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# THE HYBRID SKUA: A SOUTHERN OCEAN ENIGMA

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ABSTRACT.—Mixed pairs of South Polar Skuas (*Catharacta maccormicki*) and Brown Skuas (*C. lonnbergi*) were banded and observed during a 9-year study within a narrow zone of sympatry near the Antarctic Peninsula. A history of their territorial, mate, and other preferences disclosed that mixed pairs usually, but not invariably, reside near penguin colonies; male *maccormicki* usually, but not invariably, pair with female *lonnbergi*; some mixed pairs remained faithful, whereas members of others readily remated with the same or different species; nesting success in mixed pairs paralleled nesting success in *maccormicki*, indicating a major role of the male in securing food for the female before egg laying. Although hybrids resulting from mixed matings resembled *lonnbergi* in appearance, their mating, feeding, and migratory behavior resembled those of *maccormicki*. At least some $F_1$ hybrids were fertile, but matings between *maccormicki* and *lonnbergi* were less than expected by chance alone, and the two skuas were considered close but separate species. Field identification of hybrids was extremely difficult and likely will confuse observers along the migratory routes. *Received 29 Nov. 1986, accepted 17 Mar. 1987.*

Two widely recognized species of skuas breed in the Southern Ocean: the more southern South Polar Skua (*Catharacta maccormicki*) and the Brown or Subantarctic Skua (*C. lonnbergi*). Although these birds are allopatric over much of their vast breeding ranges, some pairs nest side by side within a narrow zone of overlap in the Antarctic Peninsula region (Watson 1975), the South Shetland Islands (Trivelpiece and Volkman 1982), and, more recently, the South Orkney Islands (Hemmings 1984) where a small number of mixed matings occur. The resulting hybrids pose questions concerning their influence on the gene pools of the two species. They also create problems in field identification of skuas, not only for biologists who study them, but also for the increasing number of enthusiasts observing birds either at sea or along the migratory routes of both Atlantic and Pacific shores of the Americas.

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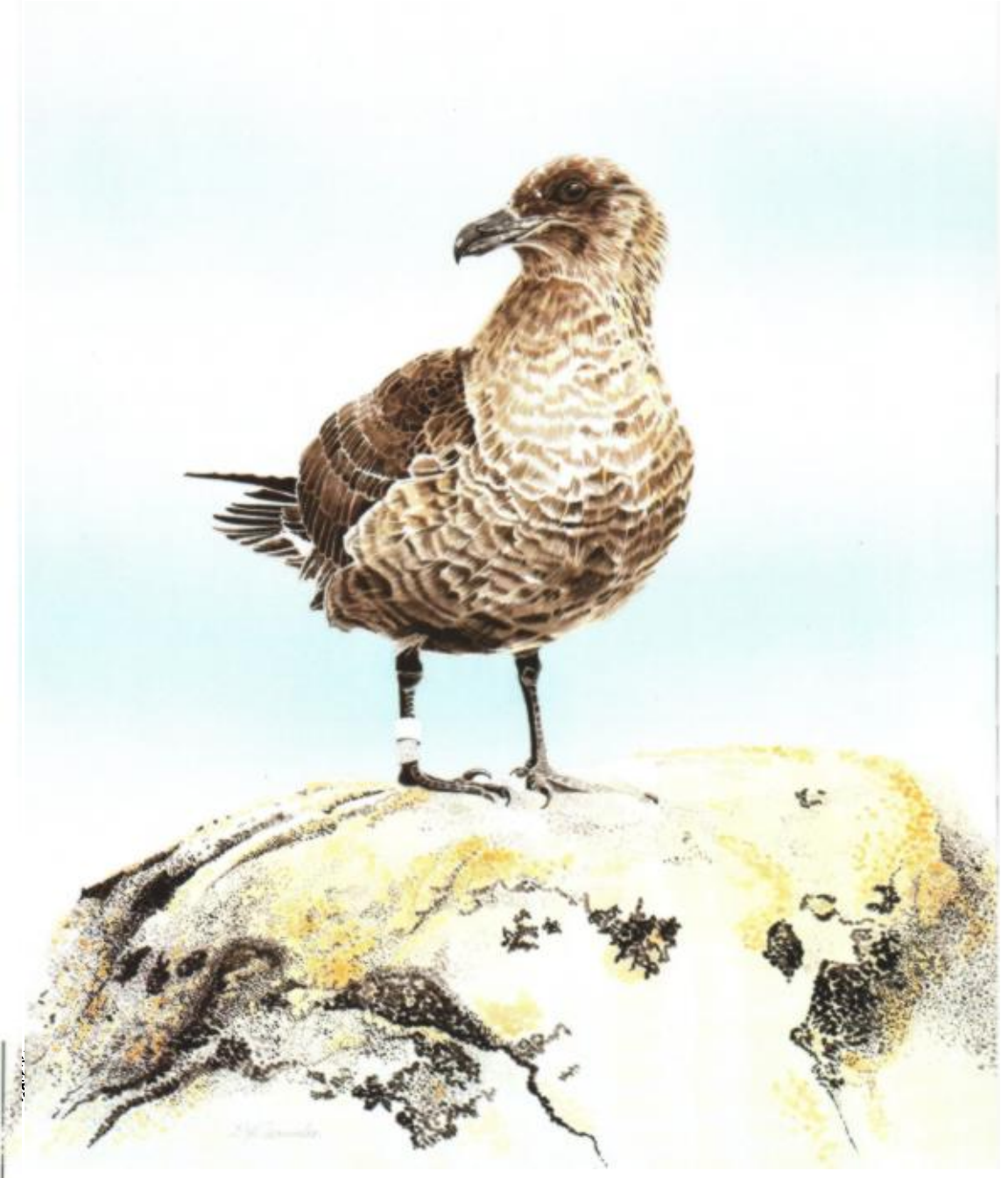

Nine-year-old $F_1$ hybrid skua *(Catharacta maccormicki X C. lonnbergi)*
on its breeding ground near the Antarctic Peninsula.
Watercolor painting by David F. Parmelee.

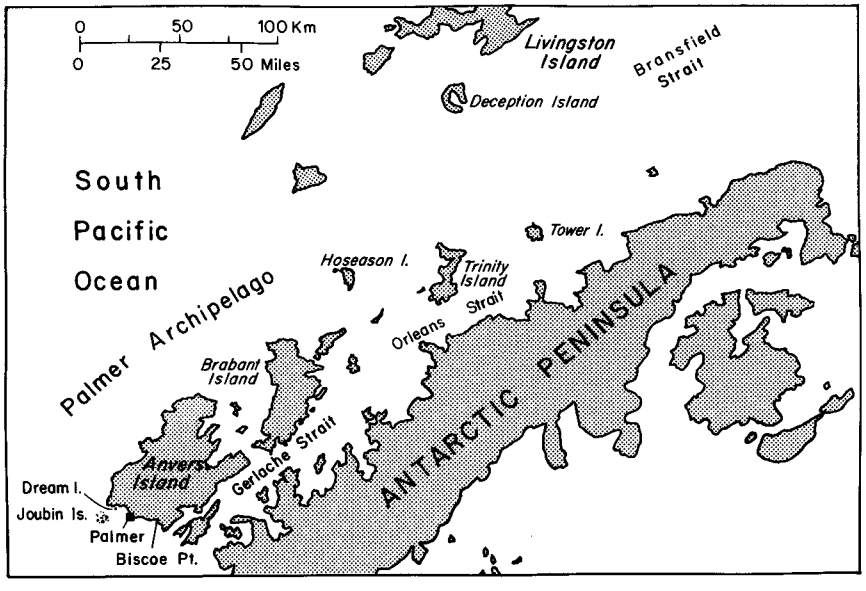


FIG. 1. Palmer Archipelago. The archipelago consists of a group of islands extending from Tower Island in the north to Anvers Island in the south, lying northeast of the Antarctic Peninsula, from which it is separated by Gerlache and Orleans Straits. The principal study area is located at Palmer, midway between Biscoe Point and the Joubin Islands.

For a period spanning 11 years, including the austral summer seasons (October–March) from 1974–75 through 1980–81, and from 1983–84 through 1984–85, the author and others observed mixed pairs and their hybrids in the vicinity of U.S. Palmer Station (64°46'S 64°03'W) on Anvers Island (Fig. 1) near the Antarctic Peninsula. In this report I attempt to identify and clarify some of the mystery surrounding the mixed matings and resulting hybrids.

## STUDY AREA AND METHODS

Anvers Island, at the southern end of Palmer Archipelago, is covered with a thick, highly crevassed ice sheet except for the peaks of high interior mountains ranging up to 2822 m elevation, and the tips of low-lying peninsulas that jut into the sea. These peninsulas and the small offshore islands close by become mostly snow- and ice-free each austral summer and provide the breeding grounds for the skuas and other seabirds. The study area (Fig. 2) included both peninsulas and offshore islands which, with the exception of Bonaparte Point, were accessible only by means of outboard engine-driven rubber boats. Tides were not a concern, but whenever windblown pack ice moved into the area it hindered or prevented travel by boat. Several hundred pairs of South Polar Skuas that bred in many places throughout the Palmer study area were dependent on at-sea foraging for their principal food of fish.

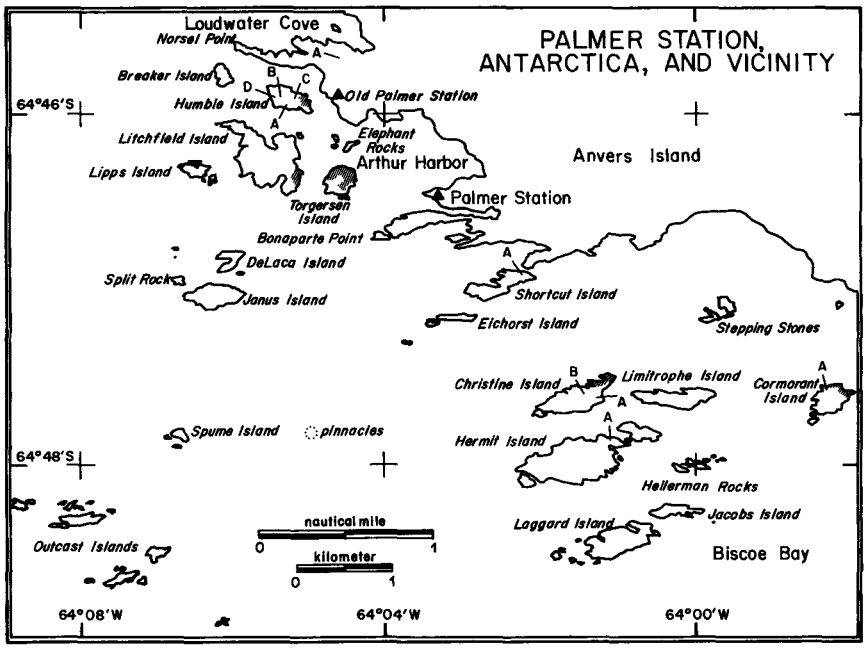


FIG. 2. Palmer Archipelago Study Area. Parallel lines show locations of Adelie Penguin colonies on Cormorant, Christine, Torgersen, Litchfield, and Humble islands. Mixed pairs of South Polar and Brown skuas produced 24 hybrids on Cormorant Island (Site A), Hermit Island (Site A), Shortcut Island (Site A), Humble Island (Sites A, B, C, D), and Norsel Point (Site A). On Christine Island Site A, an eight-year-old $F_1$ hybrid mated with a South Polar Skua and produced an $F_2$ hybrid fledgling; for two seasons a male South Polar Skua and a female Brown Skua occupied but produced no progeny at Site B.

The much less numerous Brown Skuas (6 to 12 pairs) bred near and used Adelie Penguin (*Pygoscelis adeliae*) eggs and nestlings as a source of food.

Both South Polar and Brown skuas defended their nests boldly. As dive-bombing individuals were easily caught in hand nets thrust suddenly above one's head, the majority of nesting skuas were caught, banded, and frequently marked with combinations of colored bands for convenient field identification. Apart from the nesting areas, a few were caught in cannon or simple drop nets baited with food. As a rule adults were banded with numbered bands on the left leg, chicks on the right. Although we failed to catch some individuals, 16 individuals from mixed pairs were captured and marked at 10 sites within the study area (Fig. 2). Their hybrid offspring in turn were marked with a numbered metal band and a white plastic band on the right leg.

From one season to the next a concerted effort was made to keep track of the mixed and normal pairs of skuas. Their territories were mapped, and any change in occupancy was noted. As surviving adults often returned to the original territory and paired with former mates, changes were easily detected. Personnel at Palmer also noted the return of birds that

had been banded previously as chicks. Always, a watchful eye was kept for any returning hybrid.

## HISTORY OF MIXED PAIRS WITHIN THE STUDY AREA

Within the study area, mixed pairs were not evenly distributed (Fig. 2). An abbreviated island-to-island summary of these pairs follows:

### Cormorant Island

*Site A.*—South Polar ♂ 877-34049 × Brown ♀ 877-34048 (pair banded at site on 9 January 1975) produced two hybrids each season in 1974–75, 1975–76, and 1976–77, but their attempt in 1977–78 failed when all South Polar Skua nestings also failed, after which D. Neilson collected the male. In 1978–79, the female produced no progeny with an unbanded Brown male. In 1979–80, Brown ♀ 877-34048 abandoned Cormorant Island for Christine Island where she mated with a Brown male previously banded 877-36903 at Palmer Station on 4 November 1975; the pair produced progeny that season, and again in 1980–81, and 1983–84. In 1984–85, the male was found dead at Palmer Station on 11 December 1984, and the female (rebanded 1067-25020 earlier) failed to remate and was last seen on Christine Island on 18 January 1985.

### Christine Island

*Site A.*—Hybrid 877-36556 (banded when a chick on Humble Island by Neilson [1983] on 18 January 1976) was observed by me at Site A on 2 January 1984 when it was eight years old and mated with an unbanded South Polar individual of uncertain sex. C. Rimmer later confirmed the identity but not the sex of the hybrid (rebanded 1067-25309) and also banded its South Polar mate 1067-25708 on 16 February 1984; still later he banded their single $F_2$ hybrid fledgling 1067-25841 on 24 February 1984, thus establishing beyond doubt the fertility of *maccormicki-lonnbergi* $F_1$ hybrids. The mixed pair again occupied Site A in 1984–85 but produced no progeny; shell fragments at their nest indicated earlier loss of eggs. Before its rediscovery on Christine Island, the $F_1$ hybrid was recovered from a fish net by E. Cunico at Parangual, Brazil, on 23 May 1980, when four years old and "released unharmed."

*Site B.*—Occupied by an unbanded South Polar male and unbanded Brown female in 1983–84, and 1984–85 but no evidence of nesting was recorded.

### Hermit Island

*Site A.*—South Polar ♂ 977-31563 × Brown ♀ 977-31562 (banded at the site respectively on 15 and 11 February 1975) produced two hybrids each season in 1974–75 and 1975–76, but both adults were not seen since.

## Shortcut Island

*Site A.*—Unbanded South Polar male × left-leg banded Brown Skua of uncertain origin produced one hybrid in 1975–76, but only South Polar Skuas have since occupied Shortcut Island. Site A was about 1.5 km from the closest penguin colony.

## Humble Island

*Site A.*—South Polar ♀ 977-31504 (banded at site on 10 January 1975) × unbanded male Brown Skua produced two hybrids in 1974–75. In 1975–76, she produced two hybrids with Brown ♂ 877-36911 (banded at Palmer Station on 9 November 1975). In 1976–77, a different mixed pair occupied Site A: a left-leg banded South Polar male of uncertain origin × Brown ♀ 877-36908 (banded at Palmer Station on 6 November 1975) produced one hybrid, which died before fledging. In 1977–78, Brown ♀ 877-36908 paired with an unbanded Brown male but failed to produce eggs.

Brown ♂ 877-36911 was next recorded in 1977–78 on Litchfield Island where he participated in a trio (three adults occupying one nest) with two Brown Skuas that produced no young. In 1978–79, Site A was unoccupied, although visited occasionally by ♀ 877-36908, which did not mate that season; meanwhile ♂ 877-36911 died from fowl cholera on Litchfield Island. Site A was unoccupied in 1979–80 after ♀ 877-36908 abandoned it for Site C. It was also unoccupied 1980–81, but the site was occupied by South Polar Skuas 1983–84, 1984–85. Of the four hybrids produced at Site A, one later bred within the study area (see Christine Island above), and one was kept captive at Palmer Station where it eventually died.

*Site B.*—South Polar ♂ 877-31503 (banded at site on 10 January 1975 when mated to a South Polar female) produced two hybrids with an unbanded Brown female in 1975–76. In 1976–77, he mated with Brown ♀ 877-36958 (banded at site on 21 January 1977), but they produced no hybrid that season, and the South Polar male did not nest at this site again. Female paired next with a Brown ♂ (banded 1067-25059 at site on 24 January 1979), but only one young was produced from 1977–78 through 1980–81, and the male not seen since. When next observed in 1983–84, Brown ♀ 877-36958 (rebanded 1217-00939) was paired with South Polar ♂ 877-36651 (banded at site on 13 January 1984). They had no progeny that season, but produced two hybrids in 1984–85.

*Site C.*—Occupied by South Polar Skuas in 1974–75, 1975–76, and 1976–77, but unoccupied 1977–78 and 1978–79. The site was occupied 1979–80 by South Polar ♂ 877-36953 (banded previously near Site C on 16 January 1977) × Brown ♀ 877-36908 that previously bred at Site A on Humble Island. The pair produced two hybrids that season and one

in 1980–81. In 1982–83, the pair was shot, presumably at Site C, by Hoberg (1984) for its parasites. The site was unoccupied 1983–84 and 1984–85.

*Site D.*—This was a new territory not used by any skuas during the study before 1984–85, when it was occupied by South Polar ♂ 1057-10286 (previously banded at another Humble Island site on 9 February 1980 when mated to a South Polar female) × Brown ♀ 1217-00940 (banded at site on 24 December 1984). The pair produced two hybrids.

### Norsel Point

*Site A.*—A previously banded (left leg) South Polar male of uncertain origin × Brown ♀ 1057-10449 (banded at site on 23 February 1980) produced one hybrid at the site in 1979–80. Brown female not seen since. Site A was about 0.7 km from the closest penguin colony.

## MIXED MATINGS OUTSIDE THE STUDY AREA

Limited observations of mixed matings outside the study area included the following:

At Biscoe Point (64°49′S 63°49′W), about 12 km east of Palmer Station, an unbanded South Polar male × unbanded Brown female had two eggs on 17 December 1984.

At Dream Island (64°44′S 64°14′W), about 8 km northwest of Palmer Station, an unbanded South Polar male × Brown ♀ 1067-25104 (banded at site on 7 January 1984) produced two hybrids in 1983–84 and two in 1984–85. On an unnamed island adjacent to Dream Island, an unbanded South Polar male and an unbanded Brown female had two eggs on 31 December 1984.

On one of the many unnamed Joubin Islands (64°47′S 64°27′W), about 12 km southwest of Palmer Station, Neilson (1983), on 7 February 1977, banded two hybrids produced by an unbanded South Polar male and an unbanded Brown female.

## RESULTS

Nearly a decade of repeated observations on mixed skua matings within and near the study area disclosed the following:

(1) Penguin-dependent Brown Skuas invariably nested near penguin colonies, whereas the fish-dependent South Polar Skuas and mixed pairs either nested near or far from the penguin colonies. Judging by the prey brought to the young, the mixed pairs residing far from the colonies were the least dependent on penguins for food.

(2) Within the study area, most Adelie Penguins resided in the triangle formed by Torgersen (8630 pairs, 8-year mean), Litchfield (579 pairs,

9-year mean), and Humble (2516 pairs, 8-year mean) islands (see Fig. 2). For reasons not understood, Humble Island with its modest population of both species of skuas had 45% of the mixed matings and produced 50% of all hybrids believed to have fledged, whereas nearby Litchfield Island, which had the largest population of both species of skuas, had no mixed pairs. The Brown Skuas of Litchfield hunted mostly on Torgersen Island, which had the largest penguin colony and, in many years, no nesting skuas. Nevertheless, the triangle referred to above was the heart of Brown Skua activity for all of Anvers Island, and where mixed pairing likely will occur.

(3) In 23 of 25 mixed pairings observed in the present study, a male South Polar Skua paired with a female Brown Skua. The only exception to this was at Site A, Humble Island. Other observers (Trivelpiece and Volkman 1982, Hemmings 1984) found only male *maccormicki* mated to female *lonnbergi.* Neilson (1983), who studied mixed pairing at Palmer, believed that an advertising male South Polar Skua on territory was joined by one of a surplus of Brown Skua females in search of a mate, especially before the arrival of many South Polar Skua females. This explanation may be oversimplified, for we now know that some Brown Skua females return to and remain at a nest site even when they have lost their mates. A few of these birds then form new pairbonds with South Polar Skua males, suggesting that occasionally a female may hold a territory and attract a male to it. Also, mixed pairs per se remained faithful to an established site for as many as four seasons, possibly longer. On the other hand, some individuals of both sexes readily changed territories and mated with members of the same or different species. In any event, it appears that the formation of mixed pairs is not strictly random.

(4) In observing marked skuas over a period of years, it is clear that both South Polar and Brown skuas show a trait that may best be described as sometime absenteeism, i.e., some individuals return to the breeding grounds and do not breed, or they fail to return altogether, but then later return and breed at old or new sites. With respect to mixed pairs, a site that is abandoned by the birds for one or more seasons may be reoccupied by either member of the pair that then mates with a new individual of the same or different species. We have not yet documented whether a mixed pair ever reunites following absenteeism.

(5) In the study area, the fish-dependent South Polar Skuas showed dramatic fluctuations in fledging success, whereas the penguin-dependent Brown Skuas did not (Parmelee et al. 1978). Nesting failure in mixed pairs paralleled that of widespread nesting failure in the South Polar Skuas, indicating the important role of the male in securing food for the female before egg laying (Pietz 1987). According to Pietz, the female Brown

Skua of a mixed pair nesting close to penguins on Humble Island preyed heavily on penguins; food records for its hybrid chicks were half penguin and half fish. Hybrid chicks observed by me far from the penguin colonies regurgitated only fish or krill, and the ground occupied by them had no penguin remains which invariably litter the nesting sites of Brown Skuas.

(6) We had so few observations on the one $F_1$ hybrid (sex unknown) × South Polar Skua nesting that we cannot say for certain where the birds hunted. It appeared that their food was derived from the sea, for they were not observed at a penguin colony near by, and within their territory we found no penguin remains.

(7) Palmer-banded South Polar Skuas have been recovered as far north as West Greenland in the North Atlantic, and Oregon in the North Pacific. Most South Polar Skuas, however, and one $F_1$ hybrid have been recovered along the coast of Brazil (Parmelee 1985). To date none of our Brown Skuas has been recovered outside the Palmer area. Unlike the South Polar Skuas, the Brown Skuas commence molting their flight feathers before departing the Palmer breeding ground (Neilson 1983), suggesting a short migration. On the basis of a single long-distance return, I know that hybrid skuas behave like South Polar Skuas in that they migrate at least as far north as Brazil.

## MORPHOLOGY OF THE $F_1$ SKUA HYBRID

As a rule South Polar Skuas and Brown Skuas were easily identified in the field despite the fact that the large majority of *maccormicki* at Palmer and elsewhere along the Antarctic Peninsula are medium to dark plumaged. Not only did the species differ in behavioral characteristics (Parmelee et al. 1978, Neilson 1983, Pietz 1985, 1987), their morphology was quite distinct. Neilson (1983) took tarsal, culmen, gonys, and 7th primary measurements and weights of adults and showed *lonnbergi* to be the larger of the two. In the field, the larger body, heavier bill, and longer tarsus identified *lonnbergi.* Moreover, *lonnbergi* had a less variable plumage, characterized by somewhat rufous underparts and prominent yellow to white tipped back feathers that were lacking in *maccormicki.* Some South Polar adults showed a mottled rather than a uniform dorsum; most showed prominent golden hackles on the neck and, in flight, central rectrices that extended beyond the others.

By employing a nonparametric rank correlation test, Neilson (1983) showed that *lonnbergi* females had significantly larger tarsi, wing, and weight values than did their mates. On this basis we were quite certain of our sex determinations of live *lonnbergi.* Such measurements overlap between the sexes in *maccormicki,* and we were forced to rely on behavioral characteristics. Banded birds found dead during the 9-year study verified many earlier sex determinations.

Identifying the hybrid skua in the field, not to mention its sex, was quite a different matter. From the beginning we were puzzled by certain individuals whose size and plumage simply did not conform to our standards. The birds looked like small *lonnbergi* but behaved like *maccormicki*; some of these mystery birds were paired with South Polar mates, but none, to our knowledge, with *lonnbergi* mates. Once we began to observe mixed matings, we were convinced that hybrids likely were responsible for most of our problems in field identification.

Hybrid eggs and young measured by Hemmings (1984) were intermediate in size. Four eggs of one mixed pair measured by Pietz (pers. comm.) over two seasons were, however, typical of Brown Skua size: For samples of 16, 4, and 114 eggs, mean volumes ($V = 0.00048 \times l \times w^2$) were 100, 102, and 84 $cm^3$ for Brown, hybrid, and South Polar skuas respectively; the Brown and hybrid skuas differed significantly from the South Polar Skuas but not from each other, indicating that the size of the egg is not influenced by the male. One would expect that the size of the resulting hybrid may be intermediate to the parental types. Hemmings (1984) found that hybrid chick growth rates, with respect to weight and bill and tarsal lengths, generally fall between those of *lonnbergi* and *maccormicki*. Pietz (pers. comm.) also found that tarsal length in hybrid fledglings was intermediate and that the three groups differed significantly: For samples of 10, 3, and 11 chicks, means were 77.0, 70.0, and 67.0 mm for Brown, hybrids, and South Polar skuas, respectively. In outward appearance hybrid fledglings looked more like *lonnbergi* than *maccormicki*. A captive hybrid at Palmer Station continued to have the outward appearance of *lonnbergi*, although its development seemed abnormal, and it never learned to fly, possibly because of hand rearing.

C. Rimmer took several measurements of the eight-year-old $F_1$ hybrid: culmen 54.3 mm, gonys 19.9, and tarsus 76.5. These measurements were intermediate between those taken at Palmer by Neilson (1983) for *maccormicki* (culmen 45–52, gonys 16–18, tarsus 63–72) and *lonnbergi* (culmen 52–59, gonys 20.5–22.5, tarsus 73–86). Overall, the hybrid had the appearance of a small *lonnbergi*, but its behavior with respect to mate preference, nesting, and migration pointed to *maccormicki*. Although additional examples of banded hybrids are needed to confirm this hypothesis, I believe that most, if not all, of the mystery skuas that plagued our studies probably were hybrids.

## DISCUSSION

With few exceptions the behaviorial distinctions between the two taxa were subtle. One obvious distinction mentioned earlier was the difference in their feeding behavior when breeding sympatrically. The Brown Skuas were so dependent on penguins for their food source that their breeding

schedules were attuned to those of their prey (Parmelee 1985). As a consequence, they bred early and within a relatively short time span, whereas, the at-sea foraging South Polar Skuas were not nearly so synchronized in their breeding, as is clearly reflected in their egg-laying dates that spanned a period of many weeks (Neilson 1983). Also, South Polar Skuas had a greater choice of nesting habitat, often far removed from the penguin colonies. This distinction breaks down, however, where the two species breed allopatrically, even as close as the west coast of Anvers Island where South Polar Skuas too depend on penguins (Parmelee 1985).

Pietz (1985) observed far more subtle differences while studying the two species within the Palmer Station study area. In examining several aspects of the skua long-call display, she found no significant species differences in call composition, call duration, or note duration. She did, however, find that the species differed significantly in four parameters. On the average, the notes of South Polar Skua had a faster repetition rate, lower pitch, lower average frequency, and more harmonics than those of Brown Skuas. Film analysis revealed that South Polar Skuas tended to lean farther back at some point in the long call display. Unfortunately, Pietz did not have the opportunity to observe the known $F_1$ hybrid discussed above.

I observed nothing in the behavior of known or suspected hybrids that clearly set them apart from the parental types. The hybrids resembled *maccormicki* in certain obvious behavior, particularly mate preference. It probably is no coincidence that our mystery birds recorded as probable hybrids were invariably mated to *maccormicki,* some of them nesting a long way from the penguin rookeries. Whether the hybrids select *maccormicki* mates through choice, or simply because those skuas far outnumber *lonnbergi* skuas in our study area is, at this time, a moot question. Nevertheless, if the pattern of $F_1$ hybrid skuas mating with *maccormicki* predominates, the influence of *lonnbergi* genes should diminish.

In another paper on Anvers Island skuas (Parmelee 1985), I stated that the Palmer study area appeared to be fairly typical of Short's (1969) description of a zone of overlap and hybridization where secondary intergradation has occurred. Parental phenotypes far outnumbered the hybrids, and mixed matings were comparatively rare. Certain premating isolating mechanisms also were evident for keeping the two skuas apart, notably asynchronous arrival and breeding times. Ecologically, the two have different territorial and feeding strategies when sympatrically situated. Based on the number of breeding pairs of skuas in the study area, the expected number of mixed pairs through chance mating was calculated to be no fewer than 15 pairs—considerably more than the one to four pairs recorded annually during the 9-year study. The Anvers Island skuas

showed a very close though separate relationship and are thus best considered separate species even though there appear to be no postmating isolating mechanisms with respect to hybrid fertility.

Of 15 banded hybrids believed to have fledged during the early part of the study (1974–75 through 1978–79), including 14 within the Palmer study area, there has been only one recovery (6%) of a returning hybrid to date. This compares with the recovery rates of 2% for 541 Palmer banded *maccormicki* chicks and of 3% for 80 *lonnbergi* chicks for the same period (Parmelee and Rimmer 1984).

Apart from the breeding grounds where experienced observers have the advantage of observing the birds closely on their territories, $F_1$ hybrid skuas are extremely difficult to identify in the field. $F_2$ hybrids will prove even more difficult. As it seems likely that the hybrids are long-distance migrants, observers along the coasts of the Americas should be cognizant of this problem.

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COLOR PLATE

The Frontispiece painting by David F. Parmelee has been made possible by an endowment established by George Miksch Sutton.