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Order **CHARADRIIFORMES**

A large, diverse assemblage of small to medium-large (12–75 cm long) limicoline, pratincoline, aquatic or terrestrial birds. Cosmopolitan from Arctic to Antarctic regions; in all sorts of maritime, freshwater and open terrestrial habitats (including deserts) with a few (woodcocks and snipes) even using dense forests. Once known as Limicolae or Laro-limicolae (e.g. Mayr & Amadon 1951); colloquially, the assemblage (excluding alcids, skuas, gulls, terns and skimmers) is often referred to as waders (especially in Britain) or shorebirds (especially in North America).

About 350 species in 19 families, though taxonomic treatments vary. Following families recognized (mostly based on recent reviews of Order [Sibley *et al.* 1988; Sibley & Ahlquist 1990; Sibley & Monroe 1990]):

Thinocoridae	seedsnipes; four species, S. America.
Pedionomidae	Plains-wanderer; monotypic, Aust.
Scolopacidae	sandpipers, snipes and allies; *c.* 85 species, cosmopolitan.
Rostratulidae	painted snipes; two species, s. America and Old World.
Jacanidae	jacanas; seven species, pantropical.
Chionididae	sheathbills; two species, Antarctica and subantarctic islands.
Burhinidae	thick-knees, stone-curlews; nine species, widespread in Old World and two in Neotropics.
Haematopodidae	oystercatchers; *c.* 11 species, worldwide in tropics and temperate regions.
Recurvirostridae	avocets and stilts; about seven species, worldwide in tropical and temperate regions.
Ibidiorhynchidae	Ibisbill; monotypic, central Asia.
Charadriidae	plovers and lapwings; *c.* 60 species, cosmopolitan.
Pluvianellidae	Magellanic Plover; monotypic, S. America.
Dromadidae	Crab Plover; monotypic, Arabian region.
Glareolidae	pratincoles, coursers, and Egyptian Plover; *c.* 15 species, widespread in Old World.
Stercorariidae	skuas and jaegers; about seven species, mostly in Arctic and Antarctic regions.
Rhynchopidae	skimmers; three species, pantropical.
Laridae	gulls; *c.* 47 species, cosmopolitan.
Sternidae	terns; *c.* 42 species, cosmopolitan.
Alcidae	auks; *c.* 20 species, Arctic and temperate regions of n. hemisphere.

Apparently monophyletic. Pteroclididae (sandgrouse) probably sister-group of Charadriiformes (e.g. Fjeldså 1976, 1977; Sibley & Ahlquist 1990; BWP), though whether best placed within Charadriiformes or in separate order is debated. Flamingoes (Phoenicopteridae) and divers (Gaviidae) have also been treated as Charadriiformes (Olson & Feduccia 1981; Fjeldså 1976, 1977) but DNA–DNA hybridization studies (Sibley & Ahlquist 1990) inconsistent with these theories. Affinities to other orders still controversial; DNA–DNA hybridization has suggested closest links are to large waterbirds, such as storks, herons and allies, Pelicaniformes, Procellariformes, penguins, grebes, divers (Gaviidae) and also Falconiformes. All these were combined in huge order Ciconiiformes by Sibley & Ahlquist (1990).

Taxonomy and relationships reviewed in Sibley & Ahlquist (1990), Christian *et al.* (1992) and BWP (and references therein). Recent reviews have included: patterning of downy young (Jehl 1968; Fjeldså 1976, 1977), osteology (Strauch 1978; Mickevitch & Parenti 1980; Olson & Steadman 1981), DNA–DNA hybridization (Sibley *et al.* 1988, Sibley & Ahlquist 1990) and electrophoresis of tissue proteins (Christian *et al.* 1992). The studies of allozymes, DNA–DNA hybridization and the most recent osteological study of the entire order (Strauch 1978) have agreed in finding two or three well-knit, monophyletic assemblages within the Charadriiformes: scolopacids and allies (Thinocoridae, Pedionomidae, Scolopacidae, Rostratulidae, Jacanidae) and charadrids and allies (Chionididae, Burhinidae, Haematopodidae, Recurvirostridae, Ibidorhyncidae, Charadriidae, Pluvianellidae, Dromadidae, Glareolidae, Stercorcariidae, Rhynchopidae, Laridae, Sternidae, Alcidae); Strauch (1978) treated Alcidae as separate lineage, but skeletons may be so highly modified for foot-propelled diving that they do not reflect relations well (Sibley & Ahlquist 1990); gulls and allies have also been regarded as a separate lineage (Christian *et al.* 1992) or as allied to charadrids (e.g. Sibley & Ahlquist 1990). Further relationships within the Order discussed in introductions to families.

Because the Order comprises so many species and adaptations are so diverse, few characters shared by all species; those that are shared are mostly anatomical features of the skull, e.g. most or all have schizorhinal nostrils, schizognathous palates, well-developed vomer, lachrymals fused with ectethemoid and pre-frontal bones, well-developed supra-orbital grooves; see Olson & Steadman (1981) for more information on osteological characters. Wings usually have 11 primaries, with p10 longest and p11 minute; 15–24 secondaries; diastataxic except in *Scolopax minor*, as far as is known. Usually 12 tail-feathers. Necks usually rather long with 15–16 cervical vertebrae. Oil-gland bilobed and tufted. Syrinx, tracheo-bronchial; two carotids (type A-1 of Glenny 1955); caeca present. Legs usually rather long; hind toe small or lacking in most but all toes greatly elongated in Jacanidae. Feathers with small thin afterfeathers. Normally two moults annually: complete post-breeding and partial pre-breeding; some jacanas and alcids have flightless periods when moulting remiges. Young, downy, usually with intricate cryptic patterns on upperparts of three chief types: pebbly, spotted and striped, matching characters of habitat (Fjeldså 1976, 1977): precocial, nidifugous usually, self-feeding or not depending greatly on parents.

Thirteen families recorded in HANZAB region, with 54 species breeding, 41 occurring as regular non-breeding migrants and *c*. 38 as accidentals or probable accidentals. Scolopacidae, Stercorcariidae, Laridae and Sternidae will be dealt with in Volume 3 of HANZAB.

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Family **LARIDAE** skuas, jaegers, gulls and terns

A large assemblage of small to very large charadriiform seabirds. We recognize four subfamilies within the Laridae following Mayr & Amadon (1951), AOU (1983).[1]

Stercorariinae	Skuas and jaegers; about six species; cosmopolitan.
Larinae	Gulls; *c*. 47 species; cosmopolitan.
Sterninae	Terns; *c*. 42 species; cosmopolitan.
Rynchopinae	Skimmers; three extralimital species, pan-tropical.

Taxonomic rank given to above groups varies greatly. Considered four families within suborder Lari (e.g. Campbell & Lack 1985; BWP), or four tribes within subfamily Larinae (e.g. Sibley *et al*. 1988; Sibley & Ahlquist 1990; Sibley & Monroe 1990). Others have divided Lari into three families (Stercorariidae, Laridae and Rynchopidae) with gulls and terns usually considered subfamilies within Laridae (e.g. Wetmore 1960; Judin 1965; Hackett 1989; Peters). Moynihan (1959) divided the group into two subfamilies, Stercorariinae, containing the skuas, and Larinae, containing gulls, terns and skimmers in three tribes. Study of skeletal and external morphology of suborder 'Lari' (our Laridae) was mostly unable to cluster gulls and terns satisfactorily and found group surprisingly uniform (Schnell 1970a,b). Despite lack of agreement on taxonomic ranking of above groups, monophyly of Laridae is not in doubt. Studies of biochemistry (Christian *et al*. 1992), DNA–DNA hybridization (Sibley & Ahlquist 1990), downy young (Fjeldså 1977) and skeletal morphology (Strauch 1978; Mickevich & Parenti 1980; Chu 1995) generally agree in finding close relation with Glareolidae (pratincoles) and Dromadidae (Crab Plover *Dromas ardeola*). DNA–DNA hybridization suggests Alcidae (auks) also closely related (Sibley & Ahlquist 1990), though this contradicted by studies of skeletal morphology (e.g. Strauch 1978; Chu 1995).

Body-form varies greatly, from small and slender in some gulls and terns, to robust and thickset in skuas, jaegers, some gulls and a few terns. Differences in size between sexes slight; males usually larger but females larger than males in Stercorariinae. Wings usually long, narrow and pointed, but broader and more rounded in some; 11 primaries; p10 longest, p11 minute; 17–24 secondaries. Tail has 12 rectrices; shape varies: in Stercorariinae, central rectrices project beyond rest of tail and greatly elongated in adult breeding plumages of *Stercorarius*; in most Sterninae and Rynchopinae, outer rectrices elongated and tail forked; in Larinae, usually square. Bill, varies, though usually rather short and stout, with prominent gonydeal angle; rather fine in some Larinae and Sterninae; tip pointed in Sterninae, decurved in strong hook in Stercorariinae. Bill highly modified for unique foraging methods in Rynchopinae (Zusi 1962). Lack cere, except in Stercorariinae. Nostrils schizorhinal and perforate, with no median septum. Legs, short and stout; attached near centre of body; tibiae partly bare; tarsi, short and typically scutellate in front. Four toes; hindtoe, short, raised, sometimes rudimentary or absent; front toes, fully webbed (webs somewhat incised in some). Claws, moderately long, strong, laterally compressed. Caeca ranges from large (Stercorariinae) to poorly developed (Rynchopinae, Sterninae). Supra-orbital salt-glands well developed.

Plumages mainly browns, black, white and greys. Colours of bare parts often striking and often showing marked variation with both season and age. Adults moult twice annually: (1) a post-breeding (pre-basic) moult to non-breeding plumage, which is complete (with apparent exception of *Larus sabini*); and (2) a pre-breeding (pre-alternate) moult to breeding plumage, which is almost always partial (but see *Larus pipixcan* and *L. sabini*); some terns also undergo one or two pre-supplemental moults of inner primaries. Primaries moult outwards.

Hatch in natal down, which is replaced by juvenile plumage; downy young precocial but more dependent on

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[1] This treatment differs from the arrangement presented in the introduction to the Charadriiformes in Volume 2 of *HANZAB* (p. 648), where these four subfamilies were listed as families. Recent major studies in avian classification (particularly by Sibley and co-workers) and the publication of a revised species list of Aust. birds (Christidis & Boles 1994) since the preparation and publication of Volume 2, have brought much rearrangement. In this and subsequent volumes of *HANZAB*, taxonomy, nomenclature and arrangements of species follow Christidis & Boles (1994) (though they do not present subfamilial taxonomy). Their sequence of families of Charadriiformes occurring in HANZAB region is: Pedionomidae, Scolopacidae, Rostratulidae, Jacanidae, Chionididae, Burhinidae, Haematopodidae, Recurvirostridae, Charadriidae, Glareolidae and Laridae. However, work on Volume 2 was too advanced to follow their sequence and taxonomy fully. The Scolopacidae are out of place in the arrangement of subfamilies in Volumes 2 and 3; other families follow the order of Christidis & Boles (1994).

Plate 23

Oriental Pratincole *Glareola maldivarum* (page 366)
1 Adult breeding; **2** Adult non-breeding; **3** Juvenile;
4, 5 Adult

Australian Pratincole *Stiltia isabella* (page 373)
6 Adult; **7** Downy young; **8** Juvenile;
9 First immature non-breeding;
10, 11 Adult

parental feeding than other Charadriiformes. Post-juvenile (first pre-basic) moult complete or partial, varying within and between families; moults of subadults complicated and vary between subfamilies (see subfamily accounts). Generally slow to mature, attaining adult plumage when 2–4 years old and first breeding at 2–4 years (smaller gulls and terns) to 4–9 years (many skuas and larger gulls and terns); some may breed in first year (e.g. *Sterna albifrons*).

Inhabit wide range of marine and freshwater habitats from Tropics to polar regions; many species strongly migratory, especially those breeding at high latitudes, e.g. South Polar Skua *Catharacta maccormicki* and Arctic Tern *Sterna paradisaea*, which migrate between polar regions. Most nest in terrestrial colonies near water (see subfamily accounts); some species highly pelagic in non-breeding season. Use wide range of foraging methods (see subfamilies; for discussion of feeding methods, see General Introduction).

See subfamily accounts for summaries of social organization and breeding.

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Subfamily **STERCORARIINAE** skuas and jaegers

Medium to large (50–65 cm) predatory and scavenging seabirds. About six species in two genera: (1) *Catharacta* (skuas) comprises three or four species (but their taxonomy complex, see below), mostly of Subantarctic and Antarctic; two species occur HANZAB region; (2) *Stercorarius* (jaegers) comprise three species that breed in n. hemisphere and migrate to s. hemisphere for boreal winter; all three are non-breeding migrants to HANZAB region. Morphological and behavioural studies often agree in finding these genera to be distinct (Devillers 1978; Furness 1987; Christidis & Boles 1994), but Olson (1985) found no osteological basis for recognizing two genera, and recent preliminary study of mitochondrial DNA (Peter *et al.* 1994) found unexpected similarity between *S. pomarinus* and *C. skua*; further biochemical research needed. Relationship between skuas and other Laridae unclear; morphological studies generally suggest closest to Larinae (e.g. Strauch 1978; Furness 1987; Chu 1995) while studies of behaviour (Moynihan 1959) and DNA–DNA hybridization (Sibley & Ahlquist 1990) suggest they are equally related (sister-group) to all other Laridae. Major review of biology, morphology and taxonomy in Furness (1987).

The genus *Catharacta* comprises six closely related forms (all but one of which breeds in s. hemisphere), and boundaries between species and subspecies difficult to define: *skua* breeds North Atlantic; *lonnbergi*, circumpolar, breeding subantarctic islands and Antarctic Pen.; *hamiltoni* breeds Tristan Grp and Gough I., South Atlantic Ocean, and it is probably this form that occurs Iles Amsterdam and St Paul, Indian Ocean; *antarctica* breeds Falkland Is and Patagonia; *chilensis* breeds coastal Chile and Patagonia; and *maccormicki* is circumpolar on Antarctic Continent, continental islands and South Shetland Is. Both *maccormicki* and *chilensis* usually treated as separate monotypic species. Other four usually treated as one or two species, but treatment complicated by nomenclatural priorities: the three s. circumpolar taxa *antarctica*, *lonnbergi*, and *hamiltoni* almost always treated as subspecies of a single species, and North Atlantic *skua* treated as separate species or fourth subspecies with s. taxa. If all four treated as one species, *skua* has nomenclatural priority (thus *C. skua* with four subspecies); if treated as two species, *C. skua* monotypic, and *C. antarctica* has three subspecies. (The specific name used for s. hemisphere

Plate 24

Great Skua *Catharacta skua* (page 388)
1 Adult on breeding grounds, austral summer; **2** Downy young; **3** Juvenile

South Polar Skua *Catharacta maccormicki* (page 412)
4 Adult pale morph, in worn plumage at breeding grounds, austral summer; **5** Adult dark morph, in fresh plumage at breeding grounds, austral summer; **6** Downy young; **7** Juvenile

Pomarine Jaeger *Stercorarius pomarinus* (page 438)
8 Adult female breeding, light morph; **9** Juvenile, intermediate phase

Arctic Jaeger *Stercorarius parasiticus* (page 448)
10 Adult breeding, light morph; **11** Juvenile, intermediate phase

Long-tailed Jaeger *Stercorarius longicaudus* (page 459)
12 Adult breeding, light morph; **13** Juvenile, intermediate phase

forms has little biological implication beyond whether *skua* has differentiated sufficiently to be considered a species; *Catharacta* clearly radiated in s. hemisphere and *skua* is a recent offshoot from a s. ancestor [Furness 1987; cf. Brooke 1978].) Here we treat *skua*, *antarctica*, *lonnbergi and hamiltoni* as subspecies of C. *skua* and recognize *maccormicki* and *chilensis* as separate species (following Devillers 1977, 1978; Furness 1987; Christidis & Boles 1994; BWP; NZCL). Forms of *Catharacta* mostly allopatric; some hybridization occurs in all areas of contact between breeding forms. For fuller discussion of hybridization, variation and taxonomy in *Catharacta*, see Great (Subantarctic) Skua: Geographical Variation.

Body, robust and thickset, especially in *Catharacta*. Females larger than males: females 11–17% heavier during breeding season, and wings 1–4% longer, but differences slight or absent in other linear measurements. Wings, long; narrow and pointed, with angled carpal joint in *Stercorarius*; broader, straighter and blunter in *Catharacta*; 11 primaries; p11 minute; 17–20 secondaries. Tail, short, slightly wedge-shaped to rounded in *Catharacta*; 12 rectrices; central pair (t1) project slightly in *Catharacta* and most plumages of *Stercorarius*; greatly elongated in adult breeding plumages of *Stercorarius*, forming long tail-streamers (the shapes of which are diagnostic of species); tail-streamers often broken off (or intentionally bitten off) during breeding season. Bill, short, heavy and powerful, with strongly hooked tip to upper mandible and prominent gonydeal angle; superficially gull-like, but rhamphotheca complex, with four distinct sheaths on upper mandible: (1) sheath of lateral edge; (2) strongly curved distal sheath (unguis), smoother and more rounded than tip of bill of gulls; and (3) pair of separate, soft, thin dorsal plates covering nostrils, forming distinct cere (absent in all other Laridae). Head, rounded; neck, thick and strong. Coracoids do not overlap. Sternum has one notch on each side. Legs, short, superficially gull-like, but with very short bare part on tibia. Tarsi, short; scutellate in *Stercorarius*; with single row of scutes at front and reticulate scaling elsewhere in *Catharacta*; scales hard (soft and fleshy in other Laridae). Four toes; hindtoe, short, raised; front toes, fully webbed. Claws, moderately long, strong, laterally compressed, strongly hooked and sharp; combination of strongly hooked claws and fully webbed toes unique among birds. Oil-gland feathered. Caeca present, large, much longer than in Larinae. Supra-orbital salt-glands, well developed. Down occurs on both pterylae and apteria.

Sexes similar in plumage. Bare parts not brightly coloured, unlike Rynchopinae and many Larinae and Sterninae. Iris, black-brown. Bill, dull brown to black. Legs, blue-grey to black. In most *Catharacta*, plumages dark brown, with varying red and yellow tints; great individual variation in plumages within populations (though variation associated with wear, age and season poorly understood). South Polar Skua C. *maccormicki* and all *Stercorarius* polymorphic, with dark morphs (very rare in Long-tailed Jaeger S. *longicaudus*) and varying light morphs (including so-called intermediate morph, which often recognized for convenience); ratios of morphs vary geographically in some species. White bases of primaries form conspicuous patches in wing of all species, but less conspicuous in *Stercorarius*. Light morph *Stercorarius* have white in underbody of adults and subadults. Similarity of plumages between species and great individual variation complicates field identification. Adults moult twice annually: a complete post-breeding (pre-basic) moult and a partial pre-breeding (pre-alternate) moult; both occur mainly while migrating or in non-breeding areas. Young hatch with long soft woolly down, mostly uniform greyish-brown but slightly paler on belly, tips of wing-pads and around and in front of eyes; chicks of C. *maccormicki* very pale all over. Although precocial, chicks dependent on parents for some time. Bill, legs and feet of juveniles paler than in adult and area of black increases with age in *Stercorarius*. Juveniles strongly barred below in *Stercorarius* (unique among Laridae) but not *Catharacta*, one of main reasons for generic separation (Brooke 1978; Furness 1987). Juvenile plumages of *Stercorarius* polyphasic; coloration of juvenile plumage not necessarily related to colour of immature or adult plumage (hence use of phase in accounts, q.v.). Immatures of *Stercorarius* recognized by barred underwing-coverts; gradually attain adult plumage through a series of immature plumages; length of central rectrices increases with age until adult plumage attained. Transition to adult plumage also gradual in *Catharacta*, but immatures difficult to age and subadult moults poorly known. Minimum age of first breeding probably 4–8 years old in *Catharacta* (Furness 1987); *c*. 4 years old in *Stercorarius*; in Arctic Jaeger S. *parasiticus*, average age of first breeding appears to vary with morph (see Arctic Jaeger: Plumages).

Catharacta breeds s. hemisphere, except for outlying population (C.s. *skua*) breeding in North Atlantic. *Stercorarius* circumpolar breeders in high latitudes of n. hemisphere. Migratory, but non-breeding range of all species poorly known. Marine in non-breeding season, in pelagic or (less often) coastal waters. *Stercorarius* migrate S in boreal winter to poorly known wintering areas in Pacific, Indian and Atlantic Oceans. Migrations of *Catharacta* more varied and poorly known, but at least South Polar Skua long-distance trans-equatorial migrants, and almost all leave breeding colonies in non-breeding periods; some Great (Subantarctic) Skua stay near breeding islands in non-breeding periods.

Opportunistic predators, scavengers and, notably, kleptoparasites, though importance of kleptoparasitism varies greatly between species. Feed on land and at sea, taking a variety of carrion, small mammals, eggs and young of seabirds, burrowing petrels, land birds and fish, crustaceans, molluscs, offal and garbage. At times, approach or follow boats, feeding on offals or scraps thrown overboard or stealing food from other seabirds. Pomarine Jaeger and some populations of Long-tailed Jaeger depend almost exclusively on lemmings during breeding season. At sea, food taken mostly by dipping, surface-diving, pattering and aerial pursuit; also piracy. On land, use a variety of methods, including direct attacks, stealing and scavenging. Feeding behaviour of South Polar Skua influenced by presence of Great (Subantarctic) Skua in areas where both species breed (see South Polar Skua: Food). Some individuals defend feeding territories or type-A territories.

Behaviour well studied. Established pairs normally monogamous, with pairs re-forming at start of each breeding season on traditional territories. However, Pomarine Jaegers do not retain same mates or territories but roam nomadically and breed opportunistically and Great (Subantarctic) Skuas in some locations, including HANZAB region, breed in trios as well as pairs (e.g. Bonner 1964; Burton 1968a,b; Young 1978; Hemmings 1989). Trios usually consist of two males and a female (Hemmings 1989). Trios not recorded for South Polar Skua. Nests well-spaced and territories vigorously defended. Clubs a feature of large colonies, generally where non-breeding birds gather to rest together or to practice displays and behaviours. Most jaegers and skuas have same patterns of displays, though only jaegers use a distraction display as well as diving at intruders near nest. During most activities, *Catharacta* typically display white patches in wings by stretching wings vertically. Jaegers and skuas have fewer displays than gulls, and displays generally aggressive, with fewer appeasing postures than gulls. Fight often. Main types of aggressive behaviours involve Upright (equivalent to Upright of gulls), Oblique, Bent, and Long Call Complex. Most conspicuous display, Long Call Complex, combines Oblique and Bent displays with Wing-raising and Long Call; involved in territorial advertisement and in agonistic and sexual encounters. Long Call Complex differs between taxa of skua. Tail-raising important display between prospective mates; performed on ground within territory and displays central rectrices (which are diagnostic of age and species in jaegers). In established pairs, Scoop-making or Scraping may begin only a couple of days after a pair reforms. Young precocial and, if undisturbed, semi-nidifugous; fed by both parents, food being given in bill or regurgitated onto ground. Dependent on food from parents for long period. When food short, usually only one chick fledged by each successful pair; second-hatched chick, younger by 1–2 days, often killed by sibling. Chicks of all species show cryptic behaviour when predators present. Adults show alarm by calling or attacking, sometimes swooping and striking intruder. Only Arctic Jaeger has full distraction-lure display, though Pomarine and Long-tailed Jaegers less often use an incomplete distraction-lure type display. No such displays by *Catharacta* species. Often bathe in fresh water, though will bathe communally in seawater where no freshwater sites. Interspecific hybridization occurs between *Catharacta* species (see above, accounts, and Great Skua: Geographical Variation).

Breed seasonally. *Stercorarius* in high latitudes of n. hemisphere in boreal summer; *Catharacta* in austral summer (except outlying population *C. skua skua* breeding North Atlantic in boreal summer). In *Catharacta*, season broadly Sept.–Feb. but onset of laying varies with latitude, Sept.–Nov. in mid-latitudes, later in Antarctic (Young 1977). S. hemisphere *Catharacta* nest in or round penguin colonies; in sheltered snow-free areas on flat or sloping ground, in valleys, on small hills, moraines, cliff edges; *Stercorarius* on tundra and, in Arctic Jaeger, in moorland. Nest, a scrape or scoop in gravel, soil or vegetation, sometimes with rim; lined or unlined; nests sometimes more substantial. Colour of eggs vary from light grey, pale green or greenish blue to olive-brown or dark stone, with irregular blotches of light or dark brown, yellow-brown or purple. Usually two eggs per clutch, occasionally only one. Eggs laid at intervals of 2–8 days in *Catharacta*. Both sexes incubate, either beginning with first egg (e.g. South Polar Skua) or when clutch complete (Great Skua). Incubation period, 24–34 days, mostly 28–30 days. Hatching asynchronous. Young, semi-precocial. Both sexes feed and brood young. Chicks may leave nest within 24 h but chicks of South Polar Skua may stay in nest for up to 27 days. Parent regurgitates food onto ground then picks up pieces, which chick takes; older chicks catch food as it is being regurgitated or take food from ground. Age of first flight, 49–65 days. Young fed by parents after fledging though start feeding themselves at *c.* 7 weeks. May remain in parents' territory for 3–4 weeks after fledging.

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Catharacta maccormicki **South Polar Skua**

COLOUR PLATE FACING PAGES 385 & 416

Stercorarius maccormicki Saunders, 1893, *Bull. Br. Orn. Club* 3: 12 — Possession Island, Victoria Land (17°14'S, 171°15'W).

Named in honour of Robert McCormick (1800–90), English naval surgeon and naturalist who collected the first specimen of this Skua on Possession Island in 1841.

OTHER ENGLISH NAMES McCormick's or Antarctic Skua.

MONOTYPIC

NOTE: For clarity, standard practice of this work is varied. Only subspecies *lonnbergi* of Great Skua C. *skua* occurs in HANZAB region; throughout this account, Subantarctic Skua is used to refer to C. *skua lonnbergi*.

FIELD IDENTIFICATION Length 53 cm; wingspan 127 cm; weight 1.2 kg. Large thickset gull-like seabird, with rather broad pointed wings; short, gently wedge-shaped tail, with central rectrices projecting slightly; and short heavy bill, strongly hooked at tip. Very similar in size and shape to Subantarctic Skua but appears smaller and slimmer, with slightly finer head, bill and tarsi when directly compared. Much bigger and bulkier than Pomarine Jaeger *Stercorarius pomarinus*, with broader wings, shorter tail and thicker bill. Polymorphic, with a varying pale morph and a dark morph and continuous gradation between. Pale morph shows diagnostic contrast between pale head and underbody and dark upperparts and underwing-coverts; or, in darker birds, diagnostic pale hindneck collar. Much rarer dark morph, darker, more uniform, though usually with slight contrast between head, neck and underbody and darker upperparts and underwing-coverts; some have distinctive faint pale collar. All plumages show large striking clear-cut white patches on bases of primaries of upperwing and underwing, which flash as wings beat. Sexes similar, though female of breeding pair often slightly paler. Slight seasonal variation. Juvenile and immature separable. Hybrids (*C. maccormicki* x *C.s. lonnbergi*) occur Antarctic Pen. and in South Atlantic but not likely in A'asian waters, see Plumages.

Description Adult PALE MORPH: Darkest birds (so-called intermediate morph; see Plumages): Head, neck and underbody, dark buffish-grey or brown, contrasting with blackish-brown upperparts, upperwing-coverts, axillaries and underwing-coverts. Many have creamy lores and lower forehead, forming pale band at base of bill and slightly darker area round eye or on ear-coverts. Most have prominent and diagnostic pale-buff or cream collar on nape and hindneck, often continuing onto sides of neck; in breeding season, collar covered with golden hackles (visible only when close), which often continue round foreneck. Many birds appear faintly hooded. Some have delicate pale-brown scaling to saddle and innerwing-coverts (lost with wear) or fine pale streaks on mantle and scapulars, visible only when close and in good light, though upperparts still appear uniformly dark; exceptionally, some have pale mottling on saddle. Remiges and tail, slightly darker than rest of upperparts, with white basal third or so of primaries forming clear-cut and conspicuous wing-flash, visible at considerable distance. Underwing: axillaries, subhumerals and most coverts, blackish brown, contrasting with paler underbody; median secondary coverts, greater coverts, secondaries and distal parts of primaries, glossy dark-grey; striking clear-cut white crescent across bases of primaries as on upperwing but slightly broader. Typical (paler) birds: As above, except head, neck and underbody, paler, pale buffish-grey, showing less contrast with pale collar and band at base of bill but greater contrast with dark upperparts and underwing-coverts; fine pale streaks of saddle may extend onto larger innerwing-coverts, and pale mottling on upper mantle often more prominent and may extend onto scapulars, producing pale-mottled saddle contrasting with darker upperwing-coverts (similar to pattern of typical Subantarctic Skua). In all birds, head, neck and underbody become paler with wear and fading, yellowish buff, cream or almost white in palest birds, contrasting greatly with dark upperparts and underwing-coverts; on very worn birds, belly and flanks can appear scruffy (almost barred) in close view. Bill, dull black, though in bright light can sometimes appear to have paler base and dark tip. Legs and feet, dull black. DARK MORPH: Saddle, wings and tail as darkest pale morph, but with fainter or no pale streaks on mantle and scapulars. Head, neck and underbody vary, from dark grey-brown to almost black, usually contrasting with darker upperparts and underwing-coverts, though some appear uniformly dark. Most show faint nuchal collar and pale band at base of bill and, in breeding season, all show golden hackles as in pale morph. Plumage remains dark despite effects of wear and fading, though some paler mottling may appear along flanks of paler birds. Bare parts as pale morph. **Juvenile** Distinctly greyer than adult, with almost no brown in plumage; generally darker than darkest pale-morph adults but paler than lightest dark morph. Differ from adult by: head and underbody, dark to medium grey, without pale collar or golden hackles; some show suggestion of pale band at base of bill. Darkest birds show only slight contrast between grey of head, neck and underbody and darker blackish upperparts and underwing-coverts; palest show obvious contrast. Further differ by slate-black upperparts with delicate pale-grey scaling to saddle and innerwing-coverts (visible when close but much reduced with wear). White patches in primaries generally slightly smaller. Bill, paler, blue-grey with black tip, giving obvious two-tone pattern; at least some have only faintly paler grey-black base to bill, with paler grey stripe along sides of lower mandible. Legs and feet bicoloured: dull black, with front of tarsus bluish pink. **Immature** Separable, at least in austral spring and summer of second calendar year, by combination of adult-like plumage and lack of pale hackles during breeding season; also by differences in timing of moult of primaries; see Plumages.

Similar species Paler adult pale morph, unmistakable: striking contrast between pale head, neck and underbody and dark upperparts and underwing-coverts, diagnostic; in flight, when wings raised, contrast between pale body and dark underwing conspicuous. In darker adult pale morph, contrast between pale head, neck and underbody and dark upperparts and underwing-coverts less pronounced, and normally have diagnostic pale collar on hindneck. Darker pale morphs, with faint or no collar, dark morphs and juveniles can be confused with **Subantarctic Skua** (see text for Great Skua for distinctions). Dark morph might also be confused with darker immatures and juveniles of **Pomarine Jaeger** which differs from dark-morph South Polar Skua in much the same way as it does from Subantarctic Skua (q.v.). Could be confused with juvenile and second-year Pacific *Larus pacificus* and Kelp *L. dominicanus* Gulls, but these easily distinguished by lack of white wing-flashes; Skuas also have faster, more direct and purposeful flight; and more menacing appearance and piratical behaviour.

Circumpolar in Antarctic waters during austral spring–autumn, with pale morph predominating in all areas except Antarctic Pen., where dark morph is common; only pale morphs and juveniles reported from A'asian waters and then only during austral spring and autumn when birds on passage between breeding grounds and wintering areas in n. Pacific and Indian Oceans. In Antarctic waters, occur on coast, in pack-ice and in adjacent open waters. Rarely seen on migration in open waters of Southern Ocean. In A'asian seas and wintering areas, normally encountered in shelf-break or pelagic waters, only rarely farther inshore. Loosely gregarious at breeding areas; at other times, mainly singly or in pairs, though occasionally gather in small groups round trawlers. Often approach ships, though usually only circle or attend briefly; occasionally alight. At least in wintering areas, regularly attend trawlers for offal or to chase seabirds. Flight, gait and behaviour similar to that of Subantarctic Skua (q.v.). At breeding grounds, when breeding near other seabirds, predator of penguin chicks and smaller seabirds, otherwise piratical or scavenging as Subantarctic Skua; also obtain much food by fishing in open Antarctic or pelagic waters; foraging behaviour varies with presence of breeding Subantarctic Skuas. Normally silent at sea; at breeding grounds, utter variety of high-pitched squeals and screams.

HABITAT Breed Antarctica, mainly on coast, especially offshore islets or peninsulas; some colonies 1–2 km from coast (Ainley *et al.* 1986) and, occasionally, much farther inland, e.g. Mühlig-Hofmannfjella, Dronning Maud Land, *c.* 200 km from open sea (Mehlum *et al.* 1988) and Theron and Prince Charles Mts, 250 km from coast (Furness 1987; Howard 1991). Prefer dry areas, free of snow and ice (Peter *et al.* 1990); but often near open water, such as fjords, inlets or bays, or in areas with scattered small freshwater or saline lakes or melt-streams (Spellerberg 1967; Johnstone *et al.* 1973; Ainley *et al.* 1990; Peter *et al.* 1990). Usually in areas with exposed rocky out-crops (Eklund 1961; Ricker 1964; Broady *et al.* 1989; Peter *et al.* 1990), or strewn with scree, morainic or volcanic deposits. Also gravelly beaches and spits, and talus shelves; valleys and basins; bluffs and headlands; cliffs, at base, on shelves and edges; crests of rock-strewn ridges; and gently sloping tablelands at top of cape, up to 300 m above beach (Reid 1962; Ricker 1964; Spellerberg 1967; Pascoe 1984; Peter *et al.* 1990). Rocks bare, or covered with moss or lichen (Pascoe 1984; Pietz 1985). Often near or in colonies of penguins or, sometimes, petrels, such as Snow Petrels *Pagodroma nivea* or Antarctic Petrels *Thalassoica antarctica* (e.g. Trillmich 1978; Broady *et al.* 1989); at coastal sites, such associations may result from lack of suitable ice-free breeding sites (Trillmich 1978) rather than for feeding. However, birds breeding at sites far inland are entirely dependent on petrels for food (T. Howard). One breeding site on S. Shetland Is was *c.* 25 m from rubbish tip (Trivelpiece & Volkman 1982). During breeding season, failed breeders may congregate at meltwater ponds near colonies (Maxson & Bernstein 1982). Vagrants occur on ice-cap hundreds of kilometres inland (Falla 1937; Ricker 1964; Spellerberg 1967; Furness 1987; Ryan & Watkins 1988).

Few records at sea away from breeding colonies (Zink 1981), mostly over ice-shelf (van Oordt & Kruijt 1954; Spellerberg 1971a; McGarry 1988) in dense pack-ice or fast-ice. Prefer pack-ice to open water: recorded at densities of 0.3–0.6 birds/km² over pack-ice, and 0.1–0.2 birds/km² in adjacent open water; 92.7% recorded in heavy pack-ice (5–8 oktas), 6.4% in light pack-ice (1–4 oktas) and 0.9% in open water (Zink 1981; Ainley *et al.* 1984). During a voyage between NZ and McMurdo Stn, only recorded in waters between −1 and 0 °C (Darby 1970). Outside Antarctic waters, generally offshore or pelagic: off s. Aust., recorded over waters 92 m and 166 m deep (Barton 1978; K. Bartram); off Washington, USA, most records over waters 100–900 m deep (Wahl 1975). Occasionally recorded inshore, but rarely in harbours (Wahl 1975; K. Bartram). In Pacific Ocean, recorded at sea surface temperatures of 10 °C off se. Aust. (Barton 1978), and from 10.6 ° to 24.9 °C between Alaska and Hawaii (Gould 1983).

Often forage in open sea, plunging from heights of 3–6 m to take food from just below, or on, surface of water, especially where sympatric with Subantarctic Skua (Young 1963b; Spellerberg 1971a; Pietz 1987). Method of feeding depends on amount of pack-ice: when little open water, may land on ice to eat seal placentae or krill; or steal food from other birds in flight (see Food), catching regurgitated food in mid-air or retrieving it from water (Ricker 1964; Cowan 1979; Maxson & Bernstein 1982; Ainley *et al.* 1985; Pietz 1987). Occasionally forage in open water along shore (Ricker 1964); once seen feeding on beach (Johnstone *et al.* 1973). Where Subantarctic Skua absent, forage much in colonies of penguins, and sometimes in colonies of petrels. Take penguin chicks and eggs while foraging on ground or in flight (Young 1963b; Müller-Schwarze & Müller-Schwarze 1973; Trillmich 1978; Pietz 1987; Young 1994). Regularly drink from meltwater ponds (Eklund 1961) and once seen feeding there (Pietz 1987).

Roost or loaf on ice-floes or on pack-ice (Darby 1970; Ainley *et al.* 1984). Near breeding colonies, non-breeders gather at edges of small lakes and ponds of meltwater from glaciers or sea-ice to roost (Young 1963b; Spellerberg 1967; Maxson & Bernstein 1982); breeders and non-breeders also bathe and preen in these ponds (P. Pietz).

DISTRIBUTION AND POPULATION Circumpolar Antarctic breeding distribution. Most recorded breeding colonies on Antarctic Pen., in Wilkes Land and edge of Ross Sea (Furness 1987), though occurrence away from these areas not well known. Colonies also on S. Shetland and S. Orkney Is and scattered elsewhere on coast of Antarctica; some well inland (e.g. Theron Mts, 79°S, 28°W, the most s. breeding site of any bird) (Furness 1987). Distribution of colonies may be linked with distribution of colonies of penguins, especially Adelie Penguins *Pygoscelis adeliae*, or petrels. During breeding season, scattered records of singles or small groups throughout Antarctica; recorded at South Pole, Vostok Base, at s. Kirwanveggen, and at the inner edge of Ross Ice Shelf (Spellerberg 1967; Furness 1987; Ryan & Watkins 1988; Murphy). Records at sea during breeding season generally not far from land (Darby 1970; Fowler 1973a; Hicks 1973; Bretagnolle & Thomas 1990; Woehler *et al.* 1990).

Long-distance trans-equatorial migrant (Furness 1987), though non-breeding distribution not well known. Some possibly remain within Southern Ocean, within limit of pack-ice (Eklund 1961; McGarry 1988) but no details. In Pacific Ocean, regular records in N, off Japan, Kuril Str. and at sea between British Columbia and California (Kuroda 1962; Slepstov 1963; Robertson 1972; Wahl 1975; Devillers 1977; Balch 1981; Furness 1987); recorded Oregon (Parmelee 1994); single record, Icy C., n. Alaska (AOU 1983). Recorded e. Tropical Pacific Ocean (Spear & Ainley 1993), Mexico (Parmelee 1994), and probably off Panama (AOU 1983); occasional records Hawaii, Kiribati, Tonga and Solomon Is (Jenkins 1980; Weimerskirch *et al.* 1985; Pratt *et al.* 1987). In Atlantic, several records Brazil (Parmelee 1994); occasional records in Caribbean (Manolis 1981); unconfirmed records in waters off nw. Europe (Bourne 1989); more regularly to nw. Atlantic (Veit 1978; Lee 1989) with two records from w. Greenland (Salomonsen 1976). Small numbers visit n. Indian Ocean, rarely N to Gulf of Aden (van den Berg *et al.* 1991) and Somalia (Urban *et al.* 1986), but more regularly to waters round Indian subcontinent (Ali & Ripley 1969; Devillers 1977; Furness 1987; Simpson 1990; De Silva 1991; van den Berg *et al.* 1991). Occasional records off Malay Pen. (van den Berg *et al.* 1991), and unconfirmed records off Sumatra (van Marle & Voous 1988). Rare off South Africa (Urban *et al.* 1986). Single vagrant recorded North Dakota, USA, probably this species (Anon. 1989).

Aust. Few records with adequate descriptions or submitted to RAC and most records unconfirmed. (Singles unless stated.) **Qld** Unknown number, Runaway Bay, 18 Apr. 1980 (Aust. Atlas); off Pt Lookout, 4 (or 14) May 1985 (Qld Bird Rep. 1985). **NSW** Specimen, *c.* 12.5 km SE of Tathra, 13 Nov. 1977 (Barton 1978); 5 km off Sydney Heads, 22 Oct. 1983 (NSW Bird Rep. 1983), single bird, not three as stated (D.W. Eades); off Ballina, 2 and 5 Dec. 1986 (NSW Bird Rep. 1986); *c.* 50 km off Wollongong, 24 June 1990 (Brandis *et al.* 1992; NSW Bird Rep. 1990; NSWORAC). Unknown number, 500 km ENE of Eden, summer 1978–79 (Barton 1982). **Vic.** E. Bass Str. (37°S, 150°E), 28 Nov. 1984 (Vic. Bird Rep. 1984); specimen, Discovery Bay, 21 Apr. 1985 (Vic. Bird Rep. 1985); off Portland (38°36'S, 141°16'E), 20 Apr. 1986 (Vic. Bird Rep. 1986); other claims include: off Portland, 26 Apr. 1992. First claimed record, a single specimen, Queenscliff (Campbell 1924) was a Subantarctic Skua (Anon. 1924). **Tas.** Two, between King I. and C. Otway, 9 Apr. 1984 (Tas. Bird Rep. 14; RAC); edge of shelf NW of King I. (39°S, 143°E), 17 Apr. 1984 (Bartram 1986; Tas. Bird Rep. 14; RAC). Also, three singles at sea (year unknown: 1981–90): SW of Tas. (45°S, 142°E), July; SSE of Tas. (46°S, 150°E), Nov.; and SW of Tas. (47°S, 141°E), Nov. (Woehler *et al.* 1990). Other claims include: off w. coast (14°S, 144°E), 14 Sept. 1985; S of Tas. (41°S, 148°E), 24 Mar. 1986; off Eaglehawk Neck, 1 Feb. 1992. **SA** Specimen (banded), Hardwicke Bay, Yorke Pen., 19 May 1958 (Eklund 1959, 1961); three, Outer Harbour, 1 Mar. 1980 (SA Bird Reps 1977–81); specimen (banded), 60 km SE of Head of Great Aust. Bight, 19 Apr. 1990 (Anon. 1991). **WA** Two, at sea off Geraldton (28°30'S, 114°30'E), 2 Nov. 1980 (Aust. Atlas); Two People's Bay, 9 May 1986 (RAC); nine, The Gap (35°S, 117°E), 12 May 1986 (RAC).

NZ All singles: specimen, Rangitikei, 2 Jan. 1940 (Falla 1940); specimen, Muriwai, 21 Apr. 1940 (Falla 1940); specimen (skull), Multi-miti Beach, N of Hokianga, date unknown (winter 1946 to early 1947) (Sibson 1950); specimen, Waikanae Beach, 29 Mar. 1953 (Fleming 1953); Himatangi, June 1965 (Spellerberg 1967); specimen, Dargaville, Oct. 1972 (Veitch 1980); Taumutu, L. Ellesmere, 9 Dec. 1972 (CSN 20). Farewell Spit, 6 Jan. 1993 (P.F. Battley; accepted RBC). First claimed record, a single specimen, Paterson Inlet, Stewart I., 1887 (listed as 1885 in some literature) misidentified Subantarctic Skua (Falla 1940).

Macquarie I. No confirmed records. Unknown number at sea N of Macquarie I. (53°S, 158°E), Nov. (year unknown: 1981–90) (Woehler *et al.* 1990).

Heard I. Single (banded), 28 Nov. 1987 (Woehler 1989).

Kermadec Is Single, W of Kermadec Ridge (32°47'S, 179°18'E), 28 Aug. 1951 (MacDonald & Lawford 1954).

Campbell I. Single, 20–29 Feb. 1968 (Kinsky 1969).

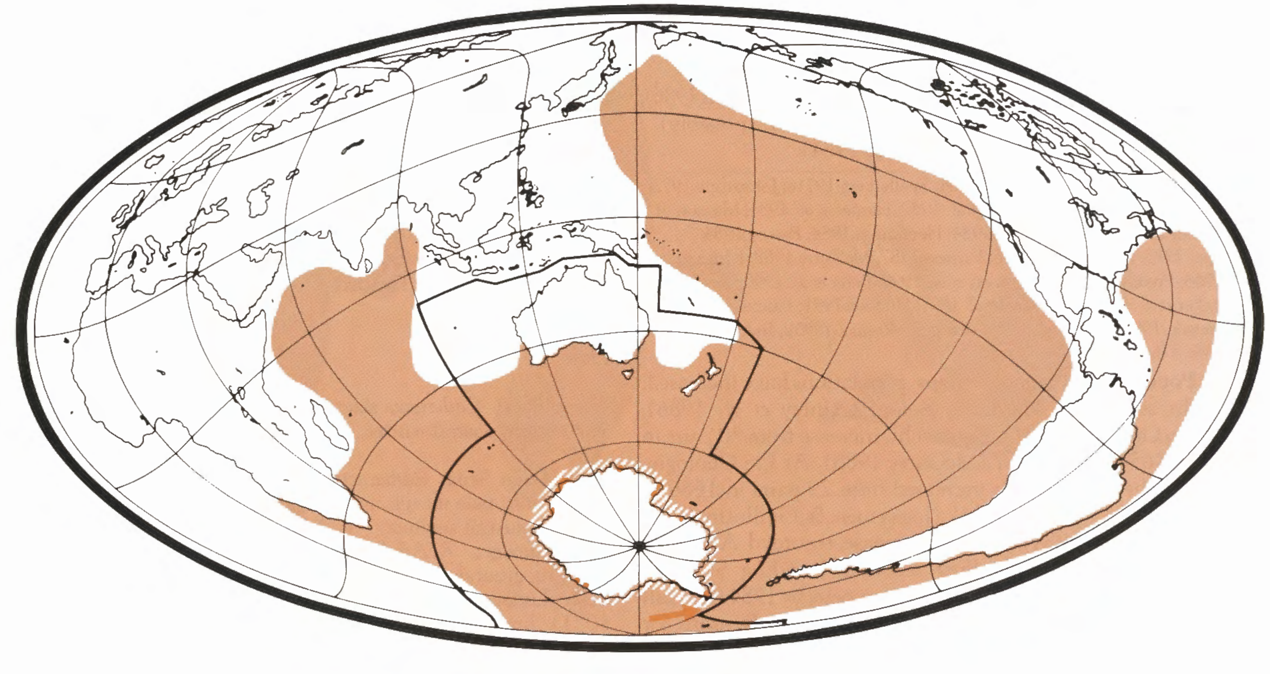
Iles Kerguelen Unverified report of single, SE of Iles Kerguelen (51°S, 72°E), June (year unknown: 1981–90) (Woehler *et al.* 1990).

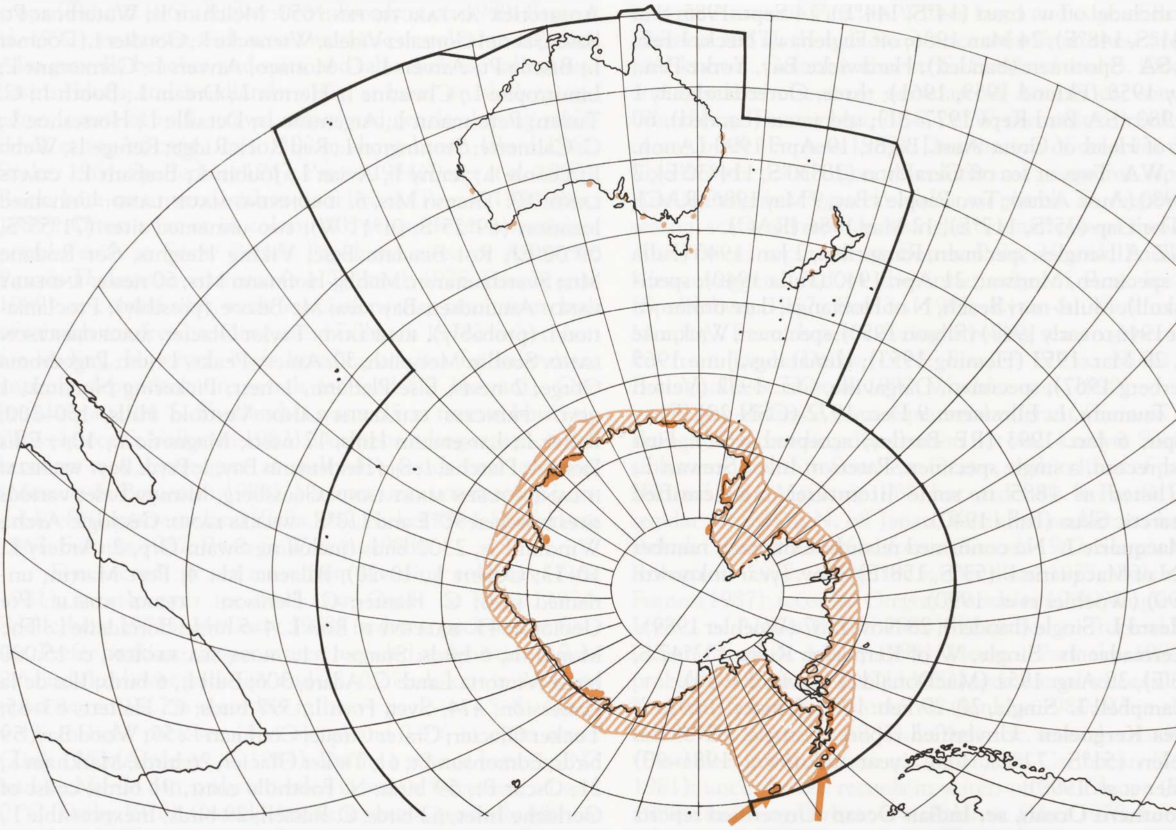
Southern Ocean, se. Indian Ocean Unverified reports of singles at sea: 50°S, 155°E, 13 Apr. 1993 (R.P. Scofield, D.W. Eades); 54°S, 141°E, 23 Oct. 1991 (D.W. Eades); 41°S, 104°E, Sept.; 46°S, 98°E, Oct.; 48°S, 126°E, Oct. (years unknown: 1981–90) (Woehler *et al.* 1990).

Breeding Summarized following (pairs unless stated); see also summary in Watson *et al.* (1971).

Antarctica ANTARCTIC PEN.: 650: Melchior Is; Waterboat Pt; Base Gabriel Gonzalez Videla; Wienecke I.; Goudier I.; Doumer I.; Biscoe Pt, Anvers I.; C. Monaco, Anvers I.; Cormorant I.; Limitrophe I.; Christine I.; Hermit I.; Dream I.; Booth I.; C. Tuxen; Petermann I.; Argentine Is; Detaille I.; Horseshoe I.; C. Calmette; Stonington I.; Red Rock Ridge; Refuge Is; Webb I.; Leonie I.; Jenny I.; Avian I.; Joubin I.; Brabant I. COATS LAND: 10: Theron Mts, 6. DRONNING MAUD LAND: Unnamed location (69°25′S, 01°11′W); two unnamed sites (71°55′S, 09°00′E); Roi Bauduin Base; Viking Heights, Sor Rodane Mts; Svarthamaren, Mühlig-Hofmann Mts, 50 nests. ENDERBY LAND: Amundsen Bay area; Mt Biscoe (possibly); Proclamation I. (probably). KEMP LAND: Taylor Glacier. MACROBERTSON LAND: Scullin Monolith, 30; Amery Peaks, 1 nest; Pagodroma Gorge, 2 nests; Else Platform, 1 nest; Pickering Nunatak, 1 nest. PRINCESS ELIZABETH LAND: Vestfold Hills, 150–200; Rauer I.; Larsemann Hills, 17 nests; Magnetic I., 10+; Ellis Fjord, 1; Platcha, 1; S of Heidemann Bay, 1; Prydz Bay. WILHELM II LAND–QUEEN MARY LAND: Gaussberg; Mirnyy Base; various sites between 90°E and 110°E. WILKES LAND: Géologie Arch.; Windmill Is, 2300 birds (including Swain Grp, 2; Ardery I., 10–13; Odbert I., 10–20); Balaena Isl., 4; Port Martin; unnamed sites; C. Hunter; C. Denison. TERRE ADÉLIE: Pte Géologie, 43. BALLENY IS: Row I., 4–5 birds; Borradaile I.; The Monolith, 6 birds; Sturge I., 1. ROSS SEA REGION: *c.* 15,000 birds: Victoria Land: C. Adare, 306; Bull I., 6 birds; Iles de la Possession, 474; Sven Foyn I., 397 birds; C. Hallett, 83–85; Tucker Glacier; Crater Cirque; Coulman I., 55; Wood Bay, 59 birds; Edmonson Pt, 61; Tinker Glacier, 26 birds; Markham I., 21; Oscar Pt, 59 birds; N. Foothills coast, 91 birds; coast of Gerlache Inlet, 62 birds; C. Russell, 29 birds; Inexpressible I., 60; n. Franklin I., 147 birds; s. Franklin I., 184; C. Day, 21 birds; Tripp I., 9 birds; C. Ross, 141 birds; Depot Pt, 72; C. Archer, 6 birds; Gregory I., 119; Lion I., 3 birds; Pt Retreat, 44 birds; Cuff C., 3 birds; Discovery Bluff, 124 birds; C. Roberts, 109 birds; Spike C., 62 birds; Dunlop I., 88; Bay of Sails, 21 birds; Gneiss Pt, 29 birds; Marble Pt, 68 birds; Taylor Valley;

Distribution of South Polar Skua. Solid red indicates breeding sites; cross-hatching is at-sea distribution while breeding; faint red is passage and non-breeding distribution.





Distribution of South Polar Skua. Solid red indicates breeding sites; cross-hatching is at-sea distribution while breeding; faint red is passage and non-breeding distribution.

New Harbour coast, 132 birds; C. Bernacchi, 31; Strand Moraines, 190; Blue Glacier, 226; C. Chocolate, 35; Dailey I., 77; C. Armitage, 1; Delbridge Is, 49; C. Evans, 237; Tent I., 42; C. Barne, 104; C. Royds, 76; Rocky Pt, 66; C. Bird, 399; Beaufort I., 209; C. Crozier, 1000; Horseshoe Bay. MARIE BYRD LAND: Rockerfeller Mts: Drummond Peak; Mt Frazier; Melbert Rocks; Mt Paterson; Mt Schlossbach; Fokker Rocks; Washington Ridge; Mt Nilsen; Breckenridge Peak. Scott Nunataks, Alexandra Mts. Peter I., possibly 1.

S. Shetland Is Penguin I.; King George I., 37 nests (Jablonski 1986); Ardley Isl., 81; Nelson I. (possibly); Deception I. (possibly).

S. Orkney Is Signy I., 10 (Hemmings 1984).

REFERENCES: Eklund 1961; Ricker 1964; Spellerberg 1971a; Johnstone 1972; Johnstone *et al.* 1973; Robertson *et al.* 1980; Harper *et al.* 1984; Maxson & Bernstein 1982; Jouventin *et al.* 1984; Hemmings 1984; Pascoe 1984; Cooper 1985; Ainley *et al.* 1986; Furness 1987; McGarry 1988; Mehlum *et al.* 1988; Broady *et al.* 1989; Bassett *et al.* 1990; Peter *et al.* 1990; van Franeker *et al.* 1990; Heatwole *et al.* 1991; Howard 1991; Parmelee 1992; Robertson 1992; Hull *et al.* 1994; Wang & Norman 1993b; Indian Ocean Seabird Atlas.

Populations In many regions, populations have increased: at eight sites in s. McMurdo Sound (Ainley *et al.* 1986); between Gneiss Pt and C. Bernacchi, increase from 20 pairs in 1965 to 165 pairs in 1987 (McGarry 1988). At Pte Géologie, Terre Adélie, populations increased from 29 pairs in 1966 to maximum of 43 pairs in 1981 (Jouventin & Guillotin 1979; Jouventin *et al.* 1984). Similar increase recorded Antarctic Pen. and S. Shetland Is. First recorded breeding Signy I., 1977–78, with numbers increasing to ten pairs by 1984 (Croxall *et al.* 1984; Hemmings 1984; W.Z. Trivelpiece). Reasons for increases not known (but see below) (Croxall *et al.* 1984). On e. shores of n. McMurdo Sound, populations have declined or been stable since early 1960s. At C. Hallett, between 1959–60 and 1971–72, fell from 180 pairs to 98 pairs; possibly through human disturbance, though numbers fell to c. 84 pairs in 1983, after the station was closed in 1971 (Johnston 1971; Trillmich 1978; Harper *et al.* 1984; Pascoe 1984; Ainley *et al.* 1986); continual decline possibly result of hazards left at site, e.g. wires (causing collisions or entanglement) and poisons (P. Pietz). At C. Royds, numbers fell from 68 pairs in 1959–60 to 57 pairs in 1964–65 (Harper *et al.* 1984), and numbers round Edward VII Pen. thought to be fewer than 50 years ago (Broady *et al.* 1989). **Survival and longevity** At Palmer Stn, of 34 adults banded 1974–75 (including 28 adults of known sex: 13 males, 15 females), 53% seen in area in 1984–85, 32% in 1987–88, and 21% in 1989–90; average years known to be alive 9.5±5.2, and not significantly different between sexes (males, 11.1±4.2, females 9.0±6.4), though of birds of known sex, 100% of males but only 60% of females were seen in the third year after banding; for adults of known sex, mean

Plate 25

Great Skua *Catharacta skua* (page 388)
1, 2 Adult, austral winter; **3, 4** Juvenile

South Polar Skua *Catharacta maccormicki* (page 412)
5, 6 Adult, pale morph, in worn plumage at breeding grounds, austral summer; **7** Adult, intermediate morph, fresh plumage; **8** Adult, dark morph, in fresh plumage at breeding grounds, austral summer; **9** Adult, dark morph, in fresh plumage at breeding grounds, austral summer;
10, 11 Juvenile

estimated annual survival rate was 95%±6% (Pietz & Parmelee 1994). At C. Crozier, Ross I., mean annual survival of birds >10 years old, 0.96±0.01; 2–10 years old, 0.89±0.02; to 2 years old, 0.36 (1–2, 0.83; 0–1, 0.44); mortality appeared to differ slightly between sexes, with change in ratio of males:females from 54:46 to 59:41 between age 6 and age 19; an average 19.3%±7.2% of males and 35.8%±6.1% of females known to be alive at age 6 had died by age 19 (Ainley *et al.* 1990).

Scavenge for food round human settlements and stations (Austin 1957; Ryan & Watkins 1988); sometimes fed by people (Trillmich 1978; Cowan 1979), but mainly scavenge at rubbish-tips and bins. Sometimes ingest plastic (Green 1986). Increases in populations round many stations attributed to availability of refuse (Jouventin & Guillotin 1979; Jouventin *et al.* 1984; Ainley *et al.* 1986; McGarry 1988). At Davis Stn, 50+ regularly attended dog-line (Johnstone *et al.* 1973) in past. Murphy noted the species was quick to take advantage of slaughter of whales.

MOVEMENTS Trans-equatorial migrant; breed Antarctica, moving N during austral winter; autumn and spring passage migrant through Aust. waters. Some, possibly population breeding Ross Sea (pale morph), move into Pacific Ocean and possibly migrate in clockwise loop round Pacific (Devillers 1977; Furness 1987). Movements in Atlantic Ocean less well known; probably population breeding Antarctic Pen. and adjacent islands (dark morph) migrates to Atlantic, though birds banded Antarctic Pen. also recovered Indian and Pacific Oceans. Movements in Indian Ocean not known (see Parmelee 1985; Furness 1987; Bourne & Curtis 1994; Banding). Suggested that some winter in Southern Ocean (e.g. Eklund 1961) but no data. Known to fly at least 50 km/h (Young 1963b). Recorded perching on icebergs at sea (Parmelee & Rimmer 1985).

Departure In Antarctica, last seen Vincennes Bay and Wilkes Stn, Windmill Is, second half Apr. (Eklund 1961). At C. Hallett, in 1959: adults and young left Mar.; last chicks present 20 Mar.; last local breeding adults left 22 Mar.–2 Apr.; last birds flew N, 6 Apr. (Young 1994). Adults and fledgelings began to leave C. Royds and farther S, late Feb. and Mar.; last departures Ross Sea region, Mar. to late Apr. (see Spellerberg 1971b), May (Ferrar 1928). Leave coast of Terre Adélie between end Mar. and 18 Apr. (le Morvan *et al.* 1967). Still at Casey, second week Apr. (Orton 1970). On islands off Antarctic Pen., present till May (Parmelee *et al.* 1977; Parmelee 1985; Furse 1987); in 1975: breeding adults left 25 Mar.–22 Apr., with most females by 4 Apr. and most males by 12 Apr.; on average, females left 4 days after their young (Parmelee 1985). On Signy I., present at breeding colonies till Mar. (Rootes 1988). From Antarctic Pen., fly N across Drake Passage and continue along Pacific and Atlantic coasts of South America to North America; do not always stay close to land (Parmelee 1985). In Pacific Ocean, records from NZ, Jan.–June (Falla *et al.* 1981; Spellerberg 1967; Oliver). Passage migrant in Aust. waters (D.W. Eades); one recorded over South Tasman Rise, Mar. (D.W. Eades); recorded off Tas. and Vic., Apr. (Tas. Bird Rep. 1985; K. Bartram); off Qld, May (Qld Bird Rep. 1985). Appear off Japan, May to late July, and off British Columbia, July–Oct. (Devillers 1977); accidental off n. Alaska (AOU 1983). Also regarded as uncommon migrant in central Pacific in waters off Hawaiian Is and Kiribati (Pratt *et al.* 1987). Unconfirmed records Tonga, Samoa, Fiji (Jenkins 1980, 1986). In Atlantic Ocean, Port William, Falkland Is, in Feb. (Bourne & Curtis 1986), and in Caribbean Sea (e.g. Manolis 1981). In Indian Ocean, seen moving W off sw. WA, May 1986 (Patterson 1991; K. Bartram); unconfirmed records off Sumatra, May and July (van Marle & Voous 1988); recorded off s. Africa, May (Urban *et al.* 1986).

Plate 26

Pomarine Jaeger *Stercorarius pomarinus* (page 438)
1, 2 Adult male breeding, light morph;
3, 4 Adult non-breeding, light morph;
5, 6 Adult breeding, dark morph

Arctic Jaeger *Stercorarius parasiticus* (page 448)
7, 8 Adult breeding, light morph;
9, 10 Adult non-breeding, light morph;
11, 12 Adult breeding, dark morph

Long-tailed Jaeger *Stercorarius longicaudus* (page 459)
13, 14 Adult breeding, light morph;
15, 16 Adult non-breeding, light morph

Non-breeding Migration sometimes rapid, e.g. of those leaving early to mid-Apr., one bird reached Oregon, USA, by 9 July and another Greenland by 31 July (Parmelee 1992). Range includes Pacific Ocean to n. Alaska and North Atlantic Ocean as far N as Greenland, May–Sept. (AOU 1983; Harrison 1987; Lee 1989); see Furness (1987). Unconfirmed records in waters NW of Europe, June–Oct. (Bourne 1989). Also recorded N of Equator in Indian Ocean, and off South Africa (Ryan *et al.* 1989). Many collected off Washington and Japan immatures, but sampling may have been biased towards young birds. Some birds may spend austral winter farther S, possibly in pack-ice of Southern Ocean, though this not confirmed (Eklund 1961; Kuroda 1960; Devillers 1977; Furness 1987; van den Berg *et al.* 1991).

Return Recorded off California, Sept. to late Oct. (Devillers 1977). Off e. Aust., Sept.–Nov. (Barton 1982; Hoskin 1991; D.W. Eades); off Geraldton, WA, Nov. 1980 (Aust. Atlas). At sea at 54°S, 141°E, 23 Oct. 1991 (D.W. Eades). Recorded at 60°S, early Oct. (Bassett *et al.* 1988). Timing of arrival at breeding sites varies, with those nesting at more s. sites appearing later (le Morvan *et al.* 1967). First adults arrived Signy I., S. Orkney Is, late Oct. 1982 (Hemmings 1984). Arrived Pt Thomas, King George I., S. Shetland Is, late Oct. to mid-Nov., 1976 and 1977 (Trivelpiece & Volkman 1982). First return to Anvers I. area, off Antarctic Pen., mid-Oct. to late Nov.; in 1975, most between 1–27 Nov.; males return before females, usually by 1 week (Parmelee *et al.* 1977; Maxson & Bernstein 1982; Parmelee 1985, 1992; Pietz 1987). First seen Vincennes Bay and Wilkes Stn, Oct. (Eklund 1961). Arrive coast of Terre Adélie, 20 Sept.–18 Oct. (le Morvan *et al.* 1967). Farther S, first arrive Ross Sea region, mid-Oct. to mid-Nov. (Spellerberg 1971b; Trillmich 1978), in Sept. (Ferrar 1928). Ross Sea, first arrivals at C. Royds and Scott Base were young non-breeding birds; after a few days, however, these birds left C. Royds to fly farther S (Spellerberg 1971b). At Larsemann Hills, Princess Elizabeth Land, e. Antarctica, arrive mid- to late Oct. (Wang 1991).

Breeding Few recorded away from Antarctica after Nov. Most return to breed at natal colonies; usually first return when several years old. Fidelity to breeding site high (see Banding). At least some young non-breeders may spend breeding season at sea round Antarctica (Ainley *et al.* 1986);

immatures found at sea all year (Watson 1975). Some occur in Aust. during spring–summer, e.g. off Ballina, NSW, in Dec. (NSW Bird Rep. 1986) and in e. Bass Str., 28 Nov. 1984 (probably not immature) (D.W. Eades). Also record from Solomon Is in Dec. (Weimerskirch *et al.* 1985).

Breeding birds will travel at least 25 km to feed, including out to sea; on summer voyages between Tas. and Terre Adélie, most recorded within 30 km of Antarctic coast (Eklund 1961; Young 1963b; Trillmich 1978; Bretagnolle & Thomas 1990). Some movement evident in Antarctica; transient in some areas, e.g. Dronning Maud Land (Ryan & Watkins 1988) and Vanda Stn (Fowler 1973b); a few movements recorded between C. Crozier and McMurdo and Scott Bases but only before and after breeding (Ainley *et al.* 1986). Some movements apparently dispersive; in Dronning Maud Land, birds usually arrive within hours of a camp being established (Ryan & Watkins 1988). Recorded up to 400 km from open sea in Antarctica (Ryan & Watkins 1988).

Banding, Colour-marking Few breed away from natal sites, with proportion of population that breed away from natal site, and direction of movement from natal sites, possibly related to availability of food; where breed away from natal site, usually move to adjacent breeding area; maximum distance recorded between natal and breeding sites 1400 km (see Wood 1971; Pietz & Parmelee 1994; Parmelee 1992); also high fidelity to breeding sites (see also Social Organization: Breeding dispersion). Displacement experiments show some birds return to nest-site over distances up to *c.* 550 km (Eklund 1961).

Of birds colour-marked at Wilkes Stn, Antarctica, two recovered in s. Indian Ocean, 130 km and 190 km away, in Feb. Various recoveries and sighting of colour-marked birds, assumed non-breeders, indicate movement around Antarctica between seasons; maximum distance *c.* 3850 km (all distances within Antarctica assume passage round coast). Between-season banding recoveries on Antarctic Pen. indicate N–S movement along Peninsula, though apparently no interchange with birds in other parts of Antarctica. Longest confirmed movement within a season, *c.* 3850 km in 66 days (Eklund 1961).

LONG-DISTANCE RECOVERIES: Recoveries of birds banded as chicks near Anvers I. (Parmelee 1992): banded Jan. 1975: one recovered Mexico, 14 Sept. 1975; another Greenland, 31 July 1975 (longest distance recovery of any bird ever recorded by banding) (also see Salomonsen 1976); banded Jan.–Feb. 1976: two recovered Brazil, 18 Dec. 1976, winter 1976; banded Feb. 1977: three recovered Brazil, 10 Jan. 1978, 30 Oct. 1980, 26 Apr. 1982; banded Feb. 1979: two recovered Brazil, 27 June 1979, summer 1979; banded Feb. 1980: recovered Oregon, USA, 9 July 1980; banded Feb. 1984: three recovered Brazil, 28 Apr. 1984., 14 Sept. 1984, 9 Oct. 1984. Other records: One, banded Antarctic Pen., 5 Mar. 1961, recovered w. India, 7 Aug. 1964 (Ali & Ripley 1969). One banded Refugio Pas De Los Andes, Argentina, winter 1957, recovered near Anvers I., Mar. 1979 (Parmelee 1992). One banded, Dumont d'Urville, Jan. 1983, sighted Heard I., 28 Nov. 1987 (Woehler 1989). One banded Wilkes Stn, 1 Mar. 1957, recovered Yorke Pen., SA, 19 May 1958, round time of storm period that apparently originated from polar or subpolar regions (Eklund 1961). One banded Terre Adélie, recovered 3924 km NNW near head of Great Aust. Bight in Apr. 1990, over 11 years after banding (ABBBS 1991). One banded Antarctic Pen. or Ross Sea area, sighted Campbell I., NZ, 20 Feb. 1968 (Kinsky 1969). Pullus banded Pte Géologie, Terre Adélie, 28 Jan. 1976, recovered at sea near Solomon Is, 10 Dec. 1976 (Weimerskirch *et al.* 1985). Adult, almost certainly South Polar Skua, banded C. Hallett, 1 Jan. 1964, recovered Sea of Japan, 28 Apr. 1966 (McLure 1974; Fullagar 1976). Skua banded Deception I., S. Shetland Is, Jan. 1960, then recaptured and released Mar. 1961 on Antarctic Pen., and recovered Caribbean Sea, May 1967, possibly South Polar rather than Subantarctic Skua (Hudson 1968; Furness 1987). One F1 hybrid *C. maccormicki* x *C.s. lonnbergi* banded near Palmer Stn, recovered as 8-year-old, Parangual, Brazil, 23 May 1977 (Gelilen & Gelho 1977; Parmelee & Rimmer 1984; D.F. Parmelee); another banded Humble I., 1976, recaptured Brazil, 1980 (Parmelee & Rimmer 1984; Parmelee 1992).

FOOD Mainly carnivorous, taking eggs, and young and adult birds; remains, milk and placentae of seals; fish; molluscs; and euphausid crustaceans. When breeding, feed at sea, at breeding colonies of other seabirds, or scavenge; during non-breeding season, appear to feed mostly at sea. Importance of foraging at sea, and thus fish in diet, varies with site and time of year, and influenced by presence of Subantarctic Skuas in areas of sympatry. **Behaviour** Diurnal; on Anvers I., minimum foraging occurs round twilight (24:00) (Pietz 1986, 1987); on Ross I., little foraging takes place 01:00–05:00 (Spellerberg 1969). Breeding populations often associated with breeding colonies of other seabirds, especially penguins, and seals, e.g. on Windmill Is, 95% or more of all nesting sites near colonies of Adelie Penguins. In many areas, penguins important source of food (Eklund 1961; Wang & Norman 1993a), see below. In some areas, other seabirds, such as Antarctic Petrels *Thalassoica antarctica*, Snow Petrels and Southern Fulmars *Fulmarus glacialoides* (e.g. Brook & Beck 1972; Ryan & Watkins 1988) important food; at Larsemann Hills, 22 of 23 boluses collected Jan. 1989 consisted entirely of remains of Snow Petrels (Norman & Ward 1990), as were hundreds of samples collected throughout 1989 (Wang & Norman 1993a). At Pagodroma Gorge, Prince Charles Mts, two pairs, observed from late Dec. 1990 to end Jan. 1991, each successfully raised two chicks, feeding entirely on Snow Petrels (T. Howard).

BREEDING SEASON: Foraging behaviour varies with presence of breeding Subantarctic Skuas. Where both species present, food resources appear to be sharply partitioned (Trivelpiece & Volkman 1982; Hemmings 1984; Pietz 1987); South Polar Skuas are excluded from penguin colonies and forage almost exclusively at sea, while Subantarctic Skuas monopolize some terrestrial sources of food, such as penguin eggs and chicks; at such sites, South Polar said to be almost totally dependent on fish *Pleuragramma antarcticum* (Neilson 1983; Hemmings 1984; Pietz 1984, 1987); Subantarctic Skuas can monopolize colonially nesting birds but not scattered, secretive nesting birds like Wilson's Storm-Petrel *Oceanites oceanicus* (P. Pietz). In areas of allopatry, South Polar Skuas forage at sea and within colonies of seabirds, such as penguins, and at seal pupping sites. TERRITORIES: When breeding, most do not defend feeding territories; some defend all-purpose territories and others defend separate breeding and feeding territories (for discussion, see Social Organization: Territories). Generally specialize in nearest source of food. Mostly scavenge within penguin colonies (Young 1963b); no differences in breeding success of those penguins within territories of Skuas and those nesting in preferred feeding areas of Skuas (which have six times greater density of Skuas) (Trillmich 1978). FORAGING TIME: At Palmer Stn, 1979–80, average foraging time (three pairs): 7.7 h/day before laying, 6.6 h/day during incubation and brooding, and 6.7 h/day after brooding; before laying, male did most foraging (91% of total for pair), while female remained on territory and was fed by male; after laying, foraging time by female approached that of male: 46% during incubation and brooding, and 48% after brooding (Pietz 1987). In 1979–80, presence of heavy ice made fishing difficult and usual foraging time per day probably less than recorded above (P. Pietz). FORAGING BOUTS: Length of bouts influenced by availability of food and weather: at Palmer Stn, 1979–80, average 198 min (SE: 17.43; four pairs, 123 foraging bouts), though varied from 145.1±12.72 (SE) when little ice-cover to 453.2±77.04 (SE) when ice-cover heavy; in 1980–81, when food apparently more plentiful, 25% of trips were <60 min (cf. 12% in 1980–81) (Pietz 1986); also at Palmer Stn, 1976–77, average length 58 min in calm weather and 112 min in period of storms; average 1977–78, 1–2 h (Neilson 1983; also see Young 1994). At C. Royds, in early summer, some feed at edge of ice, still 16–24 km from colonies (Young 1963b). On Windmill I., daily feeding range up to 13.5 km or more from nesting site (Eklund 1961). At Davis, presence of hair of Southern Elephant Seal *Mirounga leonina* showed that Skuas were moving at least 7 km to nearest wallow to feed (Green 1986). Food taken may change in regular sequence over time. At Windmill Is, Skuas arrive about mid-Oct., about 1 week after arrival of penguins (Eklund 1961) and at time when Weddell Seals *Leptonychotes weddelli* pupping; at this time Skuas feed on seal placenta and at sea, on fish and krill; 3–4 weeks later Adelie Penguins begin laying, and from second week Nov. till mid-Dec., when Penguin chicks start hatching, mostly on eggs (K. Green). Said to take euphausiids and other marine life after penguins leave (Eklund 1961; Murphy; also see Young 1994). METHODS OF FEEDING: (1) Take pelagic fish and crustaceans along ice-edge by surface-seizing and surface-plunging (Young 1963b; Pietz 1987), though possibly take krill only incidentally when feeding on schools of fish (Pietz 1987). Take krill washed up onto top of ice-floes (Pietz 1987) or frozen to underside of ice-floes that have flipped over (R.P. Scofield). Turn fish from crosswise in bill to lengthwise and swallow whole (Young 1963b; Spellerberg 1971a). (2) SCAVENGING: Near Davis Stn, East Antarctica, as little as one-third of Adelie Penguins eaten were from colonies of Penguins, with most coming from Penguins that died or were killed elsewhere, possibly from faeces of Weddell Seals, which Skuas often eat (Green 1986). Take remains of adult Adelie Penguins that have been killed in water by Leopard Seals *Hydrurga leptonyx* (Young 1963b; Müller-Schwarze & Müller-Schwarze 1973). At Vanda Stn, Ross Sea (46 km from coast), ate only food waste during summer (Fowler 1973b). At beginning and end of penguin breeding season, eat carcasses frozen from previous years (Reid 1964; but see Young 1994). (3) Steal eggs by hovering over colony and scarcely landing (Siple & Lindsey 1937). Eggs carried away whole, in bill (Sladen 1958), and opened by hammering them with bill (Sladen 1958; Eklund 1961) or even dropping them from the air (Sladen 1958). Said to take or investigate eggs in preference to chicks (Müller-Schwarze & Müller-Schwarze 1973). (4) Grab unprotected penguin chicks (<2000 g) by neck and shake or knock head on ground till dead (often taking <6 min) (Young 1963b); larger chicks often pecked to death. Smallest chicks swallowed whole (Sladen 1958). Selection of chicks at nests related to how well they are guarded; at crèches related to size of bird (Young 1994). (5) KLEPTOPARASITISM: Theft of food from Antarctic Shags *Phalacrocorax bransfieldensis* studied at Palmer Stn, Antarctica; not a major source of food (Maxson & Bernstein 1982; Pietz 1987). Attack by biting back, rear or belly of Shag; sometimes simply flew close behind Shag or swooped at it; if Shag regurgitates, food caught in mid-air or retrieved from water. Single Shags or small flocks avoided Skuas by swerving away, which sometimes ended chase; larger flocks (10–20 birds) split into smaller groups when attack was imminent, flying in different directions, the Skua switching to one of the smaller groups or individual Shag; flocks of 30 or more birds did not split up. Landing on water best method of escaping harassment, though Shags did not do so till struck or about to be struck; Skuas sometimes tried to stop Shag from landing by flying beneath it and biting at its belly; Skuas usually gave up if Shag landed on water, though some persisted in attack. Of 280 chases, only 13 (4.6%) were successful; success of single Skuas chasing single Shags, 4.6% (2 regurgitations/43 chases); several Skuas chasing single Shag, none successful (0/7); single Skua chasing flock of Shags, 5.5% (2/36); success of groups of Skuas (3.9 [3.1; 2–10]) chasing flocks of Shags was 21% (8/38), though success of individual Skuas not significantly different (5.3%). Success appeared to increase when Skuas struck Shags. When dense pack-ice present, chases most frequent, because Skuas cannot feed at sea, and success highest, because Shags cannot escape attack by landing on water; all successful attacks occurred when pack-ice dense. At Palmer Stn, also observed to chase Antarctic Terns *Sterna vittata* and Kelp Gulls (combined, <10 chases in two seasons; outcome not known); not observed to chase Southern Giant-Petrels *Macronectes giganteus*, which also bred there. Not observed to steal food in Ross Sea (Young 1963b; Spellerberg 1971a) or Signy I. (even though a large colony of shags [770 pairs] within 1 km of a study site) (Hemmings 1984). (6) CANNIBALISM: Occurs often; non-breeding Skuas may drive incubating Skuas off nest and take eggs or chicks (Spellerberg 1971a); more prevalent when food scarce (Pietz 1987) or when unfavourable conditions stop Skuas from feeding at sea (Parmelee *et al.* 1978; Neilson 1983). Eat own young (if dead) and eggs; not known if kill and eat own chicks (Eklund 1961). CO-OPERATIVE FEEDING: Often co-operate to steal eggs (Eklund 1961). May work in pairs when feeding in penguin colonies (see Young 1963b); members of pair often co-operate when tearing up food (Young 1994). COURTSHIP FEEDING: See Social Organization. HYBRID PAIRS: Members of hybrid pairs appear to follow pattern of behaviour and activity of its species, e.g. in pair consisting of a male South Polar and female Subantarctic Skua, male brought only fish to chick and female only penguin (see Pietz 1987 for full details). NON-BREEDING SEASON: Poorly known. Probably eat mainly fish (e.g. Eklund 1961; Murphy). Route of migration during winter suggests that Skuas may follow movements of Pacific Saury and, by implication, eat them (Furness 1987) but see Parmelee (1993: Fig. 11). In Aust., observed to steal food from Wedge-tailed *P. pacificus* and Fleshy-footed *P. carneipes* Shearwaters and immature Yellow-nosed Albatross *Diomedea chlorohynchos* (Barton 1982); and, extralimitally, California Gulls *L. californicus* and Sooty Shearwaters *P. griseus* (Wahl 1977). For details of kleptoparasitism in e. Tropical Pacific, see Spear & Ainley (1993).

Food remains used to estimate size of items taken: pieces of skull of Snow Petrel and South Polar Skua indicated skull sizes of 67.7 mm (2.93; 62.4–73.1; 26) and 111.4 mm (2.51; 109.3–114; 23) respectively (Wang & Norman 1993a). Pieces of eggs of Antarctic Petrels indicated length of eggs averaged 71 x 48 mm (n=110 eggs), and those of Southern Fulmar, averaged 74 x 45 mm (n=40) (Norman & Ward 1990). Drink fresh water and eat snow and ice (Eklund 1961). Shake head to dispel salt water from salt-excretion gland in nasal passage (Spellerberg 1971a). Believed to use smell to detect food over long distances.

Adult During breeding season. EAST ANTARCTICA: At **Larsemann Hills, Princess Elizabeth Land** (1666 pellets containing 2165 individual food items and 1711 food items from food remains; Wang & Norman 1993a): Fish and invertebrates (incl. *Pagothenia*, *Sterechinus*, echinoderms, polychaetes, and amphipods) 0.7% occur. in pellets, 2.6% occur. in total items. Birds: Adelie Penguins 1.7, 1.0; Snow Petrel 66.2, 79.9; Wilson's Storm-Petrel 5.6, 1.2; South Polar Skua 1.2, 2.6; Weddell Seal (incl. placenta and remains [bones 74.5%, skin 14.6%]) 2.5, 3.6. Gravel 20.6, –; unident. 2.2, <0.1; refuse 6.8, 11.6. On **Hop I., Rauer Grp** (571 pellets containing 739 food items; Norman & Ward 1990): Fish: Nototheniidae: *Pleuragramma antarcticum* 0.7% occur. Birds: Adelie Penguin: ads 39.9, young 12.3, eggs 1.4 (frequency of chicks negatively correlated with distance from their colony); Antarctic Petrel ads 3.3, young 1.0; Southern Fulmar ads 21.5, young 3.0; Snow Petrel 15.6; Wilson's Storm-Petrel 4.0. Gravel 19.8; unident. 6.8. On **Hop I.** (466 pellets from six sites; Green 1986): Molluscs: cephalopods 0.9% freq. Fish 2.1. Birds: eggs 22.3; Adelie Penguin 27.7; Procellariidae: unident. 16.3; Southern Fulmar 25.3; Antarctic Petrel 3.8; Cape Petrel 3.7; Snow Petrel 12.4; Wilson's Storm-Petrel 7.3; South Polar Skua 1.1. Mammals: Weddell Seal 1.7; Southern Elephant Seal 0.4. Leopard Seal faeces. Stones 33.9; plastic 0.4. At **Windmill Is, Wilkes Land** (obs.; Eklund 1961): marine life; Crustaceans: Euphausiidae: *Euphausia*; Fish; Birds: Adelie Penguin eggs; South Polar Skua chick. Mammals: Weddell Seal placentae.

ANTARCTIC PEN.: At **Palmer Stn** (270 food items, 1974–78; Neilson **In** Pietz 1984; 90 food items [84 food items were fed to young; see below], 1979–81; Pietz 1987): Crustaceans: Euphausiidae: *Euphausia superba* 6% freq. 1974–78, 12% freq. 1979–81 [estimated from diagram]. Fish (mostly *Pleuragramma antarcticum*, c. 10 cm) 71, 74. Birds: penguin 5, 4; skua 14, 3. Other (incl. crustaceans: *Branchinecta*; Wilson's Storm-Petrel; Kelp Gull; Antarctic Tern eggs and chicks) 4, 6. At **Signy I.** (obs. and regurgitations; Hemmings 1984): Crustaceans: Euphausiidae: *E. superba* (possibly from fish stomachs). Fish: Nototheniidae: *P. antarcticum* (c. 150 mm). Birds: possibly Antarctic Prion *Pachyptila desolata* and Wilson's Storm-Petrel. On **Ardley I.** and **Fildes Pen. S. Shetland Is** (food remains from 154 nests; Peter *et al.* 1990): Fish 79% freq. Birds: penguins 12; other birds 7. Garbage 2.

ROSS SEA AREA: At **C. Royds, Ross I.** (obs.; Young 1963b): Fish: Liparidae (11 cm); Nototheniidae: *Pleuragramma antarcticum* (<10–21 cm; 75 g); Birds: Adelie Penguin eggs and young; Mammals: seal remains and placentae. In **Ross Sea** (four stomachs; Ainley *et al.* 1984): Molluscs: cephalopods: Gonatidae: *Gonatus antarcticus*, two stomachs; Crustaceans: Euphausiidae: *Euphausia chrystallorophias*; Fish: *Manaenolepis*; Nototheniidae: *P. antarcticum*. On **Balleny Is** (five stomachs; Robertson *et al.* 1980): Fish; Birds: penguin; Snow Petrel chicks; Wilson's Storm-Petrel *Oceanites oceanicus*.

Other records Plants: Algae (Fleming 1953). Animals: Molluscs: cephalopods (Siple & Lindsey 1937); Gonatidae: *Gonatus moroteuthis*; Psychroteuthidae: *Psychroteuthis* (Norman & Ward 1990). Crustaceans (Gain 1914): Euphausiidae (Murphy); Anostracans: *Branchinecta* (Pietz 1987). Fish (Gain 1914; Maxson & Bernstein 1982; Parmelee & Rimmer 1985): Nototheniidae: *Pleuragramma antarcticum* (Siple & Lindsey 1937). Birds: eggs and chicks (le Morvan *et al.* 1967; Orton 1970); penguin eggs and chicks (Gain 1914); Adelie Penguin eggs and chicks (Siple & Lindsey 1937; Sladen *et al.* 1958; Taylor 1962; Reid 1964; le Morvan *et al.* 1967; Pryor 1968; Spellerberg 1971a; Müller-Schwarze & Müller-Schwarze 1973; Trillmich 1978; Cowan 1979); petrels (Cowan 1979); Snow Petrels ads and fledgelings (Siple & Lindsey 1937; le Morvan *et al.* 1967; Brook & Beck 1972; Ryan & Watkins 1988; Broady *et al.* 1989; Heatwole *et al.* 1991); Antarctic Petrel (Brook & Beck 1972; Broady *et al.* 1989); storm-petrel *Oceanites*; Common Diving-Petrel *Pelecanoides urinatrix*; Mottled Petrel *Pterodroma inexpectata*; White-headed Petrel *P. lessoni*; Broad-billed Prion *Pachyptila vittata* (Stead 1932); Southern Fulmar chicks and eggs (Pryor 1968); Antarctic Tern eggs and chicks (Pietz 1987). Mammals: Weddell Seal placentae (Siple & Lindsey 1937; Reid 1964; Müller-Schwarze & Müller-Schwarze 1973); Crabeater Seal *Lobodon carcinophagus* placentae (Siple & Lindsey 1937); seal faeces (Müller-Schwarze & Müller-Schwarze 1973). Sealing and whaling offal (Gain 1914; Siple & Lindsey 1937); cast ewes and new-born lambs (Stead 1932). Kitchen waste (Reid 1964; Fowler 1973b; Müller-Schwarze & Müller-Schwarze 1973). Pebbles (Siple & Lindsey 1937).

Young First fed 14 h after hatching (Reid 1966). Both parents feed young till after fledging. For first few days, chicks offered food in bill. Later food regurgitated onto ground in front of chick and if not eaten, reingested by adult (Eklund 1961; Young 1963b); *Pleuragramma* 150 mm in length broken into 30–50 mm pieces (Hemmings 1984). At **Palmer Stn** (26 regurgitates from chicks; Eppley *et al.* 1989): Crustaceans: krill 62% freq.; fish 58. In same area (84 food items; P. Pietz): Euphausiidae: *Euphausia superba* 13% freq. Fish: 75% freq. Other records: Crustaceans (Gain 1914): Euphausiidae (Eklund 1961); Fish (Gain 1914; Eklund 1961; Young 1963b); penguin chicks (Eklund 1961; Young 1963b); South Polar Skua chick (Eklund 1963); carrot and apple (Wang & Norman 1993a).

Intake In 6 h, one captured male regurgitated four large (18–21 cm) *Pleuragramma antarcticum* and six smaller fish (<11 cm). Pairs take 2–6 eggs/day when maximum number of eggs available (Young 1963b). Estimated to need 274.4 kcal/day and to take maximum 60 g in stomach contents (Ainley *et al.* 1984). Penguin eggs and chicks provide as much, if not more, energy as alternative foods (krill & fish) (Norman *et al.* 1994); also see Young (1994).

SOCIAL ORGANIZATION Well known during breeding season, with major studies: on Windmill Is (Eklund 1961); on Ross I.: at C. Royds (Young 1963a; Spellerberg 1971a), C. Bird (particularly on territories) (Young 1972, 1994), C. Crozier, (Wood 1971; Ainley *et al.* 1990) and C. Hallett (particularly on territories) (Trillmich 1978); and near Palmer Stn, Anvers I. (including comparisons with Subantarctic Skua) (Pietz 1984, 1985, 1986, 1987; Pietz & Parmelee 1994). Account includes material from original contribution by K. Green. Outside breeding season, little known; do not maintain pair-bonds (Neilson 1983; Furness 1987; Wood 1971). During breeding season, if not in breeding pairs, generally solitary except in **Clubs**: temporary or permanent gatherings of non-breeding birds that form on edges of breeding colonies or near small ponds with open water (where birds bathe); at C. Royds, Clubs separated from breeding colonies by high lava peaks (Spellerberg 1971a; K. Green). At C. Bird, Club contained up to 120 birds and occurred in small area among colonies of penguins (Young 1972). At C. Hallett, Club of 79–83 birds usually formed near a pond 300 m from colony of Adelie Penguins (Pascoe 1984). At Larsemann Hills, Clubs contained 4–28 birds, sometimes including failed breeders; numbers increased Nov. and declined after Feb. (Wang & Norman 1993a); on S. Shetland I., maximum number of non-breeding Skuas (South Polar and Subantarctic) in Club, 136 (Peter *et al.* 1990). For details of birds in Clubs at C. Bird, see Court (1992).

During breeding season, seen feeding singly, though birds fishing or feeding at a carcass can attract others, e.g. 60–70 gathered at carcass of Weddell Seal within 20 min (Young 1963b). Steal food from Antarctic Shags, attacking alone or in small groups (of 3.9 birds [3.1; 2–10]) (Maxson & Bernstein 1982). Non-breeding birds sometimes gather round nests of Skuas and try to steal eggs (see Social Behaviour), though this probably not co-operative, but merely attraction to other foraging birds (Spellerberg 1971a). Birds may co-operate when feeding on penguin carcasses: one holds carcass while other tears pieces off; seen in both breeding pairs and non-breeding birds (Young 1963b). Eklund (1961) found paired Skua allows only mate to feed nearby (see Territories). Much co-operation between members of pair when hunting (Young 1994). At end of breeding season, unlike juveniles, adults leave singly (Parmelee 1992).

Bonds Long-term monogamy; pair reunites on same breeding territory each season unless one bird fails to return (e.g. Wood 1971; Spellerberg 1971a,c; Ainley *et al.* 1990; Pietz & Parmelee 1994); do not maintain pair-bonds in non-breeding season (Wood 1971; Neilson 1983). Co-operative breeding not recorded. Some pairs together for at least 16 years (Ainley *et al.* 1990). At C. Crozier, of pairs recorded in two consecutive seasons, only 1.5% (n=267 pairs) did not reunite though partner present (Wood 1971). In much longer study at same site, of 242 birds, 44% had only one mate, 43% changed mates once, 10% changed mates twice, and 3% changed mates three times; switching most common among breeding birds aged 14–15 years, and those that had bred together <4 years; age at first switching for both sexes, 11.8 years (n=20) (Ainley *et al.* 1990). On Anvers I., over 16 years, 34 birds had an average 1.7 mates each (n=34 adults) and spent average of 6.8 years in longest pair-bond; nearly 53% had only one mate, 32% had two, 6% had three and 9% had four; most changes occurred after disappearance of original partner; males showed slightly higher fidelity to mates than females (Pietz & Parmelee 1994). At Pte Géologie, reproductive success correlated with number of years pair bred together (Jouventin & Guillotin 1979). Missing partners may be replaced quickly (Spellerberg 1971a,c), e.g. one female disappeared after laying and was immediately replaced by new female who helped male raise chicks of previous female to fledging; remaining mate sometimes does not find new mate in first year of desertion (Pietz & Parmelee 1994). At C. Crozier, of 27 pairs in which mate failed to return, 26 paired again in first year, producing eggs either in first or second year; 18 (67%) paired with unbanded mates, suggesting latter were breeding for first time; four survivors combined to form two pairs, another four paired with Skuas that had separated from previous mates, and one paired with Skua that had previously bred outside study area. Of original 27, 85% remained on their territories, while three birds moved to adjoining territories and only one moved farther (Wood 1971). In longer-term study at same colony, when changing mates, only 63% of these new pairs bred in year of switching (cf. 100% of established pairs). Of 53 birds that changed mates, 27% stayed in same quadrat, 30% moved to an adjacent quadrat, and 43% moved farther; no differences between sexes. Rarely, intact pairs switch breeding areas (Ainley *et al.* 1990). On Anvers I., changes of territories always involved changes of mate (see Breeding dispersion); newly formed pairs usually produced eggs in first season together; change of mate and reproductive failure in previous years appear not to be related (Pietz & Parmelee 1994). Pietz & Parmelee (1994) found most females retained territories when previous mates failed to return; cf. suggestion by Spellerberg (1971a,c) and Jouventin & Guillotin (1979) that if female disappears, male re-mates in old territory, but if male disappears, female usually abandons territory and seeks another mate. At start of season, member of established pair may accept temporary mate until previous mate arrives; temporary pairs mostly occur away from breeding territories, particularly at communal bathing and feeding sites. In Clubs some temporary pairs form, lasting from a few hours to a day (Spellerberg 1971a). Will pair with Subantarctic Skuas, see that account for details. Pietz & Parmelee (1994) once observed copulation outside pair and food-begging outside pair. TIMING OF PAIR-FORMATION: Renew bonds at beginning of each breeding season (Pietz & Parmelee 1994). Do not arrive at breeding grounds in pairs (e.g. Neilson 1983; Spellerberg 1971a). Usually male awaits arrival of mate at territory or pair re-forms away from colony; co-ordinated activities in old territory begin soon afterwards (Spellerberg 1971a). At C. Crozier, at least some Skuas paired *c.* 2 weeks after first arrival (Wood 1971); at C. Denison, arrived end Oct., but little indication of nesting till toward end Nov. when seen pairing and occupying definite sites (Falla 1937); on S. Shetland Is, started arriving late Oct. and continued arriving and establishing breeding territories till mid-Nov. (Trivelpiece & Volkman 1982; see Movements). See Eklund (1961) for further observations of pairing.

At C. Crozier, long-term demographic study by Ainley *et al.* (1990) found: a few 1-year-olds returned to natal colony; most returned when 2–5 years old (no difference between sexes); median age of first breeding for females, 6–7 years, for males, 8–9 years; rarely, 4 year-old females recorded laying; most 9-year-olds or older attempted to breed. Life expectancy appears shorter for those that began breeding at youngest ages. Tended to pair with mates of similar age; average differences in age 2.0±0.5 years (n = 20 long-term monogamous pairs); of 18 pairs, 50% had older males, 28% same age, and 22% had older females (see Ainley *et al.* 1990 for further details). Other notes on age of first breeding: in second year, birds possibly returned as non-breeders (Eklund 1961); some first return to natal area when 3–4 years old; possibly pair this first summer but do not lay till fifth or sixth year, or, in Ross Sea area, typically when 7–9 years old (Sladen *et al.* 1966; Spellerberg 1971a,c; Pietz & Parmelee 1994); one 3-year-old recorded with chick (Pietz & Parmelee 1994); 0.8% of 4-year-olds bred, increasing to 58% of 8-year-olds (Wood 1971); at Pte Géologie, average age of first breeding 5.5 years (3–8; 33) (Jouventin & Guillotin 1979). **Parental care** Both sexes incubate; both defend eggs and young though, early in breeding season, defence of territory appears to be mainly by male (though female may be nearby). In some areas, when breeding territory does not include feeding area, male forages for female and chicks from start of breeding cycle till young 3–4 days old; after this, both sexes feed chicks fairly equally (Eklund 1961; Young 1963a,b; Spellerberg 1971a). At Palmer Stn, this is not so (P. Pietz); during period before laying, male does most foraging; after laying, female forages for nearly same time as male; both sexes feed young about equally (Pietz 1987). Parents said to feed chicks: for some time after chicks fledge (Young 1963a); well beyond fledging, as late as Mar. and sometimes Apr. (Neilson 1983); till chicks leave colony (Spellerberg 1971a); Reid (1966) noted that fully grown young generally stayed within area, but not necessarily within own territories; seldom seen flying; occasionally fed themselves on dead penguin chicks, but mainly seemed dependent on parents for food till departure for non-breeding areas. Juveniles may group together on headlands late in season (E.C. Young).

Breeding dispersion Nest singly or in loose colonies. On Ross I., most territories established in sheltered, snow-free areas and form loose colonies; few pairs nest singly (Young 1972). When censusing nests, care must be taken as a territory may contain several scoops but only one nest (see Sexual behaviour), though several of these may be used if re-layings occur (E.C. Young). At C. Royds, colonies of 7–20 nests with 20–50 m between neighbouring nests (Spellerberg 1971a); in colonies of 3–21, most are 27–46 m from nearest neighbour and none closer than *c.* 18 m (Young 1963a). At C. Hallett, where density of nests probably typical for fairly uniform area close to penguin colony, of 155 pairs, 52% of neighbouring nests *c.* <11 m apart and nine nests more than *c.* 24 m apart (Young 1963a). At C. Crozier, mean distance between nests and nearest neighbour, 19 m (n=109 nests) (Wood 1971). At Pte Géologie, Terre Adélie, 40% of nests <20 m apart and 89% <50 m (le Morvan *et al.* 1967). On Signy I., in study of newly established population, one pair bred singly and eight pairs bred near each other with 28 m (12–42) between nests (Hemmings 1984). At Anvers I., nests often only 15–20 m apart (Parmelee *et al.* 1977); near Palmer Stn, Anvers I., where territories established, closest nests 12 m apart; on nearby island where seven pairs were defending new nesting sites, two nests were 2.5 m apart and a third was within 7 m (Pietz 1987). Philopatric; usually breed at natal colony or nearby (no difference between sexes; for age when first return to natal areas, see above); high fidelity to territory site from year to year (e.g. Eklund 1961; Spellerberg 1971c; Wood 1971; Parmelee & Rimmer 1984; Ainley *et al.* 1986, 1990; Pietz & Parmelee 1994; Weimerskirch *et al.* 1985). For details of short movements of nesting sites, see Breeding. At C. Crozier, most birds do not change breeding areas; of 237 birds, 12.6% did so at least once (two-thirds were females and most were young, averaging 13.6±1.2 years); of birds that moved, 75.9% stayed in new area, having spent 2–6 years breeding in old area; some moved twice but always returned to first breeding area after 1–5 years breeding in second area (Ainley *et al.* 1990). On Anvers I., over 16 years, each bird held average of 1.1 nesting territories (n=34 birds); only four (all female) of 34 birds changed territories, moving 1.5 km (0.5–2.5); males showed higher fidelity to territory than females, but most females (four of five) retained their territories when previous mates failed to return (Pietz & Parmelee 1994); higher fidelity to territories by males also suggested by Jouventin & Guillotin (1979) at Pte Géologie. For changes in site associated with changes of partner, see above. Occasionally breed away from natal colony (Sladen *et al.* 1958; Pryor 1968; le Resche *et al.* 1970). In pre-breeding season, may visit Clubs away from natal colony, e.g. many Skuas, especially young ones, from C. Bird frequent Clubs at C. Crozier. Emigration rate in C. Crozier population only *c.* 0.3% though rate can vary with site (Ainley *et al.* 1986, 1990). **Territories** TYPES OF TERRITORIES AND FEEDING AREAS: Most territories are stable breeding areas defended each year by established pairs. Usually defend only nesting territories, with defence restricted to area round nest. Some pairs also defend feeding territories near breeding colonies of other species, such as Adelie Penguins (Eklund 1961; Young 1963b; Müller-Schwarze & Müller-Schwarze 1973; Müller-Schwarze *et al.* 1975; Trillmich 1978) and petrels (van Franeker *et al.* 1990), including Snow Petrels and Southern Fulmars (Wang & Norman 1993b; Norman & Ward 1990); territories defended against Skuas flying over or landing (Trillmich 1978). On Ross I., only a small proportion of breeding population holds feeding territories (Young 1963a; Müller-Schwarze *et al.* 1975; Trillmich 1978). Do not hold feeding territories on Anvers I. (Pietz 1985) or in areas where Subantarctic Skuas also breed, e.g. S. Shetland Is (Trivelpiece & Volkman 1982; Pietz 1987). At C. Hallett, Trillmich (1978) found three types of territorial situations among birds breeding in or near colonies of Adelie Penguin; pairs held either: single all-purpose territory within Penguin colony, where they nested and fed; nesting territory on edge of colony with adjacent feeding territory within colony; nesting territory away from colony and fed in undefended 'preferred' areas of colony or out to sea. Overall pattern of territories within a breeding area stable (Young 1972, 1990; van Franeker *et al.* 1990). Density of pairs with feeding territories, *c.* 1.8 pairs/ha of penguin colony; that of pairs with preferred feeding areas, 12 pairs/ha (Trillmich 1978). Smaller penguin colonies may be completely divided among Skua feeding territories; in larger colonies, functional feeding territories only at edges (Müller-Schwarze *et al.* 1975). Breeding success of pairs with feeding territories the same (Young 1990) or higher than those without (e.g. Müller-Schwarze *et al.* 1975; Trillmich 1978). At C. Bird, many birds in Club had small temporary territories in Club area; in many, nesting displays and courtship feeding common; in two cases, eggs laid (Young 1972; Court 1992). TIMING OF TERRITORIAL BEHAVIOUR: Defence of territory begins a few days after arrival and re-establishment of pair-bond (Spellerberg 1971a). At C. Hallett, pairs associated with penguin colony start defending territories end Oct. to early Nov., with males usually arriving on established territories before females; at first, birds forage throughout colony but from about mid-Nov. those with feeding territories forage only within territories (Trillmich 1978); at C. Crozier, active defence of territories most obvious at start of hatching of Adelie Penguins (Müller-Schwarze *et al.* 1975). Birds present on territories for little more than 4 months in each year (Young 1972); at C. Hallett, territories begin breaking down early Feb. (Pascoe 1984); at C. Royds, territories occupied till early Mar. (Young 1963b). On Anvers I., males defend territories till shortly before departure (leave *c.* 1 week after females, which have left a few days after their young) (Parmelee 1992). ESTABLISHMENT OF TERRITORY: When a pair establishes itself in deserted territory, both birds explore territory, mainly on foot, till stopped by defending neighbours; when attacked, new pair retreat but do not leave; by third day pair may behave as established pair, and may even join in group defence of breeding area (Young 1978). Spellerberg (1971a) noted sequence for single bird establishing new territory: bird indicates claim by giving Aggressive Uprights (see Social Behaviour) on promontory or high ground at boundaries of established territories; neighbours try to drive it away, but new bird scarcely retaliates and roosts short distance away until no longer molested; in 6–10 days, if not forced from claim then slowly adds it to territory; at this stage, single males often start to display. BASIC PHYSICAL CHARACTERISTICS: Boundaries of territories clearly defined (Spellerberg 1971a; Young 1972). Territory size and distances between nests not necessarily correlated (Pietz 1987). At C. Hallett, all-purpose territories 1.2 ha (0.5–1.8) in size, holding 730–3190 pairs of Adelie Penguins (significant correlation between size and number of pairs of Penguins); though birds usually hunt on ground, defend larger areas when in air; overlap between adjacent territories 22±14% of total territory area; one pair appears to dominate in region of overlap, but any of the relevant territory owners will defend against intruding Skuas, other than neighbours. Nesting territories away from colony much smaller (Trillmich 1978). At C. Crozier, feeding territories 726–2871 m² and extended from edge to *c.* 32–91 m into colony of Adelie Penguins; in late Dec. held 179–711 Penguin nests (Müller-Schwarze *et al.* 1975). Usually, pairs with feeding territories have points close to nest from where they can observe feeding territory (van Franeker *et al.* 1990; F.I. Norman). At C. Royds, territories vary in size; in any colony, smallest territories grouped in lower and more sheltered areas of basin, and largest near perimeter; sometimes stretches of frozen sea included within territories on coast and pairs attack birds over the ice as far as 275 m from shore; after thaw, no attacks made over open water; some pairs defend territories which contain 90–540 Penguin pairs (Young 1963b). When chicks begin to fly, territory boundaries may change (Spellerberg 1971a; Young 1963a). Size and siting of territory influence age of first flight, see Breeding. Other observations on territory size include: at C. Royds, generally 1600 m² (Spellerberg 1971a); at C. Hallett, 9–2790 m² (Reid 1966); at C. Chocolate, average 500–700 m²; at s. tip Blue Glacier, some >10,000 m² (McGarry 1988). At C. Crozier, of 312 pairs that bred together in two consecutive seasons, only four pairs (1.3%) moved enough to change previous relationship with adjacent pairs (Wood 1971). Stability of boundaries possibly occurs because vacated territories re-settled before neighbours encroach (Young 1972). OTHER ACTIVITIES IN TERRITORIES: At C. Hallett, pairs holding both nesting and feeding territories have some characteristic activities, including: Early in breeding season, when pair rests, usually does so within territory. After laying, leave territory only to bathe (once or twice a day for 5–10 min), during brief chases, or for rare foraging flights to human settlement. During incubation period, non-sitting bird spends about half its time on nesting territory, usually resting or preening, but takes off, usually to chase intruders, *c.* 4 times/h; spends rest of time on feeding territory; about half food taken in feeding territory carried close to nest and eaten there; no differences between sexes (Trillmich 1978). In some areas, if no feeding territory held, only male leaves nest territory to forage, starting from just before and during incubation; female stays within territory, incubating and roosting (Young 1963a,b; Spellerberg 1971a). After hatching, chicks always fed in territory. **Home-range** During breeding season in some parts of Antarctica, pairs with feeding territories sometimes feed almost entirely within territory (e.g. Trillmich 1978) but mostly also forage at sea, though apparently not greatly beyond pack-ice (e.g. Young 1963b, 1994; Johnstone & Kerry 1976; Pietz 1985). Can range up to 16–24 km from nesting sites (see Movements and Food). On Anvers I. (no feeding territories), breeding birds feed mainly at sea (Pietz 1985, 1986; Eppley *et al.* 1989). On Ross I., all pairs feed at sea for at least part of breeding season, e.g. late in chick-rearing or when penguins not abundant (Young 1963b, 1972). At Larsemann Hills, do not fish locally, because little open water available, and do not bring large quantities of marine food to nests (Wang & Norman 1993b). At C. Crozier, Müller-Schwarze & Müller-Schwarze (1973) found nest territories of many pairs *c.* 1–1.5 km from feeding areas within Adelie Penguin colonies. At C. Hallett if breeding birds without feeding territories feed within penguin colonies, both members of pair feed in same part of colony (Trillmich 1978).

Roosting On Anvers I. during summer, activity of birds influenced by light levels; birds show maximum resting and minimum foraging during twilight (Pietz 1986, 1987). On Ross I. at s. end of breeding range, birds show 24-h cycle of activity even during continuous daylight; between 01:00 and 05:00 all breeding pairs roost, incubate or brood, and little or no foraging takes place (Spellerberg 1969). When on territory, breeding birds spend much time resting or preening (Spellerberg 1971a). At C. Hallett in period before laying, established pairs spend 90% or more of resting time within future nesting territories; after laying, when off-duty bird is in nesting territory, it spends 94% of this time roosting (on small mound) and preening with resting bouts averaging 12 min (n=151); when on feeding territory, 72% of time spent resting and preening, and resting periods shorter, average *c.* 9 min (n=133) (Trillmich 1978). During unfavourably cold weather, most birds settle on sheltered part of territories, often at nests; snow builds up round them quickly until they finally sit well into drift and are protected from wind (Young 1963a). To roost, tuck bill beneath scapulars and completely withdraw neck (Spellerberg 1971a). At roost, may remain alert, but neck and head still drawn down (F.I. Norman).

SOCIAL BEHAVIOUR Well known during breeding season; major studies include: detailed behavioural study (Spellerberg 1971a) and observations (Young 1963a,b,) at C. Royds; and study of Long Call Complex at Palmer Stn, Anvers I. (Pietz 1984, 1985). Behavioural comparisons with other species discussed by Devillers (1978), Spellerberg (1971a), Furness (1987) and Pietz (1986, 1987). Account includes material from review by Furness (1987) and original contribution by K. Green.

At Palmer Stn, no difference in behavioural repertoires of South Polar and Subantarctic Skuas, and calls and displays used interspecifically (Pietz 1985). Pietz's (1985) comparison of Long Call Displays between these two species indicates considerable variation within individuals and overlap between species (Fig. 1; see also Pietz 1985: Figs 1, 2). Five types of Long Call Displays; species overlap in Types 2, 3, and 4, and only most extreme postures seemed species-specific: Type 1 being Subantarctic Skua and Type 5 being South Polar Skua, though on rare occasions even these may overlap; results generally indicate South Polar Skua tends to hold neck farther back while Subantarctic tends to hold neck forward (see Agonistic behaviour for display details). Furness (1987) considered head posture held by Subantarctic Skua indistinguishable from that of subspecies *hamiltoni*, *antarctica* and *skua* of Great Skua and of Chilean Skuas *C. chilensis*; South Polar is distinctive (see Voice). White wing-flash important signal in display (Furness 1987; see Spellerberg 1971a). **Flock behaviour** In colony, when one bird gives Alarm Call (usually female), others join in (Spellerberg 1971a). Birds in colony sometimes co-operate in attack of non-breeders (Young 1963b). **Comfort behaviour** Most often seen bathing in early afternoon and preening in afternoon and twilight, but preening

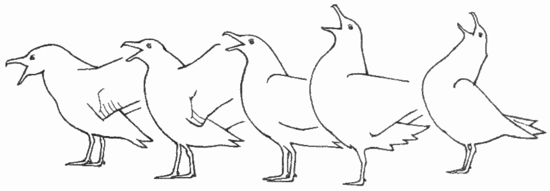


Figure 1 Long Call Displays

can occur at all hours (Pietz 1986). BATHING: Appears important; bird stands in fresh water ducking head and wings under water in scooping motion, causing water to run over back; sometimes beat wings vigorously against water, then raise and flap wings while in Oblique Posture (see Agonistic behaviour). Then preen, and usually allow plumage to dry before returning to territory or Club, though plumage sometimes freezes, preventing flight (Spellerberg 1971a). At C. Royds, communal bathing area used by breeding and non-breeding birds (Young 1963b). Five-day-old chicks show similar bathing behaviour to adults. PREENING: Continues for up to 50 min after bathing; rub both sides of bill and sides of head on uropygial gland then nibble and wipe bill over feathers of breast and neck then continue with those of (in no particular order) scapulars, dorsals, flanks and wings; with single feathers of wing in tip of mandibles, nibble from base to tip of feather (Spellerberg 1971a). HEAD-SHAKING: Recorded in roosting birds; shake head vigorously to remove small drops of liquid that form on tip of bill (Spellerberg 1971a). Two relaxed postures: (1) roosting position; or (2) bird stands or incubates with neck not stretched (Fig. 2; Spellerberg 1971a). Spellerberg (1971a) also describes CROUCHING BEHAVIOUR: in response to bird flying overhead, female crouches with head and tail almost touching ground; function unknown; seen only three times and always by females near start of incubation.

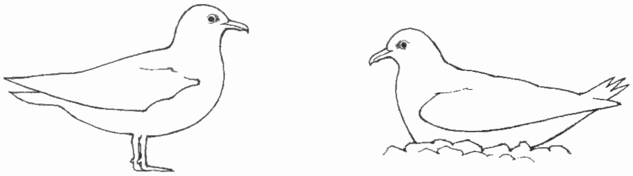


Figure 2 Relaxed posture

Agonistic behaviour Breeding birds defend territory (and eggs and young) against other Skuas and are particularly aggressive when eggs hatching or when with chicks; attack in air and on ground. Generally, birds of either sex harass other Skuas that circle above or land on their territory, but may not challenge birds flying directly across territory. During period of incubation, groups of non-breeders sometimes gather round incubating bird, each trying to steal eggs; birds settle in territory and approach sitting bird, causing it to leave nest and attack; some intruders try to take eggs and, if non-incubating partner does not return, eggs likely to be taken (Spellerberg 1971a,c; E.C. Young). Young (1963a) found egg-stealing by conspecifics rare; noted non-breeders allowed to fly about territories during incubation but not after hatching. At some colonies non-breeders fly for long periods above territories, disturbing many pairs; birds from colony co-operate in attack but non-breeders usually outfly breeding birds and seldom tackled effectively (Young 1963b). Aggression may also occur: among rival females during pair-formation (Spellerberg 1971a; see Sexual behaviour); when chicks wander into neighbouring territories (see Relations within family groups); and during communal feeding (Spellerberg 1971a). Agonistic activities occur at all hours of day (Pietz 1986). In areas of sympatry, interact aggressively with Subantarctic Skua (e.g. Pietz 1987).

Territorial advertising Often use Long Call Complex (see below). According to Young (1978), pair moving into deserted territory establishes boundaries with ground displays. Also boundaries of territory sometimes defined by one of pair flying slowly in circuits round territory, similar to that described for Long-tailed Jaeger *Stercorarius longicaudus* (Spellerberg 1971a; see Drury 1960); this may continue throughout breeding (F.I. Norman).

Threat Following displays based on Spellerberg (1971a) except where stated. Three forms of UPRIGHT posture which may merge: (1) ANXIETY UPRIGHT (Fig. 3): Head raised or directed at stimulus and often cocked to one side while neck may be stretched; given when incubating or roosting bird looks at intruder flying overhead; often associated with Alarm Call. (2) INTIMIDATED UPRIGHT (Fig. 4): Head lifted above horizontal, neck held back and bill pointing slightly downwards; body in oblique position with tail almost touching ground; sometimes associated with Short Call; a submissive posture (see below). (3) AGGRESSIVE UPRIGHT (Fig. 5): Neck stretched, with feathers of nape slightly raised and bill pointing down; wings held out and stationary; any movements, particularly walking, rigid; assume posture when approaching intruders and before attack. Following aggressive displays also involved main aggressive display, Long Call Complex (see below). BENT NECK (Fig. 6): As bird raises feathers of nape, slowly points head and bill downwards, sometimes placing tip of bill in feathers of breast, and raises tail slightly. Intimidatory posture; used when bird adopts stiff appearance and slowly moves body. No call given but often culminates in Long Call and Wing-raising. OBLIQUE (Fig. 7): Lifts head up and backwards, then tilts body backwards with tail nearly touching ground. Wing-raising almost always occurs at same time. WING-RAISING (Fig. 8): Fully extends and raises wings while body

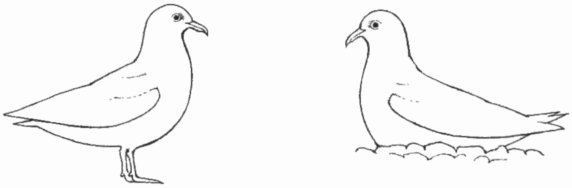


Figure 3 Anxiety Upright

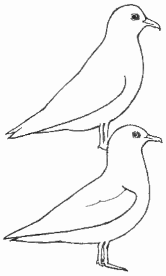


Figure 4 Intimidated Upright

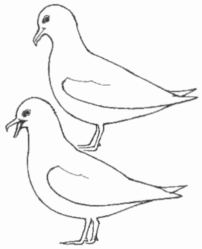


Figure 5 Aggressive Upright

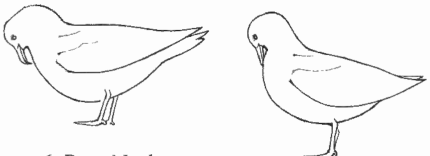


Figure 6 Bent Neck

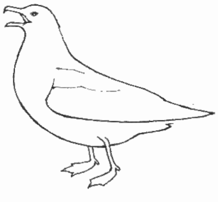


Figure 7 Oblique

Figure 8 Wing-raising

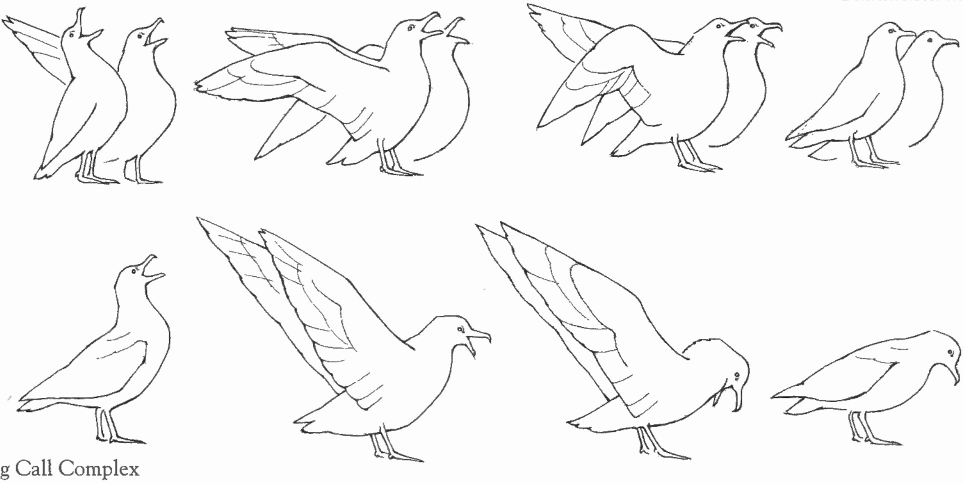


Figure 9 Long Call Complex

leans slightly backwards; white of primaries fully displayed; performed by single birds or together by pairs; often occurs during communal feeding as one bird approaches another or before jumping (as an intention movement) by attacking bird. LONG CALL COMPLEX: Common display involving wings and loud call; varies greatly. Occurs both in and out of breeding colonies; but often used for territorial advertising and seen after territorial boundary disputes; also Greeting, see below (Pietz 1985). Typically, bird assumes Oblique as Long Call begins, then slowly raises wings (Wing-raising); adopts Bent Neck posture as call ends, while wings still raised. Pietz (1985) described five different types of associated postures for this species and Subantarctic Skua (See Fig. 3 of Pietz 1985, top) and several of these may be adopted during a single call; at times postures adopted appear to be related to location of intruder or partner. Figure 9 shows Long Call Complex displays; see also Voice. GRASS-PULLING: Performed with wings raised; occasionally seen in males after nest-relief, territorial disputes and unsuccessful copulation (Spellerberg 1971a). In 86 territorial boundary disputes seen by Spellerberg (1971a), 81% of postures used by attacking bird were Bent Necks and Aggressive Uprights, singly or in combination; Intimidated Upright made up 49% of postures before retreat. Disputes always followed by resident bird giving Long Call Complex, either by itself or together with mate. Threats to intruders, in order of increasing intensity, probably: Anxiety Upright, Oblique, Bent Neck, Aggressive Upright. If stranger flies over colony without showing interest in particular territory, most breeding birds react with Anxiety Upright; if interest shown, Bent Necks and Obliques more common, with aerial attack following in all cases. If stranger lands in territory, sequence by resident: Bent Neck, Aggressive Upright, attack, or Bent Neck then attack; if resident does not attack, it usually responds by: Anxiety Upright, Aggressive Upright, Long Call Complex, or simply Aggressive Upright. Responses by bird in Club to another flying overhead: mostly Aggressive Uprights (52%; n=21) with some Anxiety Uprights (19%) and not many Bent Necks and Intimidated Uprights; aggressive responses to another on ground: usually Aggressive Uprights (41%; n=29) but often Intimidated Uprights (31%). Main displays seen in 28 interactions between birds feeding at a carcass were: when attacking, Aggressive Upright frequent (43%) whereas, when retreating, Intimidated Upright common (32%); high number of Oblique with Wing-raising in both attacking (39%) and retreating birds (57%) possibly related to frequency of fights that occur in conflicts over food. **Attack, Fighting** Aerial attacks often used if intruder flies over territory; pursuing bird sometimes appears to peck at tail or feathers near uropygial gland of intruder. When intruder on ground, attacker may SWOOP: circles over intruder on ground, then swoops down, spreading wings and lowering tarsi to hit intruder; at impact, one bird gives Short Call; Swooping often persistent and can continue for up to 3 h, with short breaks, e.g. when boundary being disputed or when females competing for mate and territory. Aerial attacks sometimes result in broken wings. Ground combat may involve two or more birds attacking each other with wings and claws; often preceded by Wing-raising, allowing feet to be used for striking opponent; attacking bird pecks downwards, trying to seize and hold tail of opponent (Spellerberg 1971a). **Escape, Appeasement** Before attacker Swoops, intruder on ground may adopt Oblique or Bent Neck and Long Call; as Swoop begins, crouches so that breast touches ground, raises tail and points head and bill upwards at attacker; once Swoop ends, gives Long Call. During territory dispute, less aggressive bird assumes Intimidated Upright then usually flees. PECKING AT THE GROUND: After boundary dispute, retreating bird occasionally pecks at objects on ground, sometimes picking them up and then tossing them to one side (Spellerberg 1971a). **Alarm** Give Alarm Calls; may change to Long Call as danger becomes less intense; and may be preceded or interspersed with Quack, a low-intensity response. Sometimes only gives Quack followed by Long Call (Spellerberg 1971a). Also see Parental anti-predator strategies.

Sexual behaviour Based on Spellerberg (1971a) unless stated. **Pair-formation, Courtship** In Clubs, where some temporary pairs form, no apparent posture or call used by males to attract females. Instead, aggressive displays by single birds moving about Club sometimes lead to encounters between males and females: two birds approach each other in Aggressive Upright, then either fight on ground then move away, or female assumes Intimidated Upright or Hunched Posture (see below); in latter case, pair-bond maintained for short period (no longer than 1 h) by both birds showing Scoop-making behaviour (Scraping by male, Squeaking by both; see below) or, less often, by female Begging and male regurgitating. No attempts at copulation seen in Clubs. Apparently, pairs establish permanent bonds in breeding colonies where pair-formation behaviour complex and varying; such behaviour usually lasts 2 h or more; some females leave after this time. Single male claims territory then starts displaying (Long Call Complex; Scoop-making) to attract females. When female approaches on ground, male initially gives Aggressive Upright; birds exchange aggressive behaviour and call, male giving Obliques or Aggressive Uprights while female alternates between Aggressive Uprights, Obliques, and Intimidated Uprights. Eventually, both birds may temporarily stop displaying and roost in territory; when displays re-start, perform similar activities or female may be intimidated before they perform mutual activities, such as Squeaking Ceremony (see below), Scoop-making, courtship feeding, and Willing postures, followed by male mounting (without cloacal contact). Pair-formation behaviour characterized by following: male sat in scoop giving Soft Calls, periodically standing, Scoop-making, and giving Long Calls; two females landed together a few metres from male and gave similar calls to male; one approached male then, when other started to approach him, first attacked and chased away second; remaining female and male both adopted Aggressive Upright and walked round one another till female assumed Intimidated Upright then Hunched Posture, and both birds settled by scoop. At start of summer, previously established pairs re-form on old territories: male assumes aggressive postures, including Wing-raising in front of female; female gives Intimidated Upright, and Hunched and Begging Postures. Within a few days of arrival, pair begins co-ordinated defence of territory, and feeding and bathing together. As laying approaches, female less active, staying on territory and settling in scoops. In established pair, Scoop-making activities preceded by male moving about territory pecking at ground, picking up and dropping objects. SCOOP-MAKING: Male begins SCRAPING while giving Soft Calls, then suddenly stops and starts elsewhere in territory; female slowly approaches male in scoop; when alongside, male leaves scoop and female keeps Scraping. Procedure repeated 3–5 times in 24 h. After *c.* 3 days, female goes to scoop without male. When female standing in scoop and male approaches, she gives HUNCHED POSTURE (Fig. 10): Head slightly lowered, but not withdrawn; body slightly bent forward and tail raised. Male shows Aggressive Upright and birds peck breast and nape of other. Generally, female then leaves scoop and copulation behaviour begins. In recently established pair, Scoop-making frequent and may continue through summer; in previously established pairs, may start 2–3 days after birds arrive and persist till laying, by which time several scoops may have been made. SIDEWAYS NEST-BUILDING: Before laying, female (usually) sits in scoop picking up objects and dropping them in or to one side of scoop, but no attempt made to line scoop (Spellerberg 1971a). Young (1963a) also refers to pairs playing with objects during pairing and scoop-building. If female does not respond to Scoop-making of male, he performs PECKING AT THE GROUND, a form of displacement behaviour. SQUEAKING CEREMONY (Scoop Selection; Fig. 11): Just before laying, female joins male as he approaches scoop (usually future nesting scoop) and both give Soft Calls; when near each other, crouch with heads pointing down and tails raised, and give high-pitched squeaks; then male stands in scoop while female makes small quick steps from side to side in front of him; finally female displaces male and shows Scraping and settling movements (Spellerberg 1971a). **Courtship feeding** Female begs from, and is fed by, male. At times, at some locations, during breeding cycle fed entirely by male: may occur from pairing till hatching (Young 1963a,b) or till young 3–4 days old (Spellerberg 1971a); in territories that include part of penguin colony, courtship feeding occurs during laying, then female forages for herself in territory during incubation (Young 1963b). Most feedings seen when male returns to territory from foraging; female appears to recognize male returning long before he arrives and leaves nest to approach him as he lands; pair then run together in hunched attitude. Feeding never occurs at nest (Young 1963a,b; Spellerberg 1971a). BEGGING: Female, in Hunched Posture, tries to move in front of male, sometimes running back and forth if male tries to move away; both birds call; when facing each other, female, still in Hunched Posture, pecks breast of male while both birds call more often; if activity lulls, female may slowly stretch wings up then lower them before continuing to Beg. In response to Begging, male adopts Aggressive Upright, then Oblique while raising neck feathers, and finally regurgitates (Fig. 12). Female takes food from ground but sometimes male offers her portions of regur-gitate in his bill (Spellerberg 1971a). After feeding, during incubation, female either drinks from pond then returns to eggs, or roosts while male incubates (Spellerberg 1971a). At times, female Begs from male that has not foraged or voluntarily offered food; commonly is fed with well-macerated fish or milky fluid, but little food passes; some males never fed females in these circumstances and either flew or pecked viciously, provoking challenge display; persistent worrying can cause male to obtain food (Young 1963b). Courtship feeding plays role in copulation (Spellerberg 1971a; see below) and probably maintenance of pair-bond (Young 1963b). **Greeting** Long Call Complex sometimes used when members of pair meet (Spellerberg 1971a; Pietz 1985). Little ceremony at change-over during incubation: relieving bird comes to nest and stands by sitting bird; outgoing bird then steps off nest, and relieving bird settles straight away (Young 1963a), may call (F.I. Norman); alternatively, sitting bird flies from nest to nearby rock where mate roosting; pair stand close together for *c.* 30 s during which both raise wings upwards and call; then relieving bird immediately starts incubating (Eklund 1961). Sometimes change-over not co-ordinated and eggs left uncovered, or both birds try to incubate at same time; if sitting bird reluctant to leave, relieving bird (usually female) sometimes quietly pecks at head and breast of sitting bird or tries to lever or push it off nest with bill and head. Relieved bird often picks up objects in bill and flicks them to side or over back, though they rarely fall close to nest; bird may continue to flick objects even though it is a metre or so away from nest; similar to Sideways Nest-building (see above); seen more often in first weeks than towards end of incubation and females continue to do so

Figure 10 Hunched Posture

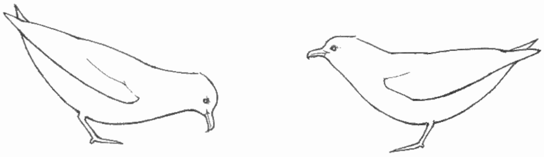


Figure 11 Squeaking Ceremony

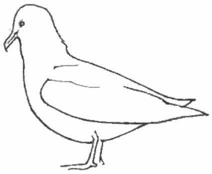


Figure 12 Begging

longer than do males (Young 1963a; Spellerberg 1971a). Relieved bird flies round territory, during which defecates; then lands near snow drift to eat snow or drink from pond in territory (Spellerberg 1971a). **Copulation** Contrary to Young (1963b), Spellerberg (1971a) found successful copulation always preceded by courtship feeding, with or without regurgitation; if no regurgitation, female may not allow male to mount. Start of copulation signalled by female settling in scoop with SIDEWAYS ROCKING movement, where tail-feathers and wing-tips project upwards. Male assumes Aggressive Upright, then Intimidated Upright while giving Copulation Call (given more often before and during mounting). In front of male, female stands in WILLING POSTURE (Fig. 13): head withdrawn and facing down, tail feathers raised, and wings held slightly away from body. In response, male struts back and forth while raising, lowering and flapping wings in Oblique posture (Fig. 14); mounts several times before sexual contact made. During contact, male rests on tarsi while bending tail downwards; he uses tips of his wings and grasps female's nape for support; both birds silent; 1–5 contacts performed. After copulation, birds may eat snow, drink from ponds in territory or preen (Spellerberg 1971a). Copulation may occur on or away from nesting territory (Eklund 1961). After losing eggs or chicks, birds resume courtship feeding; at C. Royds, some resurgence of pairing and nesting behaviour in late summer (Young 1963b).

Figure 13 Copulation: Willing Posture

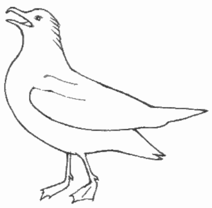
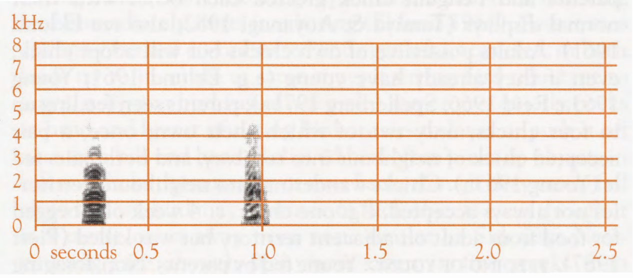


Figure 14 Copulation

Relations within family group Soon after hatching, chicks wander round nest and, later, round parent's territory; usually do not wander beyond territory, but may if neighbouring territory deserted or if neighbours tolerant of chick or submissive to parents. Chicks walk, stand or sit with stooped or crouched postures (cf. erect stance of adults). During first 3–4 weeks, chicks hold wings fairly close to body; when *c.* 1 month old, wings droop slightly; when 40–45 days old often walk with wings loosely folded (Reid 1966). When 2+ days old, chicks can show aggressive postures similar to those of adults (Spellerberg 1971a). Parents appear not to be good at recognizing their eggs and young (Young 1963a). When egg of Adelie Penguin substituted for Skua's egg in nest, Skuas incubated it for 20 days till hatching, then guarded and brooded Penguin chick, even though Penguin eggs and chicks look very different from those of Skuas (though eggs similar in size); parents and Penguin chick greeted each other with their normal displays (Tamiya & Aoyanagi 1982; also see Eklund 1961). Adults possessive of own chicks but will adopt chick, even if they already have young (e.g. Eklund 1961; Young 1963a; Reid 1966; Spellerberg 1971a); parents seen feeding up to four chicks, only two of which their own; once, a pair accepted chick of neighbour into territory, and both pairs fed it (Young 1963a). Chicks wandering into neighbours' territories not always accepted, e.g. one chick, *c.* 4 week old, begged for food from adult on adjacent territory but was killed (Pietz 1987). FEEDING OF YOUNG: Young fed by parents. Non-foraging adult helps feed young (Young 1963b). When chick <5–6 days old, and foraging male returns, female begs, pecking at his breast and bill; male regurgitates and female picks up and presents food to, or drops it in front of, chick; during feeding both adults call repeatedly. BEGGING: When chick >5–6 days-old and adult returns, chick begs by jumping, with wings raised, and squeaking (Spellerberg 1971a). Even without stimulus of returning adult, chick sometimes aproaches adult in BEGGING POSTURE (similar to Hunched posture of adults) and calls; when in front of adult, chick stands on toes with neck stretched and wings raised, and pecks at breast and bill of adult; adult regurgitates or moves away; if adult moves away, chick follows, calling more often; may follow till food given or adult flies to another area in territory (Spellerberg 1971a). Sometimes, parent feeds chick voluntarily, with food from crop, at regular intervals; parent attracts chick with Food Call and regurgitation movements (Young 1963a). During normal feeding, food offered to young usually appears little digested (whole fish and pieces of penguin flesh) and is not broken up by chicks before being eaten; within 30 min of feeding, some chicks (up to 25 days old) regurgitate and peck at food, as though trying to break it up, then eat it again (Spellerberg 1971a). Food can be shredded before being fed to chicks (Young 1963b). Generally, younger chicks have food held or dropped before them. Older chicks catch food as it is regurgitated; chicks *c.* 30 days old can swallow entire fish and dispense with help from parents in preparing food (Young 1963b; Spellerberg 1971a). SIBLING RIVALRY: Siblings often fight. Aggression begins as soon as second chick hatches (Spellerberg 1971a) or 1–2 days afterwards (Young 1963a). Older chick initiates unprovoked attacks. At first, elder sibling pecks younger on head and back without any associated calls or postures; by end of first week, adopts postures. Before attacking another chick or when approached by another chick, assume AGGRESSIVE UPRIGHT: aggressor stands on toes with neck stretched, head facing upwards, and wings held out slightly; then, if sibling within pecking distance, attacks uttering Long Call (Challenge Call; Young 1963a,b) and pecking head and back of sibling as it tries to chase sibling from area of nest. Victim, usually younger sibling, seldom retaliates effectively and if knocked down, often crouches; usually tries to escape and driven from area of nest (Young 1963a); when driven from nest, often returns soon after (Reid 1966). Once, adopted chick killed two resident chicks (Young 1963a). In captivity, chicks give Long Call and defend water supply; when fighting, peck each other on wings or nape and keep hold until both appear exhausted; attacked chick screams and, if escapes, runs and hides with head withdrawn and bill pointing down (Spellerberg 1971a). Adults try to stop chicks fighting by a number of methods; may intercept them; attempt to feed them individually; give Alarm Call, after which chicks move away and crouch (Spellerberg 1971a); or sit with one beneath wings on either side of body (Young 1963a). If unsuccessful in stopping chicks from fighting, parent starts Scraping and Scoop-making at nest and giving Alarm Call. Not uncommonly, siblings may be maintained separately within territory, each parent attending one chick: begins when parents try to separate fighting chicks during feeding; later, younger chick covered and fed separately by one parent while older sibling cared for at nest by second parent; if this continues for 1–2 days, one parent seems to associate with one chick, feeding and brooding it and, except in defence, virtually ignores second chick, which is attended by other parent; if pattern becomes established, chicks survive well (Young 1963a). This behaviour successfully used by breeding pairs that had abundant food available (Trillmich 1978) but not successful at C. Hallett, where adults also never intervened in fighting (Reid 1966). Sibling rivalry important cause of chick mortality (Procter 1975; also see Breeding); if only one chick survives, it is usually the older (Spellerberg 1971a; P. Pietz). Young (1963a) found that generally younger chick *c.* 4 days old when displaced from nest; Reid (1966) found all fighting occurred before eldest sibling 8 days old. Younger chick once killed older chick, though this followed interference by people (Reid 1966). Predisposition of younger chick to be excluded from nest or denied parental attention makes it more susceptible to starvation, exposure and predation (Procter 1975), e.g. most ejected chicks killed by non-parental adults or by cold, as parents do not attend chicks that wander from nest in bad weather (Young 1963a); even parental attempts to rear chicks separately do not compensate entirely, because both parents cannot be in continuous attendance. Sibling aggression not always common: in area where food appeared readily available, sibling aggression rare and breeding success higher (Hull *et al.* 1994) and two chicks often fledged (P. Pietz); pairs of chicks seen peacefully moving round together (Reid 1966) and, during storms, huddling together (Spellerberg 1971c). Sibling aggression and much cannibalism more in evidence when food appears scarce (e.g. Pietz 1987). Sibling aggression assumed to be response to hunger (Procter 1975); generally recognized as density dependent response in species where there is food uncertainty during breeding (Mock 1984; O'Connor 1978; E.C. Young). Parents seen eating their own chicks but probably not responsible for their death (Young 1963a). For further details on sibling rivalry, see Young (1963a) and Procter (1975). **Anti-predator behaviour of young** Respond to Alarm Call of adults by crouching with head on ground; may run to shelter before crouching. When crouching, cryptically coloured and difficult to locate. Older chicks (20+ days) assume Aggressive Upright at start of Alarm Call; will move head quickly from side to side while looking up; will crouch if Alarm Call continues (Spellerberg 1971a). If chased, half-grown chicks extend wings almost fully, but often unable to maintain balance at speed; when *c.* 40–45 days old, fully extend and flap wings and able to maintain balance; if pursued, chicks that cannot fly will often suddenly stop running and crouch. Often during chase, a bird will run across territory and, at boundary, turn back or crouch; do not always need adult to warn of location of boundary. If sitting and approached quietly, usually remain sitting (Reid 1966). About age when capable of flying, instead of hiding during disturbance, become alert, watchful and fly when approached too closely (Young 1963a). **Parental anti-predator strategies** Parents that breed successfully rarely absent at same time but, when food scarce, both parents sometimes leave territory to forage (Eklund 1963; Pietz 1986, 1987). While incubating, when approached by person, parent usually stays on nest till observer within 6–15 m then, often with wings raised, walks stiffly away while giving loud call; occasionally, bird can be touched on nest; Swooping (see Agonistic behaviour) follows. When Swooping, parents often work together by attacking from different directions or attacking in turns; approach very close before veering away and will sometimes strike; Swooping only occurs when intruder within territory (Eklund 1961; Spellerberg 1971a). Birds give Alarm Call as they circle before Swooping. In colony, when one bird gives Alarm Call (usually female), others join in. Alarm Call changes to Long Call as danger becomes less intense (Spellerberg 1971a). Said to attack more intensely when disturbed from nest during cold weather compared with fine weather (Young 1963a). Adults said to be always aware of location of chicks, even when chicks hiding from danger; they will call at chicks to crouch if they start to move before danger passed (Furness 1987). When first fly, chicks are accompanied by parents who protect them from other Skuas. Single parents can fail to defend offspring (Young 1963a). Do not perform Distraction Displays (Furness 1987). May give Long Calls (F.I. Norman). Eggs and young also protected against other Skuas (see Agonistic behaviour) or animals passing too close by (e.g. seals and penguins) (Pietz 1985).

VOICE Well known from study by Spellerberg (1971a); Pietz (1985) studied Long Call and gave sonagrams. Many calls, varying from raucous screams to soft piping. Begging Call given only by female; Food Call To Mate and Copulation Call only by male. Differences between individuals apparent in Long Call, most marked for pitch, number of harmonics, and rate of repetition of notes (Pietz 1985). No regional differences reported. Calls very similar to those of Subantarctic Skua (q.v.). For Long Call, wide overlap between both species in all characteristics measured: in South Polar Skua, notes of call are repeated significantly faster, lower in pitch (despite generally smaller size), and have greater number of harmonics; differences in number of notes per call, duration of calls and duration of notes, not significant; temporal splitting of notes noted only in South Polar Skua (Pietz 1985; also see Brunton 1982).

Adult QUACK: Quiet low-pitched call of single syllable; given singly or at intervals of 1 s. Sonagram A shows two calls made at different times by members of a single pair. Elicited by stimulus not strong enough to trigger Alarm Call; given as danger approaches, preceding Alarm Call or sometimes Long Call, or between Alarm Calls (Spellerberg 1971a). ALARM CALL: Series of high-pitched, drawn-out notes; could be described as scream. Each note *e-e-e…ak*, with each *e* rolled and *ak* sharp; three notes shown in sonagram B. Typically given by bird with chicks or eggs; may break into Long Call as danger moves away or becomes less intense. When given by one bird in colony, usually female, taken up by birds in undisturbed territories. Also given outside territory when feeding (Spellerberg 1971a). ANXIETY CALL: 4–6 hoarse notes, repeated rapidly (see sonagram C); quieter than Alarm Call; uttered when intruder near nest but threat not sufficient to stimulate Alarm Call (T. Howard). Similar in structure to Anxiety Call of Kelp Gull. ATTACK CALL: Not described; more intense during colder weather (Young 1963a). GAKKERING (SHORT CALL): Number of short notes, repeated arhythmically. Given during aggressive encounters in air or on ground, mostly by bird being chased, but also when about to swoop; often precedes Long Call (Spellerberg 1971a). LONG CALL: 10–40 short notes rhythmically repeated at rate of 2–3 notes/s; first 1–4 notes disyllabic and higher in pitch, succeeding notes



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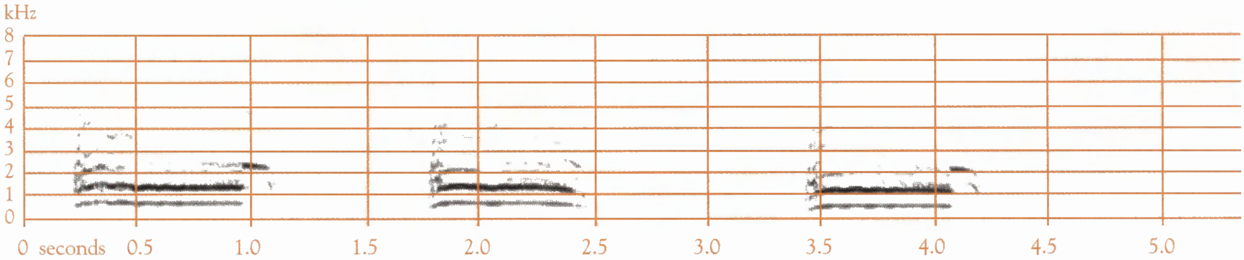

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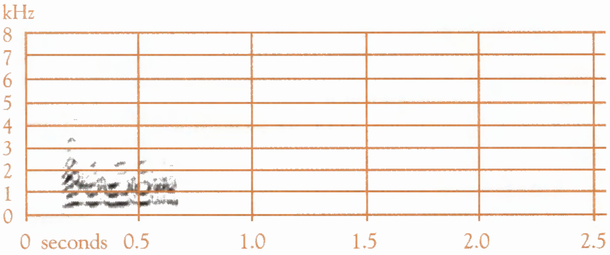


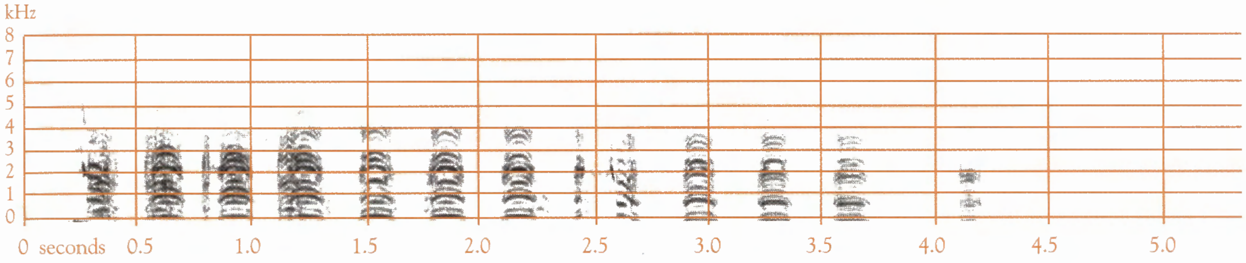
C T. Howard; Magnetic I., East Antarctica, Dec. 1987; private DA1

progressively quieter and lower in pitch; may give 2–3 calls in succession, or one call may stop or be shortened, depending on stimulus (Spellerberg 1971a). Sonagram D shows Long Call given by a pair, with both members participating in first four notes and eighth note showing temporal splitting. Given with wings extended obliquely upwards and backwards (see Social Behaviour). At Palmer Stn (39 calls of 14 birds), mean length 4.1 s (1.7–8), mean number of notes 12.0 (6–20); these data only include calls accompanied by wing-raising, thus excluding less intense calls, when notes fewer, shorter and of lower pitch; some, but never all, notes may be complex from temporal splitting (up to 0.1s), or presence of introductory components, but production and form by individuals inconsistent, so unlikely to be important for recognition of individuals (Pietz 1985). Given by both birds of pair when one joins other in territory, and by bird settling in own territory after boundary dispute (Spellerberg 1971a). YELP: Heard once during vigorous aerial fight in which one pair defended fully fledged chick from another pair (Spellerberg 1971a). SOFT CALL: Given during scoop-building, male generally calling female to participate (Young 1963a); both members of pair make this call (Spellerberg 1971a). SQUEAKING: High-pitched squeaks given by both members of pair (Spellerberg 1971a) during Squeaking Ceremony (see Social Behaviour); Squeaking rarely audible during Squeaking Ceremony (Parmelee 1992). BEGGING CALL: Ranges from short, high-pitched, chick-like call, to deep, drawn-out, rolling cackle lasting 2–3 s; given by female from start of breeding cycle until she begins to forage for herself and chicks (Spellerberg 1971a). FOOD CALL TO MATE: Soft, gull-like mew; given by male (Spellerberg 1971a). COPULATION CALL: Short, deep and harsh, repeated at short intervals by male before, but not during, copulation (Spellerberg 1971a). FOOD CALL TO YOUNG: Monosyllabic, low-pitched call, repeated at short intervals (Young 1963b; Spellerberg 1971a).

Young BEGGING CALL: Two calls distinguishable from age of 2–3 days: high-pitched, drawn-out squeaking when approaching adult before being fed; quickly repeated, high-pitched *cheep* when pecking at feathers of breast of adults before feeding and between bouts of regurgitation (Spellerberg 1971a). Shrill tremulous whistles of 2–3 s duration, at intervals of 1–2 s, from fledgeling aged 53 days, different from long quavery *cheeps* of younger chicks (Reid 1966); common call in colonies when chicks hungry (E.C. Young). LONG CALL: As in adult, but higher pitched; given as early as 12 days old (Spellerberg 1971a); used by older chick to challenge sibling, which usually flees (Young 1963a).

BREEDING Well known; studied on S. Shetland Is (Peter *et al.* 1990), Ross I. (Young 1963a; Spellerberg 1971a,b; Procter 1975; Ainley *et al.* 1978, 1990), Windmill Is (Eklund 1961), Signy I. (Hemmings 1984), and Antarctica, at C. Hallett (Trillmich 1978), Larsemann Hills (Wang & Norman 1993b) and Palmer Stn (Pietz 1987); for each site, references as above, unless stated. Breeding schedule not synchronized with that of Adelie Penguins (Spellerberg 1975; Young 1994). Hybridize with Subantarctic Skua (Trivelpiece & Volkman 1982; Hemmings 1984).

Season Laying varies between sites; starts, mid-Nov. to early Dec.; peak, late Nov., early or mid-Dec. At Palmer Stn, timing depends on availability of fish, which is often affected by ice conditions (P. Pietz). S. SHETLAND IS: For two consecutive seasons: laying, 16 Nov.–7 Jan. and 12 Nov.–15 Jan., 50% eggs laid by 9 Dec. and 30 Nov.; hatch, 16 Dec. to 5 Feb. and 13 Dec. to 12 Feb., 50% hatched by 6 Jan. and 29 Dec. WINDMILL IS: First eggs, late Nov. SIGNY I.: Mean date first eggs, 19 Dec. (12 days; 5 Dec.–13 Jan.; 13); first young, 18 Jan. (12 days; 2 Jan.–10 Feb.; 12); first fledging, 7 Mar. ROSS I.: Laying, 27 Nov. to 27 Dec., 50% by 4 Dec. and most by mid-Dec.



D T. Howard; Magnetic I., East Antarctica, Dec. 1987; private DA1

(Young 1963a); laying, 17 Nov. to 31 Dec. (Ainley *et al.* 1978). ANTARCTICA: Larsemann Hills: mean date of laying, 30 Nov. (8.1 days; 21); first eggs, 29 Nov. (7.5 days; 18 Nov.–12 Dec.; 13); second eggs, 3 Dec. (9.0 days; 22 Nov.–18 Dec.; 8); mean date of hatching, 26 Dec. (8.0 days; 14 Dec.–11 Jan.; 19); first eggs, 25 Dec. (7.1 days; 13); second eggs, 29 Dec.±9.8 days; fledging from 5 Feb.; mean fledging date for six chicks, 16 Feb.±6.4 days. Palmer Stn: mean date for start of laying, 10 Dec. (Neilson 1983); for two consecutive seasons, median hatching date of first chick, 27 Jan. (13 Jan.–9 Feb.; 15) and 15 Jan. (3–25 Jan.; 19); *c.* 3 weeks earlier for pair with supplemented diet; over six seasons, average laying dates ranged over 4 weeks. At C. Hallett, pairs with feeding territories begin breeding *c.* 8–10 days earlier than those without.

Site Often nest close to, and establish territories within, colonies of penguins, but can breed successfully away from penguins (Young 1963b; Trillmich 1978). At Svarthamaren, Dronning Maud Land (200 km inland), 50 pairs bred with 207,000 pairs of Antarctic Petrels and 500 pairs of Snow Petrels (Mehlum *et al.* 1988). On Windmill Is, Eklund (1961) says location of nesting areas governed by colonies of Adelie Penguins, with 95% or more of Skua nests close to colonies of Adelie Penguins. Often nest in association with other seabirds (e.g. Wang & Norman 1993a; Mehlum *et al.* 1988). Nest in dry areas, free of snow; on small hills, rocks, moraines, edges of cliffs, in valleys and basins, sometimes surrounding small lakes or ponds; up to 800 m from sea or sea-ice (Young 1963a; McGarry 1988; Peter *et al.* 1990). Sites traditional; breed in same territory each year, often in same scoop (Wood 1971). At C. Hallett, four of ten banded adults were recaptured at same area in next season, and two recaptured in third successive season (Eklund 1961). On Ross I., birds that did not change breeding areas moved nests average of 15.9±1.4 m (n=208) in successive years, though 134 birds did not move at all (Ainley *et al.* 1990). One replacement clutch laid within 10.7 m of original nest (Eklund 1961).

Nest, Materials Unlined scoop of fine pebbles or gravel on rocky knoll or mound; scoop usually below ground level, but sometimes rim of gravel raises nest slightly above ground (Eklund 1961); excavated in carpets of moss; more elaborate bowls heaped with plucked chunks of moss, interspersed with lichens and grasses (Parmelee 1992). At inland sites, nests may be made from bones of petrels (Howard 1991). Male generally begins building; some pairs build one scoop, others several; nest in last scoop built (Young 1963a). Female chooses scoop 2–3 days before laying (Spellerberg 1971a). Nest not always made before eggs laid; scoop lying neglected for up to 2 weeks may still be used (Young 1963a). MEASUREMENTS (cm): 15 nests on Windmill Is: diameter, 20.3–25.4; depth, 3.8–5.1; S. Shetland Is: inner diameter, 26.4 (n=52).

Eggs Ovoid, like eggs of Subantarctic Skua and other *Catharacta* (P. Pietz). Texture varies from rough and dull to smooth with faint gloss; pale green faintly blotched brown or purple, light grey distinctly blotched brown or purple, or olive brown with numerous dark heavy blotches (Falla 1937); dark stone, irregularly blotched dark and light brown, mostly at larger end (Oliver); some dark, others have clear greenish-blue ground-colour, sparsely smeared and blotched yellowish brown at larger end (Murphy); ground-colour, various shades of green, splotched light brown, with some more brown than green and with dull rather cloudy splotches of brown; eggs on Windmill Is appear much lighter than elsewhere (Eklund 1961). MEASUREMENTS, WEIGHTS: In Table 1. VOLUME: S. Shetland Is: 85.4 (7.0; 64.5–106.2; 118). At Palmer Stn, average volumes when food scarce during egg-formation, 81.5 (5.71; 67.5–97.3; 58 clutches); when food more readily available, 84.5 (5.89; 74.6–99.1; 40 clutches) (P. Pietz). At Larsemann Hills, first egg significantly longer, wider and heavier than second egg. At Palmer Stn, difference in size between first and second eggs varies with food supply (Pietz 1987). Eggs in clutches of one egg, smaller and lighter than first egg of two-egg clutches (Peter *et al.* 1990). Measurements and weights of

Table 1

Location	Length	Breadth	Weight	
Signy I.	71.3 (2.4; 66.7–76.4; 27)	49.6 (1.3; 47.1–52.1)	–	1
S. Shetland Is	71.2 (3.1; 64.3–78.1; 118)	50.5 (1.4; 47.3–54.8)	89.4 (5.0; 81–105; 41)	2
Terre Adélie	71.9 (70–73.7; 8)	–	–	3
	71.0 (65.0–74.0; 13)	50.7 (48.2–52.1)	–	4
C. Denison	70.6 (5.73; 55.0–78.0; 12)	51.5 (1.41; 49.6–54.7)	–	5
Antarctic Pen.	71.9 (65.5–75.0; 10)	49.0 (41.0–52.0)	–	6
Palmer Stn	70.9 (2.9; 64.4–78.7; 175)	49.2 (1.4; 45.8–52.4)	–	7
McMurdo Sound	70.9 (66.0–76.5; 11)	49.7 (49.0–51.0)	–	8
Larsemann Hills				
First egg	70.5 (1.31; 68.6–72.7; 13)	50.3 (0.84; 49.1–51.4)	85.6 (4.3; 80.1–91.8; 13)	9
Second egg	69.3 (1.28; 67.7–71.7; 8)	49.3 (0.58; 48.6–50.2)	80.9 (3.3; 77.1–91.8; 8)	9
C. Hallett	–	–	97.5 (n=38)	10

(1) Hemmings (1984); (2) Peter *et al.* (1990); (3) Etchecopar & Prevost (1954); (4) le Morvan *et al.* (1967); (5) Falla (1937); (6) Gain (1914); (7) P. Pietz; (8) Wilson (1907); (9) Wang & Norman (1993b); (10) Fresh eggs; Reid (1966).

Table 2

Location	Length	Breadth	Weight	
Signy I.	73.8 (3.8; 70.9–79.6; 6)	51.8 (0.4; 51.2–52.2)	–	1
S. Shetland Is	72.4 (3.4; 65.1–78.6; 21)	51.8 (1.1; 49.8–54.0)	101.2 (6.4; 95–104; 9)	2
Palmer Stn	74.5 (0.9; 73.4–75.4; 4)	53.3 (0.9; 52.5–54.4; 4)	–	3

(1) Hemmings (1984); (2) Peter *et al.* (1990); (3) All eggs from same pair; P. Pietz.

eggs of mixed pairs given in Table 2; volume: 92.9 (7.4; 77.2–109.6; 21) (Peter *et al.* 1990); 101.6 (2.9; 98.8–105.6; 4) (P. Pietz).

Laying Most (69%) newly established pairs lay in last third of laying period (Wood 1971). Laying interval, 4.6 days (1.6; 2–8; 8); hatching interval, 3.8 days (2.6; 2–8; 6) (Wang & Norman 1993b); hatching interval, 2.3 days (1.2; 1–6; 21); laying interval apparently close to hatching interval (P. Pietz). Female only leaves nest between laying of first and second eggs to be fed by male (Spellerberg 1971a). Recorded re-nesting if one or both eggs stolen before incubation begun, but not if incubation started; one pair re-laid 3 days after loss of first egg (Eklund 1961); when first egg of one pair removed, two more eggs laid within 5 days (Spellerberg 1971c). On Ross I., may lay up to three clutches if early clutches buried by drifting snow; of eight pairs laying early, three laid C/2 then C/2 then C/1, four laid C/2 then C/1 then C/1, and one pair laid three clutches of C/1 (Spellerberg 1971c).

Clutch-size Usually two; sometimes one in pairs that nest late (Young 1963a); on Windmill Is: C/2 x 32, C/1 x 8. At C. Hallett, clutch-size higher in pairs with feeding territories than those without. At Palmer Stn, clutch-size apparently depends on availability of food; in year when food abundant, 100% clutches C/2; in year when food scarce, only 45% (Pietz 1987).

Incubation By both sexes, beginning with laying of first egg; shared equally at first, female later spending more time at nest (Young 1963a; Spellerberg 1971a); during 68.25 h of observation, one pair evenly shared incubation and during 267 h of observation of three pairs, male incubated 46% of time and female 54% (Pietz 1984). Continue incubating during blizzards while snow builds up round bird, except for a small breathing hole (Spellerberg 1969). During incubation, eggs completely surrounded by brood-patches (have two separate patches), plumage and web of feet, with eggs placed on each tarsus (Spellerberg 1969). When relieving bird settles on nest, it stands with feet behind eggs, falls onto breast and brings feet underneath eggs by shuffling movement and sideways rocking; hold wings out, with tail and wing-tips high in air; bird remains stationary for few seconds, then repeats movements. When settled, makes gentle shuffling movements and wags tail. Adult will alter position of eggs with bill as it settles and will also retrieve egg placed on edge of scoop (Spellerberg 1971a). On Ross I.: average length (min) of stints of incubation, from observations of five pairs in early incubation: females, 154 (41–502; 17); males, 124 (27–255; 9); for six pairs in late incubation: females, 188 (59–348; 12); males, 115 (11–238; 12) (Young 1963a). Continuous observation of one pair on Windmill Is for 132.75 h: 13 change-overs, averaging 2.36 times/24 h; female had stints of 453 min (115–922), male 129 min (9–436) (Eklund 1961). At Palmer Stn, length of incubation stints depends on how quickly mate finds food at sea (P. Pietz). During change-over, eggs left for shortest time possible, with temperature of eggs dropping 2.3 °C/min (2.5–8.0); eggs sometimes left exposed for up to 23 min on calm days (surface temperature sometimes reach 16–21 °C) (Spellerberg 1969). Retrieve eggs placed 30 cm from nest within 85 min; will incubate Adelie Penguin eggs substituted for own egg (Eklund 1961). Female fed by male during incubation, at any time of day (Young 1963b), away from nest, by regurgitation, taking food from bill of male or from ground (Spellerberg 1971a). Before eggs laid, males did 91% of foraging, but after laying, during incubation and brooding, share of foraging by females increased to 46% (Pietz 1987). Eggs pip up to 3 days before hatching, most 2 days before (Eklund 1961); hatching process (from first crack, to shell splitting in two), usually 40–56 h (Reid 1966); time needed for pipping of eight eggs, 50–55 h for six, 45 h for one, and 41 h for one (Spellerberg 1971a). INCUBATION PERIOD: Signy I.: for four eggs in two clutches, 27 and 28 days for first egg, 29 and 30 days for second egg; Ross I.: of 46 eggs in 27 nests, one (2.2%) hatched after 27 days, two (4.3%) after 27.5 days, 14 (30.4%) after 28 days, 17 (37.0%) after 28.5 days, nine (19.6%) after 29 days and three (6.5%) after 29.5 days (Young 1963a); 26–34 days, 82% after 28–29 days (n=49) (Spellerberg 1971a). Windmill Is: 29–32 days; of 26 eggs observed daily from laying to hatching, 9 (35%) hatched after 29 days, 15 (58%) after 30 days, one in 31 days and one in 32 days. C. Hallett: 29.5 days (1.06; 26–33; 295) (Reid 1966); 24–34 days (Young 1963a). Larsemann Hills: first eggs, 25.8 days (1.1; 13); second eggs, 24.5±0.5 days. Hatching interval: Signy I., 2.1 days (1.4; 1–4; 14); Ross I.: 2.3 days (0.7; 1–3.5; 16) (Young 1963a). Infertile or addled eggs incubated for 32–41 days (n=4) (Young 1963a). No egg-shells in scoops after hatching, but method of disposal not known (Spellerberg 1971a).

Young Precocial or semi-precocial. Covered in down at hatching (Reid 1966). Can leave nest 12–24 h after hatching (Reid 1966; Spellerberg 1971a). In first week after hatching, brooded often but leave nest readily in fine weather or to be fed; may stay near nest till fledging (P. Pietz). First chick of pair, or single remaining chick, left nest after average 9.6 days (5.5–27; 15); second chicks displaced from nest after 3.8 days (0.5–8; 13) (Young 1963a). Primaries first emerge from follicles at 9–10 days (Reid 1966). Tips of wing-feathers appear at 9–12 days, tips of sheaths fraying within 24 h (Young 1963a). Begin to flap wings, with hops and small jumps, at 40–45 days; can become airborne after a short run and can fly for several metres by 45–50 days (Spellerberg 1971a).

Table 3

Location	H	5	10–11	20–21	30–35	40–41	48–50
Signy I.[1]	55	120	250	600	980	1140	1225
S. Shetland Is[2]	–	150	310	670	1000–1110	–	–
C. Hallett	69.2 (60.8–75.7; 8)	–	302 (219–419; 16)	726 (430–877; 7)	996 (802–1090; 4)	1249 (1160–1303; 4)	1254 (1140–1368; 2)
Larsemann Hills							
First chick	65.2 (1.85; 62.0–68.0; 12)	–	250	530	890	–	1190
Second chick	62.7 (1.75; 60–65; 6)	–	180	410	690	–	910

(1) Estimated from growth curve in Hemmings (1984); (2) Estimated from growth curve in Peter *et al.* (1990).

Growth WEIGHT: Increase with age in Table 3. On Signy I., first chick slightly heavier than second from about 17 days till fledging. At C. Hallett, weight of chicks generally doubled by 109–120 h old; growth of chicks fed from penguin colonies less regular, not reaching final weights attained by chicks fed on fish. At Larsemann Hills, at hatching, first chick significantly heavier than second; daily weight increase for first and second chicks, respectively: 5–10 days, 65.1 (2.02; 63–68; 10) and 62.7 (1.75; 60.0–65.0; 6); 11–20 days, 26.5 (4.11; 20.9–35.0; 11) and 19.3 (6.72; 16.0–29.3; 4); 21–30 days, 43.9 (8.24; 25.7–54.6; 10) and 31.5 (28.3–34.3; 2); 41–50 days, 15.6 (10.20; 7.0–26.3; 6) and 10.0 (n=1). Mean daily increase in weight higher at nests with feeding territories; at 5–10 days old, daily increase of 27.5 g (2.24; 25.2–31.7; 6) for nests with feeding territory, 22.5 (1.41; 20.8–23.8; 5) for nests without; at 20–30 days old, 47.2 (6.57; 39.6–54.0; 5) with, 40.7 (9.06; 25.7–49.7; 5) without; 40–50 days, 21.5 (13–30; 2) with and 15.1 (10.0; 7.0–26.3; 3) without (Wang & Norman 1993b). Asymptotic weight and mean weight at first flight, 1255.4 g (Wang & Norman 1993b). Weight at fledging, 1220–1560 g (Young 1963a). BILL, TARSUS, WING, TAIL: See Table 4.

Parental care, Role of sexes Two chicks at first brooded in nest, then separately in nearby rocks at 4 days old (Procter 1975). Brooding stops when chicks too large, at c. 14 days old and 405 g (Spellerberg 1969). After brooding, females do 48% foraging (Pietz 1987). Defend nest by swooping at intruders, occasionally striking with feet; do not attack communally, only pair owning territory dive at intruders (Eklund 1961). Chicks fed by parents till they leave colony; stay in territory till fledging, though territory boundary may change at fledging (Spellerberg 1971a). When chicks <5–6 days old, male brings food, female solicits, male regurgitates and female picks it up and feeds chicks; older chicks beg for food from adults (Spellerberg 1971a). At Palmer Stn, both parents feed chick about equally (Pietz 1984); when adults feed at sea, chicks fed whenever adult returns (P. Pietz). From observations of six pairs over two 7-h periods from midday and midnight during early growth: both sexes feed young, but not alternating regularly; feeding continued throughout 24-h period; males supplied food at 19 feedings and females at 14. Chicks <1 week old fed most regularly. Fed by regurgitation; chicks 10–15 days old fed meals of 5–65 g, mostly 20–40 g; most feedings occurred between 16:00 and 24:00 (Young 1963a). Up to 15 days old, adults generally hold food for chicks; older chicks catch food as it is being regurgitated (Spellerberg 1971a). In chicks weighing 250–300 g, weight loss between feedings c. 2–3 g/h; chicks weighing 500 g, c. 4–5 g/h; chicks weighing 1200–1400 g, c. 10–15 g/h (Young 1963a). Two chicks in brood often fed and brooded separately within territory to avoid quarrelling between siblings, older chick in nest and younger nearby (Young 1963a; Spellerberg 1971a). Displaced and stray young occasionally fed by other adults from neighbouring territories; one pair, still incubating eggs, accepted a displaced chick then neglected their eggs for progressively longer periods, finally eating them 7 days after accepting chick and 22 days after eggs laid; a chick adopted by another pair displaced original chicks (Young 1963a).

Fledging to maturity FLEDGING PERIOD: Fly at c. 50 days, though some do not leave ground till 60 days old. Size and siting of territory important factor influencing age at first flight: chicks from hillside territories seemed to fly at earlier age than those from flat beach; chicks from larger territories flew earlier than those from congested areas; and chicks on large territories with gentle ridges flew earlier than those in small territories or in rugged areas (Young 1963a; Reid 1966). Mean age at first flight: 53.5 days (49–59); at Larsemann Hills, 53.2 days (1.0; 52–55; 6) (Wang & Norman 1993b). Young still fed by parents after fledging (Young 1963b; Reid 1966). Age of first breeding: median age of first breeding 6–7 years for females, 8–9 years for males; a few females laid eggs when 4 years old; 72% birds banded as chicks breeding by 10 years old (Ainley *et al.* 1990); 5 years for one banded bird (Eklund 1961); said not to breed successfully till 5 or 6 years old (McGarry 1988).

Success On S. Shetland Is: from 75 pairs and 144 eggs, 125 (86.8%) hatched, 77 (53.5%) fledged, equalling 1.67 chicks hatched per pair and 1.03 fledged per pair. On Windmill Is: for 72 eggs, 44 (38.9%) hatched, 34 (47.2%) survived to late Jan. (c. 1 month old). On Signy I.: from 12 clutches (assumed to equal 24 eggs), 21 (87.5%) hatched, 19 (79.2%) fledged. On Ross I.: for eight consecutive seasons, 879 pairs fledged 295 young, equalling 0.34 young per pair; annual variation, 0.12 to 0.60 (Wood 1971). Over five seasons (1965–66 to 1969–70), in 774 territories, 1267 eggs laid, 346 hatched (27.3%) and 165 chicks fledged (13.0%; ranging from 0% in 1966–67 to 23.4% in 1968–69) (Young 1994). From 94 eggs, 78 (83%) hatched; eggs lost through chilling, desertion, broken by neighbouring pair, or failed to hatch after female killed;

Table 4

Location	H	5	10–11	20–21	30–35	40–41	48–50
BILL							
Signy I.[1]	15.5	22[2]	27	35	42	44.5	50
C. Hallett[3]	17.2 (17–17.5; 3)[4]	18.8 (18.0–19.6; 2)	23.8 (23.5–24.0; 2)	35.6 (34.4–36.8; 5)	43.3 (n=1)	45.7 (n=1)	48.5 (n=1)
TARSUS							
Signy I.[1]	22	32	43	54	66.5	67	67
S. Shetland Is	–	34	43	57	64.5	–	–
C. Hallett[3]	21.7 (21.0–22.0; 3)[4]	26.5 (26.0–27.0; 2)	35.5 (34.0–37.0; 2)	55.2 (53.0–58.0; 5)	61 (n=1)	61.5 (n=1)	63.8 (n=1)
WING							
S. Shetland Is[5]	–	–	–	118	210	283	–
C. Hallett[3]	–	70 (n=2)	110 (n=2)	262 (n=5)	425 (n=5)	–	–
TAIL							
S. Shetland Is[5]	–	–	–	18	64	98	–

(1) Estimated from growth curve in Hemmings (1984); (2) At 4 days old; (3) From Reid (1966); (4) At 1 day old, not at hatching; (5) Estimated from growth curve in Peter *et al.* (1990).

for 67 pairs assumed to have laid 134 eggs, 108 (80.6%) hatched, 31 (23.1%) fledged (Young 1963a). Hatching success per colony (from number of eggs laid) 73.3–92.9%; fledging success per colony, 0–41.7% (Young 1963a). For three consecutive seasons, hatching success, 58.3–81.1%; fledging success, 28.3–53.7% (Spellerberg 1971c). At Larsemann Hills: for 13 pairs assumed to have laid 26 eggs, 19 (73%) hatched, seven (26.9%) fledged (Wang & Norman 1993b). At C. Hallett: for three seasons, 472 pairs fledged 204 young, or 0.43 young per pair (Wood 1971). Breeding success higher in older birds and established pairs; on Ross I.: success of established pairs, 20% (n=266); new pairs, 6% (n=36) (Wood 1971); estimated breeding success in birds aged 4–5, 6, 7, 8 and 9 years was 0, 0.04, 0.11, 0.18 and 0.34 chicks per breeding pair respectively (Ainley *et al.* 1990). Higher survival of chicks in closely settled, sheltered areas (Young 1963a). Higher success in pairs that breed earlier rather than later (Trillmich 1978). Survival of chicks and overall breeding success higher in pairs with feeding territories than those without; abundant food supply in a feeding territory allows each parent to care for one chick nearly continuously, thus keeping chicks separate and avoiding combat (Trillmich 1978). For 108 young, 31 (28.7%) fledged, ten (9.3%) died on nest, six (5.6%) frozen, four (3.7%) killed by Skuas and 57 (52.8%) lost without record (Young 1963a). Second chick in nest rarely fledges; older chick often provokes quarrels within 1–2 days of second chick hatching, usually resulting in second chick being driven from area of nest; second chicks displaced after average 3.8 days (Young 1963a). Survival of second chick influenced by: sibling rivalry, starvation, exposure and predation (Young 1963a; Spellerberg 1971c; Procter 1975). At Larsemann Hills, only one of 13 pairs fledged both chicks (Wang & Norman 1993b). For 16 pairs on Ross I., 10 first chicks fledged, but only one second chick; second chicks survived 7.0 days (0.5–22; 15); no second chick survived beyond first (Young 1963a). Second chicks live longer if weight similar to that of first chick; Young (1963a) found that three of longest-lived second chicks (13, 15 and 22 days old) were only 10–15 g lighter than first chick at hatching; difference in weight >35 g generally led to loss of second chick within a few days. For successful (both fledged) and unsuccessful two-chick broods, respectively: mean hatching interval, 40.9 and 53.0 h; difference in weight at hatching, 6.7 and 11.4 g; difference in weight after 48 h, 9.2 and 49.6 g (Spellerberg 1971c). Stray chicks occasionally killed by adults, though much of this mortality is attributable to only a few birds in colony; adult Skuas take chicks from territories below their own, launching attacks when chick and parent well separated, advantage of downward flight carrying them easily onto victim's territory before residents have a chance to defend themselves or chicks (Young 1963a). Of 40 nests on Windmill Is: 14 had one or both eggs or young taken by Skua (Eklund 1961). Chicks dyed red or purple had significantly lower survival rate (six of 12) than natural slate-grey coloured young (28 of 32) (Eklund 1961). At Palmer Stn, heavy sea-ice in one season resulted in no breeding because birds had to fly too far out to sea to forage (Parmelee *et al.* 1978). Second chick once observed killing first chick then being fed bits of it by adults, then all three ate corpse (Reid 1966). Two chicks in a brood killed by a Subantarctic Skua (Hemmings 1984). Success of hybrid pairs at S. Shetland Is, 1.21 young fledged per nest (Jablonski 1986).

PLUMAGES Prepared by D.J. James. Begin pre-juvenile moult by Day 10. Fledge in monomorphic juvenile plumage, late Feb. to early Mar., at *c.* 60 days old (Burton 1968; Hull *et al.* 1994). Details of post-juvenile moult not known. Adults have three plumage morphs: pale and intermediate, which intergrade, and a discrete dark morph. All plumages (including juveniles and immatures) lack rufous or red tints. Adults undergo complete post-breeding moult in winter and spring; little evidence of partial pre-breeding moults or alternating non-breeding and breeding plumages. Wear and fading may produce significant seasonal change in appearance. First- and possibly second-year birds differ slightly from older birds in plumage and timing of moults but details not known (see Ageing). Adult plumage attained by at least third year (Spellerberg 1970); a banded bird 36 months old indistinguishable from adult intermediate morph (NMNZ). Minimum age at first breeding, 4–6 years (Spellerberg 1971c; Furness 1987). Sexes similar but within pairs males said to be slightly darker (see Sexing). No subspecies. Some hybridization with Subantarctic Skua (see Subantarctic Skua: Geographical Variation, and Introduction to family). Following description based mainly on specimens from Ross Sea and Aust. Antarct. Territory and not fully representative.

Adult (Definitive basic and, possibly, alternate). PALE MORPH: Strong contrast between pale head and underparts, and dark upperparts, wings and tail. **Head and neck** Head, pale to light grey-brown (119D–119C). Forehead and band round base of bill, dull-white, sometimes with pale-yellow wash. Some have cream (92) or off-white fringes to feathers of head, giving slightly scaly appearance. Darker birds tend to have more uniform grey-brown (91) to light grey-brown (27) forehead, crown, chin and throat, and appear slightly hooded. On some, ear-coverts, grey-brown (c91) forming dark patch that contrasts with rest of head. Nape and hindneck usually paler than crown and face, pale grey-brown (119D) to almost white, with fine pale-yellow to straw-yellow (56) shaft-streaks and tips to feathers, which are prominent throughout year. More yellow on nape than in Subantarctic Skua but it is often less conspicuous on pale ground; streaking occurs in broad band extending onto rear and side of neck and, on paler birds, faintly onto ear-coverts. Feathers of hindneck often have irregular off-white tips, giving slightly mottled appearance. Chin, throat and foreneck, pale grey-brown (119D) to light brown (25), sometimes with yellowish-grey shaft-streaks; inter-ramal area can be white. Head can bleach to off-white by end of summer. **Upperparts** Dark brown (219) to grey-brown (28), grading across 2–3 rows of feathers of mantle to paler neck; a few to most feathers of mantle, scapulars and back have fine off-white shaft-streaks. On some, especially pale birds, tips to feathers of mantle and anterior scapulars untidily mottled paler, markings usually disappearing quickly towards rear, though in some, rear scapulars and rump heavily marked. Pale markings fade slightly more quickly than dark parts of feathers and become more conspicuous with wear; in extreme cases, anterior mantle appears mostly off-white, with only narrow dark bases to feathers. Uppertail-coverts usually uniform, though some pale birds have faint light-grey (119C) mottling at tips of feathers. **Underparts** Light grey-brown (119D–119C) without rich tones, more or less concolorous with head. Sometimes uniform but often with narrow to broad pale-yellow (54) (soon fading to off-white or cream [92]) tips to breast and sides or whole of underparts, underparts appearing untidily scaled; in palest birds, tips so broad that little light grey-brown can be seen. Undertail-coverts generally darker, grey-brown (91) to dark grey-brown (129). **Tail** Dark brown (219) above and dark grey-brown (c129) below; small white bases concealed beneath coverts; shafts, cream (92) basally, grading to dark brown (219A) distally. **Upperwing** Coverts, dark brown (219), generally more uniform than scapulars, but can show fine off-white shaft-streaks; greater primary coverts sometimes have very narrow white tips. Remiges, black-brown (119) fading to dark brown (219) with wear. Outer five (sometimes six) primaries have bold white bases producing characteristic wing-flash; white base of p10 concealed beneath primary coverts on outer web and exposed 45–65 mm beyond coverts on inner web; of p9–p7, exposed 20–45 mm on outer web and 50–65 on inner web; of p6, 5–25 and 10–35; of p5, 5–15 on both webs. Inner primaries and secondaries have concealed white bases that are visible during moult of greater coverts. Shafts of outer primaries, cream (92) to straw-yellow (56). Shafts of secondaries and tertials, cream (92) at base, grading to dark brown (219A) at tip. **Underwing** Mostly dark with prominent white flash, *c*. 60 mm (30–80) wide at base of outer primaries. Lesser and median coverts and subhumerals, dark brown (219). Greater coverts and remiges, dark brown (119A), only slightly paler than wing-lining but more reflective, so that contrast varies with light. INTERMEDIATE MORPH: Varies much and continuous with pale morph; recognized mostly for convenience. Upperparts, tail, upperwing and underwing as pale morph. **Head and neck** Generally darker, browner and less uniform than pale morph; often with much light tawny-brown (c223D); typically richer in colour than pale morph, but still without red tones. Ground-colour of nape, paler than rest of head, forming pale nuchal collar. Head often darker than neck and underparts, appearing distinctly hooded. Straw-yellow (56) shaft-streaks on nape, sides and rear of neck to varying extent, as in other morphs. **Underparts** Light grey-brown (119C, 27) to light tawny-brown (c223D), slightly darker and richer than pale morph. Pale yellow or white tips to feathers tend to be narrower and fewer, restricted to breast and anterior flanks, not dominating ground-colour as in pale morph. DARK MORPH: Few specimens examined; supplemented with photos (Gantlett & Harrap 1992; Pringle 1987; BBC 1994). Uniform dark brown, showing little contrast between head and underparts and wings and upperparts. Darker than juvenile. Very similar to darker Subantarctic Skuas. Tail and upperwing as pale morph. **Head and neck** Head rather uniform dark brown (121); ear-coverts sometimes slightly paler than rest of head, but do not usually give impression of pale cheek or dark cap. Some have narrow pale grey-brown (119D) band over base of upper mandible. Nape and rear and sides of neck usually have profuse fine straw-yellow (56) shaft-streaks, which sometimes extend, though less densely, onto foreneck. When well developed, streaking encircles neck and contrasts with plain dark face. Ground-colour of nape usually not paler than rest of head. **Upperparts** Mantle, back, scapulars and rump, dark brown (219), similar to pale morph. Some birds have inconspicuous lighter-brown (c27) shaft-streaks and mottled tips to scattered feathers anteriorly; these not so developed as in some lighter birds and apparently rarely detract from uniform appearance (cf. adult Subantarctic Skua). Mottled or untidy appearance probably increased with wear. **Underparts** Dark grey-brown (91, 28–129), contrasting only slightly with darker wings. Most are uniform but some have yellowish (c56) to yellow-brown (c123C) tinge at tips of feathers of breast, sides and flanks, which imparts irregular scaled appearance. **Underwing** As pale morph; lesser and median coverts and subhumerals slightly darker than underbody.

Downy young Uniform off-white to blue-grey or slate-grey, often with slight brown tinge; sometimes pale grey-brown (119D) (Wilson 1907; Falla 1937; Eklund 1961; Murphy; skins: AIM, NMNZ; photos: Pringle 1987; unpubl.: S. Ward). At hatching, dark bluish-grey (blue a result of colour of skin), drying to pale, often silvery, grey; one was pale fawn or buff in some areas (Reid 1966). Murphy suggested increasing brownness of down through first weeks caused by absorption of oils from subcutaneous tissues.

Juvenile Many incorrect statements in published literature. No morphs known. Belief that juveniles have comparable morphs to adults (e.g. Veit 1978; Harrison 1983; van den Berg 1987; Lewington *et al.* 1991) has not been substantiated and is apparently wrong. Six specimens (NMNZ, TMAG) and photos of four birds (T. Howard; D.J. James) from Aust. Antarct. Terr., and a beachcast skin from NZ, Mar. (NMNZ; Fleming 1953) all fresh and all uniformly and distinctly cold-grey on head and underbody, darker than adult intermediate morph and paler than adult dark morph; upperparts, dark brown with neat grey fringes (see also Wilson 1907; Kuroda 1962; Reid 1966; Devillers 1977; Balch 1981). **Head and neck** Uniform cold brown-grey (grey 91) to light brown-grey (grey 119c) without red, yellow or tawny hues; described in Kuroda (1962) as 'warm dove-grey with a faint suggestion of brownish hue only apparent in certain lights'. No pale nape (Wilson 1907; Kuroda 1962; Reid 1966; Devillers 1977; skins, photos). At least some have narrow pale band over base of bill, but less developed than in adults. Photos of two birds show faintly darker crescent in recess under and in front of eye, and very inconspicuous paler grey eye-ring. Reports of so-called juveniles appearing hooded are unsubstantiated. Wear probably produces significant fading but extent not known. Devillers (1977) and Balch (1981) said that head and underparts vary from light to medium grey, but full range of variation and extent of individual variation and fading not known. **Upperparts** Distinctly darker than head and underparts. Mantle, back, scapulars and uppertail-coverts, dark brown (219) with slight gloss when fresh; fringes of feathers lack gloss and are less pigmented, appearing slightly duller or paler and imparting neatly scaled appearance; width of fringes varies individually and reduced by wear, but may contrast more when worn. Lack pale shaft-streaks and untidy whitish fringes of some adults. **Underparts** Uniform cold grey, concolorous with head and neck. Sides of breast scaled by dull fringes like upperparts, though less distinctly and tidily. **Tail** Rectrices, dark brown (219) with narrow, concealed white bases. Shafts, cream (92). **Upperwing** Coverts and tertials like upperparts except greater coverts lack dull fringes. Primaries, black-brown (119) on outer webs and dark brown (219) on inner webs; similar to adult but with slightly smaller white bases on average: white base of p10 concealed beneath primary coverts on outer web and exposed 30–50 mm beyond coverts on inner web; of p9–p7, exposed 10–40 mm on outer web and 20–65 on inner web; of p6, 0–25 and 5–40; of p5, 0 and 0–15; none visible p4–p1. Shafts of outer primaries, straw-yellow (56). Secondaries, dark brown (219) with small concealed white bases on both webs. **Underwing** Median and lesser coverts, dark brown (219). Greater coverts, dark brown (119A), slightly duller than median coverts. Subhumerals, dark brown (121), lacking gloss of upperparts. Remiges, dark brown (219A) with cream (92) shafts. White bases of primaries form narrower patch on average than in adult: on p10, 40–60 mm of white exposed beyond greater coverts; on p9, 50–75; on p8, 50–75; on p7, 50–60; on p6 40–50; on p5, 30–40.

BARE PARTS From descriptions in Reid (1966), photos (Pringle 1987; Gantlett & Harrap 1992; unpubl.: T. Howard; D.J. James; S. Ward) and label data (AIM, MV, NMNZ). **Adult** Bill, dull black to grey-black (92). Mouth, pale pink to white. Iris, dark brown to black. Legs, dull black to grey-black (92). **Downy young** Bill, dark grey (c82) or dark blue-grey, darkening with age; pinkish grey at gape and base of lower mandible; small white egg-tooth usually distinct for 5–7 days, then gradually disappears but can persist up to 12 days; bill often darker, black, surrounding egg-tooth. Iris, brown; pupil, blue. Narrow orbital ring, light grey (85), inconspicuous. Legs, light blue-grey to purplish grey, with pink tinges between scales; turn medium to dark blue-grey over first few weeks. Webs, fawn-grey turning dark grey. Claws, dark grey (82). **Juvenile** Bill, mostly black or grey-black; usually have blue-grey patch on lower mandible (excluding tomium) from near base to about half-way along, giving bicoloured appearance; sometimes patch absent or inconspicuous (Gantlett & Harrap 1992; skins). Mouth, cream (Fleming 1953). Iris, black. Narrow orbital ring, light grey (85), inconspicuous. Legs, grey-black (c82) mottled pale grey (86); can have blue-grey patches on tarsus or tibia not usually persisting after Apr. (Wilson 1907; Fleming 1953; Murphy). In older juveniles, toes and webs, dull black.

MOULTS Undertaken at sea where few specimens and sight records provide a sketchy picture. No good evidence of pre-breeding (pre-alternate) moults. **Post-breeding** (Pre-basic). Undertaken at sea during austral winter. Complete; primaries outwards. The following list of moult records in chronological order gives where possible date, location, feather-tracts moulting, primary-moult formula (PMF), and source: 14 Feb., Balleny Is, light moult of nape, PMF 2^2O^8 (NMNZ); 14 Feb., Balleny Is, body, N^94^1 (NMNZ); 25 May, New Jersey, *c.* $N^22^3O^5$ (photo in Gantlett & Harrap 1992); 30 May, New Jersey, *c.* 1^2O^8 (photo in Gantlett & Harrap 1992); May, Japan, breast, flanks, mantle, side of head moulting, secondaries new; scapulars, wing-coverts, tail, old; inner primaries growing (three specimens; Kuroda 1962); 31 May, Japan, nearly finished moult except for scattered feathers from neck to scapulars and wing-coverts (Kuroda 1962); 26 June, British Columbia, heavy body-moult, $4^13^12^2O^6$ (AM); July, Japan, moulting outer three primaries; July, Greenland, heavy moult on wings and tail, $N^33^12^11^1O^4$ (Salomonsen 1976); early Aug., California, almost completed moult (Devillers 1977); Aug., Washington State USA, *c.* 3^3O^7 (photo in van den Berg 1987); Aug., Newfoundland, sides and breast moulting; tail nearly complete; scapulars and upperwing, mostly new (Jensen 1982); Sept., w. Europe, moulting (Bourne 1989); Oct., Sydney, wing-coverts, $N^33^3O^4$ (photo in Pringle 1987: 461). Veit (1978) reported birds moulting wings in June and July in Massachusetts, USA. A captive in Japan moulted in Aug. and Sept. (Kuroda 1962). About 70 specimens from Antarctica (AM, ANWC, CM, MV, NMNZ) show no moult except for light moult of breast in a 5-year-old in Jan. and a breeding bird in Feb. The preceding suggest a rapid moult undertaken in wintering areas between migrations, with timing of onset apparently varying, though uncertain if variation individual or related to age. Rate of growth of primaries (3–4 at a time) is faster than in most other Stercorariinae and Larinae (Salomonsen 1976), and moult probably completed in 2 months. Some body-moult may begin on breeding grounds, but unusual (the birds from Balleny Is moulting in Feb. had immature gonads [NMNZ] but were indistinguishable from adults on plumage). The foregoing does not include birds observed not moulting, and more systematic data needed. **Pre-juvenile** Sheaths of primaries first emerge on Day 9 or 10; most rapid period of growth of primaries begins *c.* Day 17 (Reid 1966). **Post-juvenile** (First pre-basic). Details unknown. A juvenile ashore alive, Waikanae, NZ, 29 Mar. 1953 was quite fresh with a single breast-feather in sheath (Fleming 1953).

MEASUREMENTS (1–3) Antarctica, adult, skins (AIM, AM, CM, MV, NMNZ): (1) Ross Sea; (2) Terre Adélie; (3) near Prydz Bay.

		MALES	FEMALES	
WING	(1)	400.0 (6.4; 391–415; 14)	403.1 (6.9; 390–413; 15)	ns
	(2)	390.8 (8.1; 383–403; 5)	397.4 (11.6; 385–413; 5)	ns
	(3)	396, 400	399.0 (11.6; 377–410; 7)	
TAIL	(1)	150.3 (6.4; 142–163; 13)	148.9 (5.9; 143–162; 12)	ns
	(2)	147.8 (3.6; 145–143; 4)	148.5 (3.0; 145–151; 4)	ns
	(3)	148, 153	144.7 (11.1; 136–165; 6)	
BILL	(1)	49.1 (1.7; 45.7–52.0; 15)	48.7 (2.0; 44.0–51.5; 16)	ns
	(2)	47.1 (2.1; 44.4–49.2; 4)	51.0 (1.0; 49.3–52.0; 5)	*
	(3)	46.2, 51.3	50.3 (1.7; 47.8–52.5; 7)	
TARSUS	(1)	63.5 (3.2; 56.1–68.0; 14)	64.0 (2.5; 57.1–67.5; 16)	ns
	(2)	62.5 (1.8; 61.0–65.0; 5)	62.2 (2.0; 60.7–65.7; 5)	ns
	(3)	60.8, 66.9	64.2 (2.4; 61.7–67.4; 7)	
TOE	(1)	53.8 (2.5; 50.0–57.9; 15)	56.1 (1.6; 52.9–59.6; 16)	**
	(2)	54.1 (1.9; 52.2–56.5; 4)	57.1 (1.0; 55.6–58.1; 5)	*
	(3)	52.8, 58.6	56.7 (1.2; 54.4–58.2; 6)	

(4) Ross I., Ross Sea, fresh specimens (Spellerberg 1970).

		MALES	FEMALES	
WING	(4)	410 (390–420; 21)	415 (400–430; 24)	*
BILL	(4)	49.4 (48.1–51.3; 21)	50.9 (47.0–53.6; 240)	**
TARSUS	(4)	62.4 (58.6–68.0; 21)	64.8 (58.0–76.0; 24)	**

(5) Comparison of live unsexed breeding birds from Ross I., Ross Sea (Spellerberg 1970) and King George I., S. Shetland Is (Peter *et al.* 1990).

		Ross I.	King George I.
WING	(5)	405 (11; 285)	402 (14; 340–436; 77)
BILL	(5)	49.3 (2.3; 285)	47.3 (1.9; 41.5–52.7; 77)
TARSUS	(5)	63.1 (4.2; 285)	63.5 (2.1; 53.7–69.8; 77)

No significant differences found between samples (1), (2) and (3); differences between Ross and King George Is, though not significant, seem negligible; appears to be no substantial geographical variation in measurements. No comparative measurements for different morphs available. Females slightly larger, but sexual dimorphism not very strong; mid-toe appears to differ most. Samples are likely to include wrongly sexed birds. Additional measurements in Devillers (1977), Falla (1937), Friedmann (1945), Jouventin & Guillotin (1979), le Morvan *et al.* (1967), Lowe & Kinnear (1930) and Murphy. Data on growth of chicks in Breeding: Growth.

WEIGHTS (1) Ross Sea and Aust. Antarct. Terr., adults, Dec.–Feb., museum labels (MV, NMNZ). (2) Ross I., Ross Sea, fresh specimens (Spellerberg 1970). (3) Ross Sea, live birds and fresh specimens, Dec. and Jan. (after laying) (Ainley *et al.* 1985).

	MALES	FEMALES	
(1)	1247 (145; 905–1502; 16)	1350 (161; 1003–1587; 20)	*
(2)	1228 (899–1392; 21)	1366 (9660–1619; 24)	
(3)	1277 (95; 1120–1440; 26)	1421 (75; 1280–1550; 23)	**

Overlap of ranges between sexes in sample (3), 37% (Ainley *et al.* 1985).

(4) Comparison of live unsexed breeding birds from Ross I., Ross Sea (Spellerberg 1970), King George I., South Shetland Is (Peter *et al.* 1990) and Palmer Stn (P. Pietz).

	Ross I.	King George I.	Palmer Stn
(4)	1263 (128; 285)	1161 (114; 950–1600; 77)	1155 (n=89)

Birds from S. Shetland Is and Antarctic Pen. apparently weigh less than those from Antarctic continent (Peter *et al.* 1990). Data on growth of chicks in Breeding (Growth).

STRUCTURE Wing, long and pointed; broader and more rounded than in jaegers *Stercorarius*. Eleven primaries; p10 longest; p9 2–9 mm shorter, p8 16–30, p7 35–52, p6 56–77, p5 80–105, p4 106–129, p3 128–154, p2 154–174, p1 173–190; p11 minute. Eighteen to 20 secondaries, including four tertials; tips of longest tertials fall between p5 and p7 on folded wing. Tail, fairly short (34–41% of lengh of wing), slightly wedge-shaped to rounded (t2 3–10 mm longer than t6); central rectrices project less on average than in Subantarctic Skua (t1 6–18 mm longer than t2) but often flush with t2; 12 rectrices, broad, rounded at tips. Bill, very similar to that of Subantarctic Skua but slightly shorter and not so deep; tip not quite so bulbous and gonydeal angle not so steep; juveniles have slightly smoother cere than adults. Depth of bill at gonys: 17.1 mm (0.66; 16.1–18.3; 20), 17.6 mm (16–18; 34) (Neilson 1983), 17.45 mm (16.2–18.8; 84) (P. Pietz). Tibia, mostly feathered, bare distally. Tarsus, shortest of genus, laterally flattened; heavy single column of scutes on front of tarsus, small reticulate scales elsewhere. Toes, shortest of genus; outer 92–94% of middle, inner 59–65%, hind 10–16%, raised. Full webbing between inner, middle and outer toes. Claws like those of Subantarctic Skua.

AGEING JUVENILES: Distinguished, with care, by: combination of uniform grey head and underbody and neatly scaled upperparts; juvenile primaries more pointed than primaries of older birds (often visible in field); wing-flash generally narrower but this not diagnostic. Many juveniles have bicoloured bills but this is not a reliable means of ageing: some have uniformly dark bills (Gantlett & Harrap 1992; skins) and birds at sea in May with worn primaries and active wing-moult (at least in second year) had bicoloured bills (Gantlett & Harrap 1992). Use of colour of bill as character for ageing appears to have led to confusing reports of polymorphic juveniles (e.g. Veit 1978). IMMATURES: Difficult to distinguish. Transition from juvenile to adult plumage gradual and immatures tend to have more uniform upperparts than adults. However, no reliable criteria for ageing have been established. Lack of golden shaft-streaks said to indicate immature plumage (perhaps first and second year only) but not confirmed. Said to become paler with age, at least during first 3–5 years (Ainley *et al.* 1985), though probably not so for dark morphs. Some intermediate morphs possibly become pale morphs with age.

SEXING On Antarctic Pen., within pairs, males often darker and smaller than females. On Ross I., males darker in 26 of 35 pairs (Ainley *et al.* 1985); on Antarctic Pen., 11 of 12 pairs (Furness 1987).

RECOGNITION Measurements of tarsus and middle toe of Subantarctic and South Polar Skuas overlap only slightly: (1) Throughout range, adults, skins; (2) King George I., live (Peter *et al.* 1990).

		GREAT SKUA	SOUTH POLAR SKUA
TARSUS	(1)	62–92 (n=152)	56–68 (n=57)
	(2)	68–80 (n=89)	54–70 (n=77)
TOE	(1)	61.9–75.2 (n=53)	50.0–59.6 (n=56)

In sample (1), Subantarctic Skuas from Atlantic Ocean have shortest tarsi, and those from NZ, W to Indian Ocean have tarsi >68 mm. Discriminant function A = 0.22 x Bill F + 0.26 x Tarsus + 2.57 x Weight (kg) − 32.55 separated all South Polar and Subantarctic Skuas at King George I.: (Peter *et al.* 1990).

DOWNY YOUNG: Down, rich buff-brown or ginger-brown in Subantarctic; cold off-white to grey or grey-brown in South Polar. JUVENILE: Subantarctic generally has warm reddish tone to plumage and red-brown to rufous tips or fringes to upperparts, imparting reddish tone but not scaly pattern; South Polar have greyer tone and cold grey-brown upperparts with dull fringes giving distinctly scaly appearance. Differences obvious in skins but difficult to judge at sea. ADULTS: Pale and intermediate South Polar distinctive (though palest Subantarctic with slight contrast between paler underbody and dark wing-lining, and pale nape, somewhat similar to intermediate-morph South Polar). Dark morphs difficult to distinguish. Differ by: (1) some dark South Polar have diagnostic golden streaks round neck, highlighting plain dark face; (2) many Subantarctic have diagnostic, large asymmetrical white markings on webs of scattered feathers, especially on upperparts and head (which are often visible in photos but rarely so at sea); rarely, dark-morph South Polar have large pale shaft-streaks and tips to feathers of upperparts, but never asymmetrical white streaks; (3) distinct pale band at base of bill diagnostic of South Polar; present in all morphs but in probably <50% birds. OTHER CHARACTERS: A strongly bicoloured bill indicative of young (but not necessarily juvenile) South Polar. Pale nape overly emphasized as feature of South Polar and is prevalent in Subantarctic. Little information on identifying uniform dark birds, especially immatures; rufous tinges to plumage indicate Subantarctic, but these not always apparent. Hybrids have not been identified away from breeding grounds.

GEOGRAPHICAL VARIATION For discussion of relationships with other *Catharacta*, see text for Great (Subantarctic) Skua. No subspecies. Measurements do not appear to vary much between locations, though weights apparently slightly lower near Antarctic Pen. than on Antarctic continent (Peter *et al.* 1990; see Measurements, Weights).

Variation in colour of plumage generally considered to be polymorphism (Friedmann 1945; Kuroda 1962; Spellerberg 1970; Devillers 1977; Ainley *et al.* 1985), though some authors claim that variation is result of wear of plumage (dark when fresh, pale when worn) (Wilson 1907; Gain 1914; Bourne & Curtis 1994; Murphy); plumage of pale and intermediate morphs does fade but this not well described. The heterogeneous and clinal distribution of morphs has been described. Dark morphs predominate on Antarctic Pen. and S. Shetland Is; and at King George I. pale morph is rare non-breeder (Peter *et al.* 1990). At Ross I., estimated ratios of pale: intermediate: dark morphs in successive years 1:4.6:1 and 7.4:4.3:1 (Spellerberg 1970). On w. coast of Ross Sea, dark morphs extremely rare and do not breed (Kuroda 1962). In Aust. Antarct. Terr., dark morphs absent except for possible vagrants (skins; D.J. James).

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Great Skua *Catharacta skua* (page 388)
1 Adult on breeding grounds, austral summer; **2** Downy young; **3** Juvenile

South Polar Skua *Catharacta maccormicki* (page 412)
4 Adult pale morph, in worn plumage at breeding grounds, austral summer; **5** Adult dark morph, in fresh plumage at breeding grounds, austral summer; **6** Downy young; **7** Juvenile

Pomarine Jaeger *Stercorarius pomarinus* (page 438)
8 Adult female breeding, light morph; **9** Juvenile, intermediate phase

Arctic Jaeger *Stercorarius parasiticus* (page 448)
10 Adult breeding, light morph; **11** Juvenile, intermediate phase

Long-tailed Jaeger *Stercorarius longicaudus* (page 459)
12 Adult breeding, light morph; **13** Juvenile, intermediate phase

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Great Skua *Catharacta skua* (page 388)
1, 2 Adult, austral winter; **3, 4** Juvenile

South Polar Skua *Catharacta maccormicki* (page 412)
5, 6 Adult pale morph, in worn plumage at breeding grounds, austral summer; **7** Adult, intermediate morph, fresh plumage; **8** Adult, dark morph, in fresh plumage at breeding grounds, austral summer; **9** Adult, dark morph, in fresh plumage at breeding grounds, austral summer; **10, 11** Juvenile