguelen to New Zealand is explained by downwind colonisation in the belt of westerlies, taking place after the splitting and differentiation of the forms, as for *Phalacrocorax atriceps*. Tristan da Cunha may have been reached from the Falklands. The divergence of this population, and its greater resemblance to *lonnbergi*, may indicate either early colonisation, before the Falkland population diverged farther, or underwent other influences, or double origin, *antarcticus* from Falkland and *lonnbergi* from South Georgia or elsewhere, effect of the founder principle, or drift of a small population. The North Atlantic was almost certainly colonized from Tristan da Cunha or the Falklands, as Hagen (1952) suggested, since these islands have the most *skua*-like of any southern population, are closest geographically, and directly linked to the North Atlantic breeding areas by the annual migration of millions of Greater and Sooty Shearwaters (*Puffinus gravis* and *P. griseus*), species often attended by skuas at sea.

The history of skua distribution in Patagonia cannot be reconstructed with certainty. The Chilean Skuas of Santa Cruz are not distinguishable from Pacific ones and I believe that the Atlantic birds are relatively recent colonists, arrived directly overland from the Chilean fjords. Indeed, the distribution of skuas on the Patagonian coast shows a remarkable parallel to that of the blue-eyed shags. Cormorants with the cheek pattern of Falkland *Phalacrocorax atriceps albiventer* breed alone at Punta Tombo, where only *antarcticus* is found, while they share Isla Chata, off Puerto Deseado, with a majority of «*imperialis*»-type birds, indistinguishable from the Chilean fjords nesters (Devillers and Terschuren, 1978). Three Pacific coast cormorants, *P. atriceps* «*imperialis*», *P. bougainvillii*, and *P. gaimardi*, have established populations on the Atlantic seaboard without connecting links in the Strait of Magellan area, a colonisation which, as argued elsewhere (Devillers and Terschuren, 1978), is more likely to have taken place overland through the gaps of the Andean chain than around Tierra del Fuego or through the Straits of Magellan. The same applies to the Chilean Skuas, which are abundant in the maze of fjords and inner passages of Chile, far from sight of the open ocean, and can clearly travel up these fjords to their

heads near the Andean divide or across it. Such transcontinental crossings would presumably have been undertaken only after sufficient fragmentation of the Andean ice sheet that separated Patagonia from the Pacific coast, covered Tierra del Fuego, and obstructed the Straits of Magellan (Flint, 1971).

As for the *antarcticus* of Chubut, their slight plumage originality suggests a period of isolation. At the last glacial maximum the Falklands were separated from the unglaciated part of the continent by a narrow channel, and skua populations are likely to have been similar on both sides of it. They may have already had the combined *lonnbergi* and *chilensis* character of today's *antarcticus*, either as a result of their former position in a cline, or of hybridization of a *lonnbergi* type insular population with a proto-*chilensis* stock isolated on the Patagonian coast by the advance of the Andean ice sheet from the main population retreating to the northern Chilean fjords, and brought in closer contact with Falkland birds by the lowering of the sea level. As sea level rose again during the post-glacial period, the continental population of *antarcticus* would have been increasingly isolated, and would have had time to diverge somewhat from the main Falkland group before the present contact was made with the newly arrived, expanding *S. chilensis*.

It is also conceivable, however, in view of their very small present numbers, that *antarcticus* have at some time disappeared from the continental coast, and have only recently recolonized it. In that case, their morphological divergence from the Falkland stock would be the result of founder effect or of fairly rapid drift in a small population.

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SUMMARY

Two skuas of the *Stercorarius skua* superspecies breed in South America, *S. antarcticus* mainly in the Falklands, *S. chilensis* mainly in Fuegia and the Chilean Fjords. The interactions of the two forms and the limits of their respective ranges have been poorly known.

The Falkland Skua was studied in two large colonies of the Falkland Islands (New Island and Carcass Island). Adult plumages, individual variation, including frequency distribution of plumage types, juvenal plumage and behaviour, particularly the Long-Call performance, are considered. The adult plumage is very variable, with extreme light and extreme dark types bridged by more numerous intermediates. All have blackish underwing coverts. The Long-Call performance is extremely similar to that of *S. skua* and differs sharply from that of *S. maccormicki*.

The Chilean Skua, studied in the Strait of Magellan, southern Tierra del Fuego, and the Chilean channels is also rather variable in adult plumage, though the specific traits of the species, cap, red or pale underwing coverts and throat, and bicolored bill are found in all types. Juveniles tend to be brighter, redder, than adults and do or do not have rufous edges to the feathers of the upperparts. The species is considerably less aggressive at the nest than other large skuas.

The Chilean Skua has been occasionally seen in the Falklands, a new occurrence being reported in this study. On the coast of Patagonia, Falkland Skuas breed alone at Punta Tombo and at least as far south as Camarones (Chubut). The characters of this

population are very similar, though not quite identical, to those of Falkland *antarcticus*. At Puerto Deseado, Santa Cruz, breeds a mixed skua population, including *S. antarcticus*, *S. chilensis* and hybrids. Both parental forms occur side by side and apparently retain their specific behaviour at the nest, *antarcticus* aggressive, *chilensis* not.

It is proposed that *S. antarcticus* and *S. chilensis* be considered distinct species on the basis of clear-cut morphological differences in all plumages, involving signal-characters, limited hybridisation in the zone of contact, and very restricted, non-expanding, area of contact. This type of interaction is typical of many species of larids. *S. chilensis* is monotypic. *S. antarcticus* is very closely allied to *S. lonnbergi*, *S. hamiltoni* and *S. skua*. In particular, adult plumage of some individuals of the first three are practically indistinguishable, as are some juveniles of *antarcticus*, *hamiltoni* and *skua*. Some adult *skua* differ very little from *hamiltoni*. The four forms are probably best considered conspecific.

The evolutionary history of the large skuas is discussed. An orderly variation in amount of capping, and presence of red in the plumage, can be observed in the South American quadrant from light *S. maccormicki* through dark *S. maccormicki*, *S. skua lonnbergi*, *S. s. antarcticus* to *S. chilensis*. *S. s. hamiltoni* is related to both *S. s. lonnbergi* and *S. s. antarcticus*, *S. s. skua* to *S. s. hamiltoni* and/or *S. s. antarcticus*. A parallel is drawn with the distribution and history of the Imperial Shags, *Phalacrocorax atriceps*. It is suggested that the Atlantic coast of Patagonia was colonised overland by *S. chilensis* from the Chilean Fjords, while the presence of *S. s. antarcticus* in Chubut could be either a relict from glacial times or a recent recolonisation from the Falklands.

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SAMENVATTING

Twee grote jager vsan de *Stercorarius skua* supersoort broeden in Zuid-Amerika : *S. antarcticus* hoofdzakelijk in de Falkland-Eilanden, *S. chilensis* vooral in Vuurland en in de fjorden van Chili. De manier waarop deze twee soorten op elkander inwerken, alsmede de grenzen van hun respectievelijk verspreidingsareaal, waren slecht gekend.

De Falkland Jager werd bestudeerd in twee grote broedkolonies op de Falkland Eilanden, nl. op New Island en op Carcass Island. De vederkleden der adulte en der juveniele vogels, de individuele variaties — inbegrepen de frequentie waarmede deze voorkomen — en het gedrag, vooral de *Long-Call* uitvoering, worden besproken. Het vederkleed der adulte exemplaren is zeer variabel met enerzijds uiterst lichte exemplaren en uiterst donkere anderzijds; tussen beide types komen talrijke intermediaire vormen voor. Ze hebben allemaal donkere ondervleugeldekveren. De uitvoering van de *Long-Call* lijkt zeer op deze van *S. skua* en verschilt veel van deze van *S. maccormicki*.

De Chileense Jager, bestudeerd in de Straat van Magellaan (zuidelijk Vuurland) en in de Chileense fjorden en kanalen, vertoont insgelijks een variabel aduultkleed; nochtans zijn de soortgebonden kenmerken zoals het donkere kalotje, rode of bleke ondervleugeldekveren en keel, en tweekleurige snavel terug te vinden in alle types. Juveniele vogels zijn meestal roder en feller gekleurd dan de adulte exemplaren en de bovendelen vertonen niet steeds de rossige vederranden. De soort is minder agressief bij het nest dan de andere grote jagersoorten. Op de Falkland Eilanden is de Chileense Jager slechts een toevallige gast; een nieuwe waarneming wordt in deze studie vermeld. Op de kust van Patagonië broedt de Falkland Jager alleen te Punta Tombo en zuidwaarts tenminste tot in Camarones (Chubut). De morfologische kenmerken van deze populatie gelijken erg, doch zijn niet identiek op deze van de *S. antarcticus* die op de Falklands broeden. Te Puerto Deseado, Santa Cruz, broedt een gemengde populatie van *S. antarcticus*, *S. chilensis* en hun hybriden. De twee oorspronkelijke soorten vindt men er naast elkander en ze schijnen hun specifiek gedrag nabij het nest te behouden : *antarcticus* agressief, *chilensis* niet.

Er wordt voorgesteld *S. antarcticus* en *S. chilensis* als twee soorten te beschouwen. Dit op basis van de duidelijke morfologische verschillen in alle vederkleden, de verschillen in het gedragspatroon, de beperkte hybridisatie in de contactzones, alsmede de kleine hybridisatiezone die, al bestaat deze reeds langer dan een halve eeuw, zich niet verder uitstrekt. Deze wijze waarop twee soorten met elkaar in contact komen is karakteristiek voor vele soorten Laridae. *Stercorarius chilensis* is monotypiek. *Stercorarius antarcticus* is zeer verwant aan *S. lonnbergi*, *S. hamiltoni* en *S. skua*. De adult vederkleden van sommige exemplaren van de eerste drie rassen zijn nauwelijks van elkander te onderscheiden. Dezelfde opmerking geldt voor de juveniel kleden van *S. antarcticus*, *hamiltoni* en van *skua*. Sommige adulte *S. skua* verschillen zeer weinig van *hamiltoni*. Deze vier vormen mogen als één soort beschouwd worden.

De evolutie van de grote jagers wordt besproken. Een regelmatige variatie wat betreft de aanwezigheid van een donker kalotje en van de hoeveelheid ros in het gevederte, wordt in Zuid-Amerika waargenomen; van lichte *S. maccormicki* tot donkere *S. maccormicki*, *S. s. lonnbergi*, *S. s. antarcticus* tot *S. chilensis*. *S. s. hamiltoni* is zowel verwant aan *S. lonnbergi* als aan *S. s. antarcticus*, *S. s. skua* aan *S. s. hamiltoni* en /of aan *S. s. antarcticus*. Er wordt een vergelijking gemaakt met de verspreiding en de geschiedenis van *Phalacrocorax atriceps*; also wordt voorgesteld dat de Atlantische kust van Patagonië gekoloniseerd werd door *S. chilensis* overland, vanuit de Chileense fjorden. Het voorkomen van *S. s. antarcticus* op de kust van Chubut kan ofwel te wijten zijn aan een relictpopulatie uit de ijstijd, ofwel aan een recente kolonisering vanaf de Falkland Eilanden.

RESUME

Deux labbes appartenant au groupe du Grand Labbe, *Stercorarius skua*, nichent en Amérique du Sud; le Labbe des Malouines, *S. antarcticus*, principalement aux îles Falkland (ou Malouines), le Labbe du Chili, *S. chilensis*, en Fuégie et dans les fjords chiliens. Les interactions des deux formes et les limites de leurs aires de dispersion respectives étaient mal connues.

Le Labbe des Malouines a été étudié dans deux grandes colonies des Falklands (New Island et Carcass Island). Sont considérés successivement le plumage adulte, la variation individuelle, particulièrement la fréquence relative des types de plumage, le plumage juvénile et le comportement. Le plumage adulte est très variable, les types extrêmes, clair et sombre, moins nombreux que les intermédiaires. Tous ont les couvertures sous-alaires noirâtres. La Parade de Proclamation est très semblable à celle du Grand Labbe, *S. skua*, et diffère nettement de celle du Labbe de McCormick, *S. maccormicki*.

Le Labbe du Chili, étudié dans le détroit de Magellan, dans le sud de la Terre de Feu et dans les chenaux chiliens, est lui aussi variable en plumage adulte. Toutefois, les traits spécifiques de l'espèce, calotte foncée, couvertures sous-alaires et gorge rousses ou claires, bec bicolore, se trouvent dans tous les types de plumage. Les juvéniles sont généralement de tons plus vifs, plus rouges, que les adultes et ils ne présentent pas toujours de lisérés roux aux plumes des parties supérieures. L'espèce est beaucoup moins agressive au nid que les autres grands labbes.

Le Labbe du Chili a été noté occasionnellement aux Malouines et notamment au cours de la présente étude. Sur la côte de Patagonie, le Labbe des Malouines niche seul à Punta Tombo, et au sud au moins jusqu'à Camarones (Chubut). Les caractères morphologiques de cette population sont très semblables à ceux d'*antarcticus* des Falkland, mais pas identiques. A Puerto Deseado, Santa Cruz, niche une population mixte de labbes comprenant *S. antarcticus*, *S. chilensis* et des hybrides. Les deux formes parentales se trouvent côte à côte et semblent maintenir leur comportement spécifique près du nid, *antarcticus* agressif, *chilensis* pas.

Il est proposé de traiter *S. antarcticus* et *S. chilensis* comme deux espèces, en raison des différences morphologiques tranchées en tout plumage, différences qui s'étendent à des caractères-signaux, de l'aspect limité de l'hybridation dans la zone de contact

et de la faible étendue de la zone d'hybridation, qui ne s'est apparemment pas étendue, bien qu'elle soit établie depuis un demi-siècle au moins. Ce type de contact est caractéristique de beaucoup d'espèces de laridés. *S. chilensis* est monotypique. *S. antarcticus* est très voisin de *S. lonnbergi*, de *S. hamiltoni* et de *S. skua*. En particulier, les plumages adultes de certains individus des trois premières formes sont à peine distinguables. Il en est de même du plumage juvénile d'*antarcticus*, d'*hamiltoni* et de *skua*. Certains adultes de *skua* diffèrent très peu d'*hamiltoni*. Les quatre formes peuvent être considérées comme conspécifiques.

L'évolution des grands labbes est discutée. Une variation régulière, particulièrement en ce qui concerne la présence d'une calotte sombre et la quantité de roux dans le plumage, s'observe dans la zone sud-américaine, de *S. maccormicki* clair, par *S. maccormicki* sombre, *S. skua lonnbergi* et *S. s. antarcticus* jusqu'à *S. chilensis*. *S. s. hamiltoni* est apparenté à la fois à *S. s. lonnbergi* et à *S. s. antarcticus*, *S. s. skua* à *S. s. hamiltoni* et/ou à *S. s. antarcticus*. Un parallèle est mis en évidence avec la distribution et l'histoire du Cormoran impérial, *Phalacrocorax atriceps*. Il est suggéré que la côte atlantique de Patagonie a été colonisée par *S. chilensis* à partir des fjords chiliens, directement à travers le continent. La présence de *S. s. antarcticus* sur la côte du Chubut peut être soit une relique de la période glaciaire, soit une recolonisation récente à partir des Falklands.

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