

## 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.
Jacaniidae	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	pratinoles, 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, Procellariiformes, 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, Jacaniidae) and charadriids and allies (Chionididae, Burhinidae, Haematopodidae, Recurvirostridae, Ibidiorhynchidae, Charadriidae, Pluvianellidae, Dromadidae, Glareolidae, Stercorariidae, 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 charadriids (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 Jacaniidae. 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, Stercorariidae, 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).<sup>1</sup>

**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

<sup>1</sup> 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, Chionidae, 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

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| Great Skua <i>Catharacta skua</i><br>(page 388)  | Pomarine Jaeger<br><i>Stercorarius pomarinus</i> (page 438)          |
| 1 Adult on breeding grounds, austral summer; 2 Downy young; 3 Juvenile   | 8 Adult female breeding, light morph; 9 Juvenile, intermediate phase |
| South Polar Skua<br><i>Catharacta maccormicki</i><br>(page 412)  | Arctic Jaeger<br><i>Stercorarius parasiticus</i> (page 448)          |
| 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 | 10 Adult breeding, light morph; 11 Juvenile, intermediate phase      |
|  | Long-tailed Jaeger <i>Stercorarius longicaudus</i> (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 pterygiae 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 skua* Great Skua (Subantarctic Skua)

COLOUR PLATE FACING PAGES 385 &amp; 416

*Catharacta Skua* Brünnich, 1764, *Orn. Boreal.* 1764: 33 — The Faeroes and Iceland.

The generic name is a crude representation of the Greek *καταρράκτης* for a seabird mentioned by Aristotle and Aristophanes but never properly identified. The specific name is latinized from Højer's (1604) rendition *sku* of the Faeroese names *skúvur* or *skúir* for the Great Skua (from Old Norse *skúifr*).

**OTHER ENGLISH NAMES** Southern, Dark Southern, Brown and Subantarctic Skua; Falkland Skua; Tristan Skua; Sea-Hen, Skua-hen, Port Egmont Hen, Sea-Hawk; Northern Skua, The Skua, Bonxie (n. hemisphere); South Polar Skua (in error).

**POLYTYPIC** Nominate *skua* breeds n. hemisphere; subspecies *lonnbergi* (Mathews, 1912), circumpolar, breeding subantarctic islands and Antarctic Pen., and Chatham Is; subspecies *antarctica* (Lesson, 1831), breeds Falkland Is and Patagonia; subspecies *hamiltoni* (Devillers 1978) breeds Tristan Grp and Gough I., South Atlantic Ocean.

**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 64 cm; wingspan 147 cm; weight 1.5–2.2 kg. Large thickset gull-like seabird with rather broad pointed wings; short, slightly wedge-shaped tail, with central rectrices projecting slightly; and short heavy bill, strongly hooked at tip. Very similar in size and shape to South Polar Skua *Catharacta maccormicki* but appears slightly bigger, with heavier bill, when directly compared. Much bigger and bulkier than Pomarine Jaeger *Stercorarius pomarinus*, with broader wings. Larger, more thickset and powerful than Pacific *Larus pacificus* and Kelp *L. dominicanus* Gulls. Plumage of adult rather uniform, dark brown, with varying pale streaking and blotching on saddle and striking large white patches on outerwing, which flash as wings beat. Sexes alike, female slightly bigger when breeding pair seen together. Slight seasonal variation, mainly in prominence and extent of pale streaks on nape, hindneck and sides of neck. Juvenile separable when close. Hybrids (*C. maccormicki* x *C.s. lonnbergi*) occur Antarctic Pen. and in South Atlantic but not likely in A'sian waters, see Plumages.

**Description Adult** Darkest birds almost uniform, dark brown, with: Slightly to distinctly paler yellowish-brown nape, overlain with thin straw-yellow streaks (never forming distinct pale collar); on some, pale streaks continue onto ear-coverts and sides of neck and, sometimes, across foreneck. Some have small area of paler brown feathering at base of upper mandible. Typically have varying pale mottling on upperbody, most obviously on scapulars, appearing as pale saddle at distance; some very dark birds have few and indistinct pale markings; on others, sparse pale markings extend onto upper innerwing-coverts and on underbody, especially flanks. Above, remiges and rectrices slightly darker than rest of upperparts, with basal third of primaries and their shafts, white, forming clear-cut and conspicuous patches, visible at great distance. Below, remiges and greater coverts, glossy dark-grey, contrasting with dark brown rest of underwing (which contrasts little or not at all with body), and with striking clear-cut white crescent across bases of primaries as on upperwing, but slightly broader. Most birds slightly paler than above, differing by tawny-brown head and underbody, which contrasts with darker brown upperparts and underwing-coverts; tend to have more pale streaking on nape and sides of neck, and more pale streaking and blotching on upperparts and underbody; and typically show some contrast between dark crown and paler cheeks, producing slightly capped effect; pale

feathering at base of upper mandible also tends to be more prominent (though never matching that of South Polar Skua). Bill, dull black, though in bright light can sometimes appear to have pale base and dark tip. Legs and feet, dull black. **Juvenile** Like adult but darker and more uniform brown, with few or no pale markings on upperparts and no pale streaks on nape; often have slight rufous tinge to underbody, and some show some fine rufous spots and scaling to upperparts (especially scapulars) when plumage fresh; white patches in primaries often smaller, sometimes almost not visible on folded wing. Bill, black, with sides behind gonys, duller grey, giving subtle two-tone pattern. Legs and feet, black, sometimes with paler tinge.

**Similar species** All ages and morphs of South Polar Skua differ by smaller size and finer bill and tarsi when directly compared. palest birds might be confused with darkest adult light-morph **South Polar Skua**, which differs by: (1) distinctly paler brown head, neck and underbody, contrasting more with uniform and colder black rest of upperparts and underwing-coverts; and (2) diagnostic prominent pale nuchal collar contrasting with rest of head and upperparts. Main risk of confusion is with adult and immature dark-morph South Polar Skua (mainly on Antarctic Pen. and surrounding waters; unlikely to occur A'sian waters); these differ by: combination of more uniform blackish upperparts, with faint nuchal collar and colder dark greyish-brown head, neck and underbody, which still contrast with blackish upperparts and underwing-coverts; also, by often paler and more prominent patch at base of upper mandible. Juvenile Subantarctic Skua might also be confused with adult dark-morph South Polar Skua, but latter distinguished by combination of dark greyish-brown head, neck and underbody (never with rufous tinge); faint nuchal collar; and all-black bill and legs. Juvenile South Polar Skua separated from all ages of Subantarctic by distinctly pale to medium-grey head, neck and underbody contrasting with blackish rest of upperparts and underwing as on light-morph adult. Subantarctic Skua sometimes confused with adult dark-morph and darker immature and juvenile **Pomarine Jaeger**, which is: much smaller, with slimmer less barrel-shaped body, and less hunched appearance in flight; proportionately smaller head and narrower, more angular wings; slightly longer tail (with diagnostic central tail-streamers in second-year and adult birds, except when moulting); much finer and often markedly two-toned bill (especially in juvenile); less white in primaries, at least on upperwing, with obvious difference between large white patch

on underwing and small patch on upperwing (approached or matched only by some juvenile Subantarctic); and, in juveniles and immatures, usually obvious pale barring on rump, uppertail-coverts, axillaries and underwing-coverts (though barring may be very indistinct on some dark juveniles). Sometimes also confused with brown-plumaged juvenile and second-year **Pacific and Kelp Gulls** but these distinguished by lack of white patches in wing.

Widespread at sea in Southern Ocean, S to c. 60°S, dispersing N to about 30°S during austral winter; occasionally elsewhere in Antarctic waters. Pelagic but regularly range into shelf-break waters in n. part of range; sometimes seen over inshore waters, though rarely in bays and harbours. During breeding season, breed as solitary pairs and some non-breeding birds gather in Clubs; at other times, mainly solitary or in pairs, though occasionally in small groups round fishing trawlers. Often approach ships, though usually only circle for brief period before departing; occasionally follow for long periods, sometimes even perching on rigging or superstructure. Attend fishing trawlers for offal or to chase assembled seabirds. In light winds, flight leisurely but fast, direct and purposeful, with continual shallow wing-beats; sometimes fly high above water; in high winds, flight more active, with quicker, more powerful wing-beats accompanied by changes in angle of body and wing. Capable of great acceleration and agility in air when chasing other seabirds; will tackle seabirds much larger than itself, e.g. gannets or smaller albatrosses. At breeding grounds, formidable predator of small seabirds, otherwise piratical or scavenging as other skuas. Gait on land like that of large gull but heavier and more waddling on shorter legs. Look bulky when sitting on sea, appearing to float higher than jaegers. Normally silent at sea; at breeding grounds, utter variety of high-pitched squeals and screams.

**HABITAT** Breed mainly on subantarctic islands, from coasts to several kilometres inland; often on offshore islets or low peninsulas (Parmelee 1988). Generally nest among short tussock-grass (Bailey & Sorensen 1962; Warham 1967; Horning & Horning 1974; Jones & Skira 1979). On Campbell I., in tussock *Poa littorosa*, herbfields of *Bulbinella littorosa*, and clearings in *Dracophyllum* shrubland (G.A. Taylor). On Chatham Is, nest in grassy clearings, tussock-grassland, sedges, coastal swards, clearings in shrubland, and on rocks on headlands (G.A. Taylor); on South East I., in clearings on flats densely vegetated with tall grass, bracken and scattered clumps of New Zealand Flax *Phormium tenax*, or at edges of *Olearia* forests (Young 1978). On Marion I., some nest among lush vegetation round old nests of Wandering Albatrosses *Diomedea exulans*, which act as windbreaks (Rand 1954). Also nest among rocks or on ground covered with moss and lichen (Rand 1954; Warham 1969; Pietz 1985). Sometimes nest on beaches of shingle or boulders; rarely, on nearby cliffs (Westerskov 1960; Moors 1980; Skira 1984). On Macquarie I., nest in feldmark and subglacial herbfields (Jones & Skira 1979). On Antipodes Is, also recorded nesting on fern-covered flats (Moors 1980). On Auckland Is, recorded breeding in high altitude fellfields (Walker *et al.* 1991). One pair on Snares Is may have nested in dense *Olearia* forest (Horning & Horning 1974). Often breed near colonies of penguins, albatrosses or burrowing petrels, or near seal-beaches (Rand 1954; Moors 1980; Parmelee 1988; Weimerskirch *et al.* 1989; G.A. Taylor).

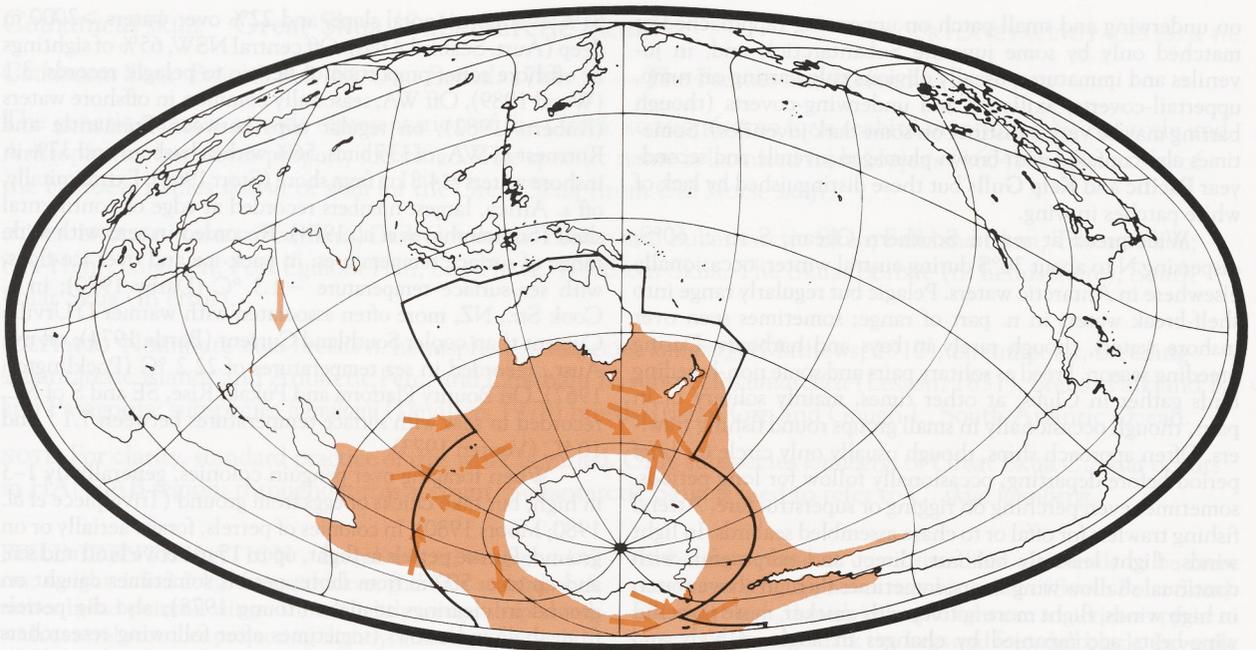
During non-breeding period, some stay in breeding areas; others occupy neritic or pelagic zones; less often inshore. Off se. Aust., in sample of 51 birds, 27% over continental shelf,

51% over continental slope, and 22% over waters >2000 m deep (Aust. Seabird Atlas). Off central NSW, 65% of sightings in offshore zone; proportion of neritic to pelagic records, 3:1 (Wood 1989). Off WA, seasonally common in offshore waters (Roberts 1982); on regular trips between Fremantle and Rottnest I., WA, of 135 birds, 56% within harbour and 37% in inshore waters  $\leq 4.8$  km from shore (Storr 1964). Extraliminally, off s. Africa, largest numbers recorded at edge of continental shelf (Summerhayes *et al.* 1974). Recorded in seas with wide range of surface temperatures: in pack-ice and over ice-floes, with sea-surface temperature  $-1.3$  °C (Darby 1970); in e. Cook Str., NZ, more often associated with warmer D'Urville Current than cooler Southland Current (Bartle 1974); off nw. Aust., recorded in sea temperatures of 22.2 °C (Pocklington 1967). On Bounty Platform and Pukaki Rise, SE and S of NZ, recorded in seas with surface temperatures between 7.1 ° and 10 °C (Vooren 1973).

When foraging over penguin colonies, generally fly 1–3 m high, but take chicks or eggs from ground (Trivelpiece *et al.* 1980; Moors 1980). In colonies of petrels, forage aerially and on ground. Pursue petrels in flight, up to 15 m above land and sea, and up to c. 500 m from shore; petrels sometimes caught on ground in clearings at night (Young 1978); also dig petrels from shallow burrows (sometimes after following researchers round colonies) (Rand 1954; Moors 1980; Sinclair 1980). Sometimes scavenge on beaches (Rand 1954; Moors 1980; Hemmings 1990a). Usually take prey back to small wetland, such as pool, seal-wallow or stream, to soak prey before eating it (Sinclair 1980; Adams 1982). Also take prey to regular feeding sites, including boggy areas, slopes or flat land, sometimes covered with tussock or herbs; sometimes at nests (Trivelpiece *et al.* 1980; Adams 1982; Cooper *et al.* 1986). One midden on Snares Is in *Olearia* forest (Horning & Horning 1974). Birds killed at sea are eaten in water (Sinclair 1980). When following ships, generally fly 10–15 m above water (Barton 1982; Wood 1989; Brandis *et al.* 1992), seizing morsels in air before they hit water; then land on surface of water well away from ship to eat (Barton 1982). Occasionally feed from surface or swim below surface to c. 25 cm (Milledge 1977; Sinclair 1980; Adams 1982; Barton 1982). Also observed feeding in farmland (Young 1978; Hemmings 1990a).

Recorded roosting and loafing on cliffs of rocky islets, on or near beaches, on mudflats, coastal sand-dunes, or adjacent grassy slopes (Spellerberg 1965; Darby 1970; Ainley *et al.* 1978; CSN 19 Suppl.); also on sandy beaches or rock platforms (G.A. Taylor). Will congregate to roost near water (Rand 1954); also recorded landing on water. Also seen roosting on jetty and on boat anchored in harbour (Learmonth 1954; Bedggood 1958). Bathe in brackish or fresh water (Westerskov 1960; Bailey & Sorensen 1962; Young 1976). Often observed in harbours. Seen to frequent coastal sewage outlet (Hindwood 1955).

**DISTRIBUTION AND POPULATION** Breeding distribution circumpolar in s. hemisphere, N to Chatham Is, and S to Terre Adélie; mostly on subantarctic islands. Outside breeding season, few stay on or near breeding islands, except in NZ region. Recorded at sea S to c. 60°S (Bailey & Sorensen 1962; Bretagnolle & Thomas 1990), though some occur farther S, to Scott I. (Darby 1970) and Antarctica, including Windmill Is, Wilkes Land (Orton 1963), Terre Adélie, where regular in very small numbers (Thomas & Bretagnolle 1988), and Ross Sea (Spellerberg 1971a; Ainley *et al.* 1978, 1984; Court & Davis 1990). In Indian Ocean, mainly S of 40°S, but regularly



recorded off s. Africa, between s. Angola and s. Mozambique; also recorded farther N, round Madagascar, Reunion and Seychelles, with vagrants off Kenya and Somalia (Weimerskirch *et al.* 1985; Urban *et al.* 1986; Indian Ocean Seabird Atlas). Single specimen, Kerala, India, Sept. 1933 (Ali & Ripley 1969); several, Sri Lankan waters (Devillers 1977; de Silva 1989). Claims from Arabian Sea and Straits of Malacca (Bruyns & Voous 1965; Bailey 1966) not verified (Indian Ocean Seabird Atlas). Specimens from Pacific coast of North America, originally identified as Subantarctic Skua, re-identified as South Polar Skua (Devillers 1977). Bird recovered Guadeloupe may have been misidentified (see Banding). Also occur off s. South America (Rogers 1980; Furness 1987). Regular visitor to A'asia.

**Aust.** Off e. Aust., recorded as far N as Sandy C., Qld, and in W, as far N as Geraldton. **Qld** Rare. Several, Moreton Bay, 20–21 Aug. 1921; Stradbroke I., June 1923; single, Sandy C., Fraser I., 19 Aug. 1925 (Alexander 1922, 1926; Alexander *et al.* 1923). Single, off Sandy C., 4 Sept. 1981 (Sutton 1990). **NSW** Widespread in w. Tasman Sea. Few records between Ballina and Coffs Harbour; more widespread at sea from Seal Rocks, S to Eden (NSW Bird Reps; Aust. Atlas; Aust. Seabird Atlas). **Vic.** Widespread e. Bass Str.; many records between C. Liptrap and w. Port Phillip Bay. Most records from w. coast, off Portland (Learmonth 1954; Vic. Bird Reps; Vic. Atlas; Aust. Seabird Atlas). **Tas.** Widespread in e. Bass Str. and in sw. Tasman Sea, off e. coast. Few w. Bass Str., King I., off nw. Tas. and rare central Bass Str. Occasionally off sw. coast. Widespread S of Tas. in Southern Ocean (White 1985; Tas. Bird Reps; Aust. Seabird Atlas). **SA** In SE, occasionally off Port Macdonnell and Robe; mostly from seas off Fleurieu Pen., W to Kangaroo I., and N to Gulf St Vincent and e. Spencer Gulf (MacGillivray 1927; Brook 1962; Baxter 1989; SA Bird Reps; Aust. Seabird Atlas). Occasional round s. and e. Eyre Pen. (Aust. Atlas), and possibly farther W into Great Aust. Bight. **WA** Recorded eight times at Eyre between 1984 and 1985 (Dymond 1988), and probably recorded elsewhere off coasts of Eucla Division (Storr 1987). Elsewhere off s. coast, recorded Arch. of the Recherche and Esperance; common Albany. Often recorded offshore and round harbours from C.

Naturaliste, N to islands in Jurien Bay (Serventy & Whittell 1976; Storr & Johnstone 1988; *West. Aust. Bird Notes*; HASB; Aust. Atlas). Recorded farther N, between Houtman Abrolhos and Dorre I. and Shark Bay; common offshore (Pocklington 1967; Serventy & Whittell 1976; Abbott 1979; Storr 1966, 1985; Roberts 1982; Aust. Atlas). Twice recorded Kimberley Division: single, C. Keraudren, 24 June 1974 (Storr 1984a); single, Bedout I., 28 May 1978 (Abbott 1979).

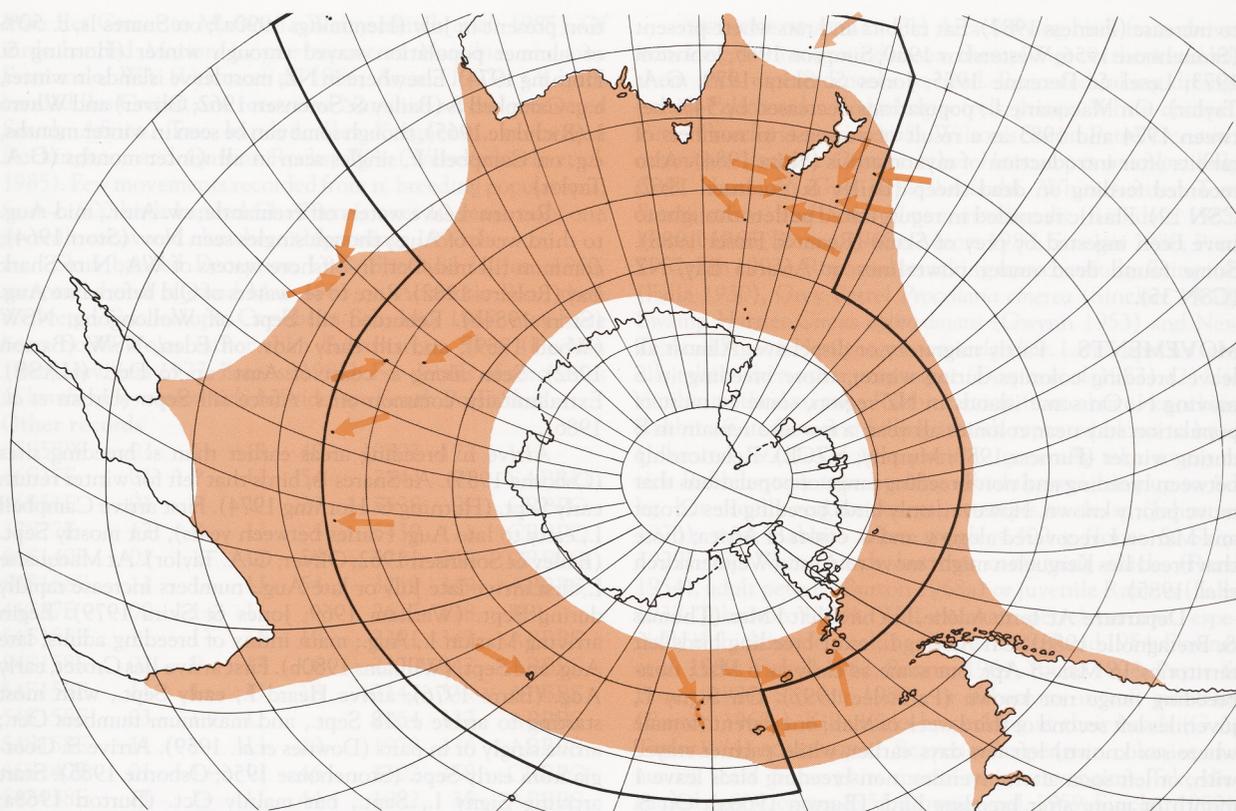
**NZ** Widespread in surrounding seas (Harrison 1983). Extreme n. record at 26°S, 176°E (Jenkins 1979). **NI** Scattered records in N from Te Pahi, Ninety Mile Beach, to Hauraki Gulf and Bay of Plenty; isolated records from Muriwai (Gisborne) and Wairoa, Hawkes Bay; recorded from Porangahau, through to Wairarapa and Wellington regions. Also recorded at Foxton Beach–Manawatu R. Estuary (CSN; NZ Atlas). **SI** Many records round Tasman Bay, Marlborough Sounds and adjacent Cook Str.; isolated records near Kaikoura. In Canterbury, mainly off coast between mouth of Waipara R. and L. Ellesmere, with a few records between St Andrews and Waitaki R. Widespread round coasts of Otago and Southland, from near Palmerston to Invercargill, with many records Foveaux Str.; also recorded Fiordland. Isolated records farther N on w. coast, round Jackson Bay, mouth of Arahura R. and Charleston (NZ Atlas; CSN). A few recorded at sea over Pukaki Rise, between Bounty and Auckland Is (Vooren 1973). Singles regularly seen on voyages from NZ to subantarctic islands, Oct.–Apr., e.g. from SI to Campbell and Auckland Is (G.A. Taylor).

**Norfolk I.** Said to be rare or casual visitor (Turner *et al.* 1968; de Ravin 1975), probably based on historical record in Iredale (1911).

**Breeding** Summarized in Table 1 (references at foot of table). Earlier information summarized by Watson *et al.* (1971).

May breed Balleny I. Extraliminally, breed Iles Amsterdam and St Paul.

**Population** Total population possibly 7000 pairs (Furness 1987). On Signy I., populations stable between 1959 and 1967 (Burton 1968a), but had nearly doubled by 1982–83 (Hemmings 1984). On Campbell Is, population appears to



have declined significantly probably because populations of penguins and seals have declined (G.A. Taylor). **SURVIVAL AND LONGEVITY:** At Palmer Stn, average years known to be alive: males  $4.4 \pm 1.3$  years, females  $8.4 \pm 5.3$  years; low figures for males a result of disproportionate loss of males during outbreak of avian cholera in one year. Mean estimated annual survival rate  $88\% \pm 18\%$ , though increases to  $95\% \pm 7\%$  if loss of birds in year of outbreak of avian cholera and one bird that was collected are excluded (Pietz & Parmelee 1994). Of 50 adults banded Palmer Stn, 30% known to have died and another 40% failed to return (Parmelee 1992). On Signy I., annual survival rate estimated at 91% (90–93%); estimated mean lifespan, 11 years (Burton 1968a).

**Table 1**

**NZ:** Breaksea Sound; Dusky Sound; Puysegur Pt, 1 nest; Solander I., 2+ pairs; Little Solander I.; Stewart I., 17 pairs; islets off Stewart I., including: Stage I., 1 pair; Codfish I., 1 pair; Whero I., 1 pair. Recorded breeding Muttonbird Is and probably still do.

**SNARES IS:** 83 territories; North-east I.: Broughton I.; Tahi Isl., 1 pair; Rua Isl., 1 pair.

**CHATHAM IS:** In 1994–95 season (E.C. Young): The Sisters, 1 pair; Forty-fours, 1 pair; Mangere I., 42 birds; Little Mangere, 15 birds; Pitt I., 2 pairs; South East I., 105 birds; The Pyramid, 1 pair; Star Keys, 21 birds. Also on Rabbit I., 1 territory; Murumurus, 4 territories; Castle I., 1–2 territories.

**ANTIPODES IS:** 50 pairs. Said to be common breeding bird on Antipodes I.

**AUCKLAND IS:** 100 pairs. Enderby I., 11 pairs, 1988; Rose I., 2 pairs; Disappointment I., many pairs; Adams I.

**CAMPBELL IS:** Campbell I., c. 100 pairs, 1984–86; also on

offshore islands, e.g. Dent, Jacquemart, and Monowai (G.A. Taylor).

**HEARD I.:** 100 pairs; also on McDonald I.

**MACQUARIE I.:** 550 pairs.

**S. SHETLAND IS:** 420 pairs, including King George, Nelson, Robert, Deception, and Penguin Is; Elephant I., 190 pairs.

**S. ORKNEY IS:** 300 pairs; Signy I., 143 pairs.

**S. GEORGIA:** c. 1000 pairs.

**S. SANDWICH IS:** 100 pairs.

**BOUVETØYA:** Possibly tens of pairs.

**PRINCE EDWARD IS:** 960 pairs; Marion I., 400 nests.

**ILES CROZET:** Ile de la Possession, 94 pairs; Ile de l'Est, 100s of pairs; Ile aux Cochons, 150–200 pairs; Ile des Pingouins, 10s of pairs; Ile des Apôtres, 10 pairs.

**ILES KERGUELEN:** 2000–4000 pairs.

**ANTARCTICA PEN.:** 150 pairs: Paulet I.; Seymour I.; Cockburn I.; Hope Bay; Melchior I. (possibly); Wienecke I.; Anvers I., 6–12 pairs; Argentine Is (Detaille, Stonington, Avian Is).

**TERRE ADÉLIE:** Pte Geologie Arch., 1 pair (unsuccessful) and hybrid pairs (with South Polar Skua).

**REFERENCES:** Guthrie-Smith 1914; Blackburn 1965, 1968; Richdale 1965; Horning & Horning 1974; Watt 1975; Best 1976; Jones & Skira 1979; Warham & Bell 1979; Jablonski 1980; Williams 1980a, 1984; Croxall *et al.* 1984; Hemmings 1984, 1990a, 1994; Jouventin *et al.* 1984; Miskelly 1984; Cooper *et al.* 1986; Furness 1987; Parmelee 1988; Thomas & Bretagnolle 1988; Weimerskirch *et al.* 1989; Walker *et al.* 1991; Woehler 1991; Freeman 1994; CSN; G.A. Taylor; E.C. Young.

Scavenge at scientific stations and human settlements (Johnston 1973; Furness 1987; Thomas & Bretagnolle 1988); increased availability of food at these sites allows some birds to winter (Hemmings 1990a) and, at some sites, local populations

to increase (Furness 1987). Eat rabbits and rats where present (Stonehouse 1956; Westerskov 1960; Simpson 1965; Johnston 1973; Lesel & Derenne 1975; Jones & Skira 1979; G.A. Taylor). On Macquarie I., populations decreased by 54% between 1974 and 1983 as a result of decrease in numbers of rabbits after introduction of myxomatosis (Skira 1984). Also recorded feeding on dead sheep (Bailey & Sorensen 1962; CSN 19). Plastic recorded in regurgitated pellets thought to have been ingested by prey of Skuas (Ryan & Fraser 1988). Some found dead under powerlines at Awarua Bay, NZ (CSN 35).

**MOVEMENTS** Partly migratory or dispersive. Almost all leave breeding colonies during winter, those breeding in S moving N. On some islands in NZ region, some or most of population stay near colonies all year; a few also remain in S during winter (Furness 1987; Murphy; NZCL). Relationship between breeding and non-breeding range of populations that move poorly known. However, only birds breeding Iles Crozet and Marion I. recovered along s. and w. coasts of Africa; those that breed Iles Kerguelen might move to Aust. (Weimerskirch *et al.* 1985).

**Departure** At Terre Adélie, last birds left 1 Mar. (Thomas & Bretagnolle 1988). On Anvers I., most breeding birds left territories 16 Mar.–8 Apr. but some as early as 6 Mar.; non-breeding range not known (Parmelee 1992). On Signy I., juveniles left second or third week of Mar.; one parent (female where sex known) left few days earlier, while partner stayed with, or left soon after, juveniles; non-breeding birds leave 1 month or more after breeding birds (Burton 1968a). On S. Georgia, young and most adults leave Apr.–May, though singles recorded till June; unsuccessful breeders leave before successful breeders (Matthews 1929; Stonehouse 1956; Prince & Payne 1979; Murphy). On Heard I., numbers decrease from Feb., with only a few remaining by third week of June (Downes *et al.* 1959). On Marion I., adults begin leaving Feb. with all, except wintering birds, gone by first week May (Williams 1980b). On Macquarie I. (1974), adults and fledgelings began leaving Feb.; fledgelings gone by last week Mar., adult numbers decreased during Apr., and few present early May; laggards recorded till first week June (Jones & Skira 1979). On Campbell I., some adults leave Feb.–Mar., most Apr.; all but a few left by end of May; birds breeding near colonies of penguins (which finish breeding Feb.) left earlier than those breeding near colonies of albatross (which finish breeding Apr.–May) (G.A. Taylor); leave from Apr., with last bird seen early June (Oliver). Leave Snares Is about May (Horning & Horning 1974).

Regular visitor to coastal waters of Aust. and NZ. E. Aust.: recorded off Wollongong, from Apr. (Wood 1989); off Eden, from May (Barton 1982); off se. Qld, from late Mar. (Storr 1984b). WA: common in offshore waters N to Shark Bay, from early Apr. (Roberts 1982); first seen off sw. Aust., end Apr., but numbers increase greatly in second week July (Storr 1964); rare visitor, Pilbara coast, May and June (see Storr 1984a).

**Non-breeding** Generally 30°–60°S (see Furness 1987), though some occur farther N in Indian Ocean (see Distribution). In se. Aust. waters, from about late Mar. to Oct., mainly late Apr. to Sept. (many are adults in moult) (D.W. Eades). A few remain in S during winter, e.g. on Iles Kerguelen (Murphy), Heard I. (Downes *et al.* 1959), Marion I. (Williams 1980b) and S. Georgia (Prince & Payne 1979). Much of n. breeding population resident through non-breeding period; on South East I., Chatham Is, at least 65% of total summer adult popula-

tion present in July (Hemmings 1990a); on Snares Is, c. 50% of summer population stayed through winter (Horning & Horning 1974). Elsewhere in NZ, most leave islands in winter, e.g. Campbell Is (Bailey & Sorensen 1962; Oliver) and Whero I. (Richdale 1965), though some can be seen in winter months, e.g. on Campbell I., singles seen in all winter months (G.A. Taylor).

**Return** Leave waters off Fremantle, sw. Aust., mid-Aug. to third week of Aug., though singles seen Nov. (Storr 1964); common till mid-Oct. in offshore waters of WA, N to Shark Bay (Roberts 1982). Rare to se. waters of Qld before late Aug. (Storr 1984b). Recorded till Sept. off Wollongong, NSW (Wood 1989), and till early Nov. off Eden, NSW (Barton 1982). Seen along s. coast of Aust. up to Dec. (HASB). Extralimitally, common off s. Africa till Sept. (Urban *et al.* 1986).

Arrive n. breeding areas earlier than s. breeding sites (Osborne 1985). At Snares Is, birds that left for winter return early Sept. (Horning & Horning 1974). First arrive Campbell I., early to late Aug. (varies between years), but mostly Sept. (Bailey & Sorensen 1962; Oliver; G.A. Taylor). At Macquarie I., first arrive late July or late Aug.; numbers increase rapidly during Sept. (Warham 1969; Jones & Skira 1979). Begin arriving Marion I., Aug.; main influx of breeding adults, late Aug. and Sept. (Williams 1980b). First arrive Iles Crozet, early Aug. (Barré 1976); arrive Heard I., early Sept., with most starting to arrive c. 18 Sept., and maximum numbers Oct.; arrive singly or in pairs (Downes *et al.* 1959). Arrive S. Georgia from early Sept. (Stonehouse 1956; Osborne 1985). Start arriving Signy I., Sept., but mainly Oct. (Burton 1968a; Hemmings 1984). Birds 1–4 years old, returning to breeding areas on Signy I. for first time, arrive Feb. (Burton 1968a). Arrive Pt Thomas, King George I., S. Shetland Is, mid- or late Oct. to early Nov. (Trivelpiece *et al.* 1980; Trivelpiece & Volkman 1982; Jablonski 1986). On Anvers I., average arrival date 7 Nov. (30 Oct.–12 Nov.; 8 males and 7 females) (Parmelee 1992); earliest date in 1975, 25 Oct. Earliest date, Terre Adélie (1976–86), 17 Oct. (Thomas & Bretagnolle 1988).

**Breeding** Outside breeding range, reported off South Africa (Sinclair 1980) and s. NI, NZ (e.g. CSN 21, 30, 34, 38); recorded off se. Aust. in all months except Oct. and Dec., though less common Nov.–Feb. (Aust. Seabird Atlas). Also recorded away from breeding colonies in s. parts of range: occasional visitor to Antarctica, e.g. Windmill Is (Orton 1963) and McMurdo Sound (Spellerberg 1971b). Non-breeders at Signy I. seemed to stay on island through summer (Burton 1968a).

**Banding, Colour-marking** High fidelity to natal breeding colony on islands. Of 22 banded Terre Adélie, five resighted at least once, and one recorded in three consecutive years (Thomas & Bretagnolle 1988). Of adults banded on Anvers I., none recovered elsewhere (Parmelee 1992). Of 116 banded fledgelings, none recovered elsewhere; a few returned as pre-breeders but only four as breeding adults (all females recovered on nest): at natal nest, <1 km from natal nest, <4 km from natal nest, and c. 15 km from natal nest; lack of recoveries probably a result of high mortality of young rather than dispersal (Parmelee & Pietz 1987; Parmelee 1992). On Signy I., of birds banded as chicks then recaptured, most returned when 3–4 years old (Burton 1968a).

Banding recoveries indicate some dispersal between Antarctic islands (between S. Shetland and S. Orkney Is, and from S. Orkney Is to Elephant I.; see Rootes 1988) and between subantarctic islands (from Marion to Heard Is; Woehler 1989;

from Iles Crozet to Marion I.; Weimerskirch *et al.* 1985). Of birds banded Marion I., one recovered Namibia, and one Fremantle, WA (Urban *et al.* 1986; Anon. 1992). Of birds banded Iles Crozet, one recovered Namibia, several recovered South Africa. Two banded, Iles Kerguelen, recovered Rockingham and Quinns Rocks, WA (Weimerskirch *et al.* 1985). Few movements recorded from n. breeding populations; from c. 500 birds banded Chatham Is over 10 years, only one juvenile recovered elsewhere (Hemmings 1990a).

Skua banded Deception I., S. Shetland Is, Jan. 1960, recaptured and released Mar. 1961 on Antarctic Pen., then recovered Guadeloupe, Caribbean Sea, May 1967, may have been South Polar rather than Subantarctic Skua (Hudson 1968; Devillers 1977; Furness 1987). For details of recoveries of *lonnbergi* x *maccormicki* hybrids, see South Polar Skua.

#### Other records

62S58W	03	1+	U	40	10502	173	VH
46S37E	01	P	U	54	7344	97	SABRU
46S51E	01	P	U	29	5578	97	CRBPO
37S77E	12	P	U	5	5439	111	CRBPO
66S140E	01	1+	U	58	3781	260	CRBPO
54S158E	11	1+	U	54	3219	349	ABBBS
46S37E	00	1+	U		2617	118	BBL
54S158E	11	1+	U	19	2391	343	ABBBS
54S158E	01	P	U	6	2370	342	ABBBS
54S158E	11	1+	U	18	2142	339	ABBBS
54S158E	03	1+	U		2064	337	ABBBS
54S158E	11	1+	U	20	1979	336	ABBBS
66S140E	01	1+	U	46	1302	258	CRBPO
54S158E	11	1+	U	44	1052	35	ABBBS

**FOOD** Opportunistic scavenger and predator; less often, steal food from other birds. Take eggs, young and adult birds, crustaceans, molluscs, fish and small mammals; also carrion, garbage, seal milk, faeces and offal. Take species roughly in proportion to local abundance (Osborne 1985). **Behaviour** Diurnal and nocturnal. May be more successful when foraging at night (Warham & Bell 1979). In permanent summer daylight of Antarctica, foraging evenly spread through day, with no difference between sexes (Pietz 1986). On Heard I., some feed only at night (Falla 1937). Food taken can vary much between islands and within island-groups because type and abundance of prey differ and birds or pairs specialize in different types of prey (Stahl & Mougouin 1986; G.A. Taylor). Food taken may change in regular sequence over time. On Heard I., first scavenged in seal colonies when seals were pupping, then changed to penguins and petrels as their breeding cycles progressed (Downes *et al.* 1959). On Macquarie I., numbers and breeding sites of Skuas linked to numbers and distribution of Rabbits *Oryctolagus cuniculus* (Jones & Skira 1979; Skira 1984). At Palmer Stn, Anvers I., almost totally dependent on penguins (Parmelee *et al.* 1978). Highly territorial during breeding season (at some sites), defending breeding site and sources of food; reproductive success is linked to proximity of territory to food source (see Social Organization: Territories). Foraging bouts averaged between 13 min (while penguins are nesting) and 77 min (when penguins gone) for Skuas defending territories, and 61 and 217 min for those without (Pietz 1986, 1987). In areas of sympatry with South Polar Skuas, only Subantarctic Skuas held feeding territories in colonies of penguins, and no South Polar Skuas observed to obtain any food from penguins during 127 h of observation (Trivelpiece *et al.* 1980). Feeding strategies differ from those of sympatric South Polar Skua (q.v.) (Trivelpiece & Volkman 1982).

**METHODS OF ATTACK:** (1) Attack flying birds from above, knocking them to ground or sea, then plunge on them and kill them with repeated pecks to head. Recorded taking diving-petrels *Pelecanoides*, fledgeling petrels, prions, White-chinned Petrel *Procellaria aequinoctialis*, Wilson's Storm-Petrel *Oceanites oceanicus*, Variable Oystercatcher *Haematopus unicolor*, Kelp Gull, Hartlaub's Gull *Larus hartlaubii*, White-fronted Tern *Sterna striata*, and Kaka *Nestor meridionalis* (Richdale 1965; Hamel 1966; Burton 1968a; Moors 1980; Sinclair 1980; Pietz 1987; Erb 1993). Reported attacking unsuccessfully: flying fish (Falla 1930), Grey Petrel *Procellaria cinerea* (Sinclair 1980), Swamp Harrier *Circus approximans* (Gwynn 1953) and New Zealand Pigeon *Hemiphaga novaeseelandiae*. Larger species usually taken when other prey scarce (Despin *et al.* 1972). (2) Use similar method to take Rabbits: stoop from above, knocking Rabbit off its feet, and killing it with repeated blows to head (Johnston 1973). On Macquarie I., generally take young or sick Rabbits; may take healthy subadults weighing up to 1.3 kg, but usually require several attempts to do so (Johnston 1973); most Rabbits taken weigh <400 g (Jones & Skira 1979). (3) Wait outside burrows containing chicks (Rand 1954), adult petrels (Burton 1968a) or juvenile Rabbits (Falla 1937; Johnston 1973). Will excavate petrel burrows, especially if chick inside is calling (Waite 1909; Rand 1954; Downes *et al.* 1959; Tickell 1962; Bonner 1964; Young 1978; Payne & Prince 1979; Sinclair 1980), or if burrows in soft substrate (Burton 1968a). Kill chicks by pecking at their heads (G.A. Taylor). (4) **SCAVENGING:** Scavenge in penguin colonies and among seals. Some pairs specialize in scavenging. Take discarded eggs (Downes 1955; Downes *et al.* 1959; Sinclair 1980); placenta of Southern Elephant Seals *Mirounga leonina* (Rand 1954); and debilitated, wounded or dead animals, including Southern Elephant Seals (K. Green); recorded scavenging on sheep carcasses in NZ (Waite 1909; Young 1978; Hemmings 1990a; CSN 19) and Campbell I. (G.A. Taylor). Take leftover scraps from colonies of giant-petrels *Macronectes* (Downes *et al.* 1959). Thrust head through small holes in skin of carcasses of Southern Elephant Seals to eat flesh (Falla 1937). Recorded scavenging along strand line (Stonehouse 1956; Burton 1968a; CSN 37); follow trawlers at sea (Milledge 1977; Sinclair 1978). At sea, recorded scavenging live and dead fish, seabirds, marine mammals, goose barnacles *Lepas australis*, and other organisms (Simpson 1965; Burton 1968a; Furness 1987; Hemmings 1990a; CSN 37; Murphy). On Marion I., recorded eating frozen Salvin's Prions *Pachyptila salvini* embedded in snow (Rand 1954) and prions that had died after striking lighthouse (CSN 19 Suppl.). (5) **KLEPTOPARASITISM:** Steal food from other birds; this especially common among non-breeding Skuas at sea (Barton 1982). Individuals or groups (especially when attacking larger species) force bird to sea or ground, allowing it to escape if it regurgitates. Observed stealing food from Southern Giant-Petrel *Macronectes giganteus* (Burton 1968a; Osborne 1985); White-chinned Petrel (Warham & Bell 1979); Buller's Shearwater *Puffinus bulleri* (Jenkins 1981); Little Shearwater *Puffinus assimilis*; Cory's Shearwater *Calonectris diomedea* (Sinclair 1980); Wandering Albatross (Sinclair 1980); Black-browed Albatross *Diomedea melanophrys* (Hall 1900); Shy Albatross *D. cauta* (Barton 1982); Grey-headed Albatross *D. chrysostoma* (Osborne 1985); Antarctic Shag *Phalacrocorax bransfieldensis* (Burton 1968a); Kelp Gull (Burton 1968a; Osborne 1985); Silver Gull *Larus novaehollandiae* (Stuart-Sutherland 1919); Crested Tern *Sterna bergii* (Milledge 1977); White-fronted Tern (CSN 22). Also recorded harassing (outcome unsuccessful or unknown): large

petrels; Broad-billed Prion *Pachyptila vittata* (CSN 37); White-chinned Petrel; Great Shearwater *Puffinus gravis*, Atlantic Petrel *Pterodroma incerta* (Sinclair 1980); Sooty Shearwater *Puffinus griseus* (G.A. Taylor); Wandering Albatross (Downes *et al.* 1959); Australasian Gannet *Morus serrator* (CSN 20); Imperial Shag *Leucocarbo atriceps* (Green 1993); White-faced Heron *Ardea novaehollandiae* (CSN 39); Kelp Gull (Green 1993; CSN 19); Silver Gull (CSN 38); Black-billed Gull *Larus bulleri* (CSN 19 Suppl.); White-fronted Tern (CSN 19 Suppl., 20, 24, 36); Black-fronted Tern *Sterna albostrata* (CSN 19 Suppl.). Will harass chicks until they regurgitate; on Campbell I., seen to harass chicks of Royal *Diomedea epomophora*, Black-browed and Grey-headed Albatrosses (G.A. Taylor). Also seen taking spilled krill from Adelie Penguin *Pygoscelis adeliae* sometimes, possibly after having harassed them (Pietz 1987). Take milk from lactating Southern Elephant Seals by feeding alongside suckling pups and taking spillage after pups have fed (Johnston 1973; Barré 1976). (6) OTHER METHODS: In Antarctica, fly 1–3 m above colonies of penguins, hover, then drop to seize prey, both when taking live prey or when scavenging. Some specialize in taking nocturnal procellariiforms attracted to lights; sometimes, if groups of Skuas are attracted to single source, feeding frenzies develop (Sinclair 1980). Cannibalism recorded at Palmer Stn, Anvers I., where breeding density high (Pietz 1987); reported to eat wounded mate (Hall 1900) and chicks (Murphy). On S. Georgia, catch Brown Rats *Rattus norvegicus* on moonlit nights (Stonehouse 1956); on Campbell I., catch Rats at dusk by flying low over vegetation and swooping onto prey (G.A. Taylor). CO-OPERATIVE FEEDING: Often feed co-operatively, especially in pairs; hold food in bills to pull item apart (Fig. 1) or shake it until it tears (Stonehouse 1956; Burton 1968a). Members of pair often co-operate to steal eggs and dismember prions. Many pairs specialize in particular prey (Falla 1937; Stonehouse 1956; Downes *et al.* 1959; Burton 1968a; Stahl & Mougouin 1986; G.A. Taylor).

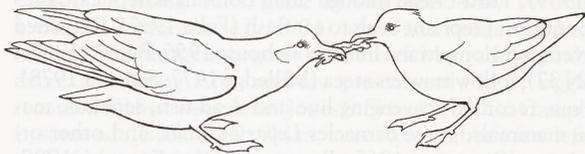


Figure 1 Co-operative feeding

METHODS OF FEEDING: On Marion I., may swallow prey whole or take it to pool where wetted, plucked and washed before breast, entrails, head and neck eaten, leaving only sternum and wings (Sinclair 1980). On Chatham Is, most birds plucked and eaten dry; diving-petrels and storm-petrels swallowed whole (E.C. Young). On Heard I., swallow bodies of prions whole (Downes *et al.* 1959; Erb 1993); on S. Georgia, prions generally plucked first (Murphy). When Antarctic Prions *Pachyptila desolata* abundant, eat only viscera and flesh of breast (Falla 1937). On Campbell I., swallow White-faced Storm-Petrels whole; chicks of penguins, albatross and cormorants torn apart and entire chick eaten, including head and feet (G.A. Taylor). Large items, such as the head of a Rabbit (Loranchet 1916) and egg of White-chinned Petrel (84 x 54 mm; Murphy), may be swallowed whole, and regurgitated several times before digestion; both adults and young regurgitate food when alarmed, then eat regurgitate after alarm has passed (Stonehouse 1956). Often feed on large penguin chicks for several hours, leaving only feet, larger bones and inverted

pelt (Pietz 1986, 1987). Usually carry eggs away from colonies, open them by hammering or pinching shell with bill, then drink contents (Stonehouse 1956; Burton 1968a; Sinclair 1980; Pietz 1987); fledgelings not able to hammer eggs open (Stonehouse 1956). Drop shellfish from air to break them (Werth 1925). On S. Georgia, catch Brown Rats, crush them in bill, tear Rats in half, then swallow them (Stonehouse 1956); on Campbell I., swallow rats whole (G.A. Taylor).

Said to make larders of uneaten food in unused petrel burrows (Szielasko 1907).

In mixed pairs (Subantarctic and South Polar Skuas), each bird followed feeding pattern of its own species (Pietz 1986).

**Adults** A summary of remains found at various sites is given in Table 2. **Antarctica** At **Palmer Stn, Anvers I.** (191 food items, 1974–78; Pietz 1987, P.J. Pietz; 71 food items, 1979–81, Pietz 1987): Crustaceans: Euphausiidae: *Euphausia superba* 10% freq. 1974–78, 14% freq. 1979–81 (estimated from diagram); Fish (mostly *Pleuragramma antarcticum*, c. 10 cm) –, 8; Birds: penguins 83, 72; skuas 6, 1; other prey (incl. crustaceans: *Branchinecta*) 1, 4. At **Signy I., Antarctic Pen.** (obs., Burton 1968a): Marine invertebrates; Crustaceans; Fish; Birds: penguin (Adelie), Chinstrap *Pygoscelis antarctica* and Gentoo *P. papua* eggs and chicks; petrel fledgelings; Cape Petrels *Daption capense* ads; Snow Petrels *Pagodroma nivea* ads; Antarctic Prion ads, chicks; Wilson's Storm-Petrel. Mammals: Southern Elephant Seal placenta. Kitchen scraps, carrion.

On **S. Georgia** (obs. and middens; Stonehouse 1956; Osborne 1985): Crustaceans: copepods; amphipods. Birds: Brown Pintail *A. georgica*; penguin (King, Gentoo, Macaroni *Eudyptes chrysolophus*) eggs, chicks, and carcasses of chicks; Common Diving-Petrel; Northern Giant-Petrel *Macronectes halli* chicks; Southern Giant-Petrel chicks; White-chinned Petrel ads, eggs; Antarctic Prion ads, eggs; albatross eggs; Grey-headed Albatross chicks; Black-browed Albatross chicks; Wilson's Storm-Petrel; Black-bellied Storm-Petrel *Fregatta tropica*; South Georgian Pipit *Anthus antarcticus*. Mammals: Brown Rat; Antarctic Fur Seal *Arctocephalus gazella* placenta, and carcasses of adults and pups. Rubbish and debris. On **Ardley I. and Fildes Pen., S. Shetland Is** (food remains from 154 nests; Peter *et al.* 1990): Fish 11% freq. Birds: penguins 69; other birds 10. Station garbage 10.

On **Marion I.** (obs.; Sinclair 1980): Birds: diving-petrels; Kerguelen Petrel *Lugensa brevirostris*; Soft-plumaged Petrel *P. mollis*; Salvin's Prion; White-chinned Petrel; Grey-headed Albatross small chicks. Eggs: Rockhopper Penguin *Eudyptes chrysolome*; Macaroni Penguin. Carcasses: Penguins: King *Aptenodytes patagonicus*; Gentoo; Rockhopper; Macaroni. Mammals: Southern Elephant Seal. Also offal, regurgitations. Also at **Marion I.** (remains at nests; Schramm 1983): penguins, mainly eggs and chicks, at 70.3% of nests; *Eudyptes* (Macaroni and Rockhopper Penguin) 63.0; King Penguins 22.2; Gentoo Penguin 3.7. No evidence of predation on House Mouse *Mus musculus*, which is abundant. On **Ile de la Possession, Iles Crozet** (obs., stomachs and regurgitations; Barré 1976): Molluscs: cephalopods; Crustaceans; Birds: Eaton's Pintail *Anas eatoni*; penguins (King, Gentoo, Rockhopper and Macaroni) eggs, chicks and carcasses; diving-petrels; petrel young; prions; Mammals: Brown Rat; Southern Elephant Seal placenta and milk. On **Heard I.** (obs., Ealey 1954): Cephalopods; Birds: eggs, chicks; diving-petrels; prions; Wilson's Storm-Petrel; bird carrion; Mammals: seal carrion and faeces.

**NZ** On **Whero I.** (obs. and middens; Richdale 1965): Common Diving-Petrel; petrels *Pterodroma*; Broad-billed Prion;

Table 2. Diet of Subantarctic Skuas at eight sites.

	1	2	3	4	5	6	7	8
	% freq							
<b>Plants</b>								
Moss	-	-	-	-	-	-	0.4	-
<b>Animals</b>								
<b>MOLLUSCS</b>								
Gastropods								
<i>Nacella deaurata</i>	-	-	-	-	-	-	1.0	-
Cephalopods	-	-	-	-	-	-	2.3	-
<b>CRUSTACEANS</b>								
Barnacles								
<i>Lepas australis</i>	-	-	-	-	-	-	4.3	-
Crabs	-	-	-	-	-	-	0.1	-
<b>FISH</b>								
Nototheniidae								
<i>Notothenia</i>	-	-	-	-	-	-	-	0.2
<b>BIRDS</b>								
Domestic Chicken	-	-	-	-	-	-	0.1	-
Eaton's Pintail	-	-	-	-	-	-	-	0.1
Penguins	-	-	-	-	-	36.8	19.7	-
King Penguin	-	-	-	-	-	-	0.1	-
Gentoo Penguin	-	-	-	-	-	-	0.1	-
Erect-crested Penguin	-	0.2	-	-	-	-	-	-
Rockhopper Penguin	-	-	tr	-	-	-	0.6	-
Macaroni Penguin	-	-	-	-	-	-	33.0	1.0
Eggs	-	-	-	-	-	10.5	-	-
Chicks	-	-	-	-	-	0.5	-	-
Little Penguin	-	-	-	tr	-	-	-	-
Pitt Shag	-	-	-	tr	-	-	-	-
Procellariidae							1.2	-
Diving-petrels	-	-	-	-	-	-	-	14.6
Common Diving-Petrel	0.2	1.1	-	tr	tr	6.8	0.1	5.1
South Georgian Diving-Petrel	-	-	-	-	-	-	4.2	19.7
<i>Macronectes</i>	-	-	-	-	-	-	0.1	-
Kerguelen Petrel	-	-	9.0	-	-	-	-	3.7
<i>Pterodroma</i>	-	0.2	-	-	-	-	-	-
Great-winged Petrel	-	-	tr	-	-	-	-	1.8
White-headed Petrel	35.5	39.3	-	-	-	-	0.1	-
Soft-plumaged Petrel	0.2	0.9	tr	-	-	-	0.1	3.0
Black-winged Petrel	-	-	-	tr	-	-	-	-
Blue Petrel	7.8	-	65.3	-	-	0.5	0.1	6.3
<i>Pachyptila</i>	-	-	tr	-	-	-	-	-
Fairy Prion	-	10.9	-	tr	-	-	-	0.7
Antarctic Prion	49.5	-	-	-	-	22.6	0.1	0.1
Salvin's Prion	-	-	-	-	-	-	5.4	55.6
Broad-billed Prion	-	-	-	tr	most	-	-	-
White-chinned Petrel	-	3.7	tr	-	-	-	1.0	1.1
Grey Petrel	-	7.4 <sup>A</sup>	-	-	-	-	-	-
Sooty Shearwater	6.7	0.4 <sup>B</sup>	-	tr	-	-	-	-
Short-tailed Shearwater	0.2	-	-	-	-	-	-	-
Little Shearwater	-	43.3	-	-	-	-	-	-
<i>Diomedea</i> chick	-	-	-	-	-	0.3	-	-
<i>Phoebetria</i>	-	-	-	-	-	-	0.8	0.1
Wilson's Storm-Petrel	-	-	-	-	-	0.3	0.1	0.4
Grey-backed Storm-Petrel	-	0.4	-	tr	-	-	0.1	0.1
White-faced Storm-Petrel	-	-	-	tr	many	-	-	-
Black-bellied Storm-Petrel	-	0.9	-	-	-	0.3	0.2	0.9
Black-faced Shearwater	-	-	-	-	-	-	0.3	0.7
Antarctic Tern <i>S. vittata</i>	-	0.2	-	-	-	-	-	-
<i>Cyanoramphus</i>	-	0.2	-	-	-	-	-	-
<b>MAMMALS</b>								
Rabbit	-	-	-	-	-	-	-	4.3
Black Rat <i>Rattus rattus</i>	-	-	-	-	-	-	30.2	0.4
Antarctic Fur Seal	-	-	-	-	-	10.3	-	-
Unident.	-	-	7.7	-	-	-	-	-

(1) Macquarie I., 1193 remains (Jones 1980); (2) Antipodes Is, 457 remains (Moors 1980); (3) Prince Edward I., 455 remains (Adams 1982);

(4) Star Keys, Chatham Grp (CSN 37); (5) South East I., Chathams Grp (Young 1978); (6) S. Georgia, 76 middens, 2888 items; expressed as freq. per midden (Osborne 1985); (7) Ile de la Possession, Iles Crozet, 1546 items (Stahl & Mougin 1986); (8) Ile de l'Est, Iles Crozet, 1546 items (Stahl & Mougin 1986).

<sup>A</sup> Fledgelings; <sup>B</sup> Adults and fledgelings

Fairy Prion *P. turtur*; Sooty Shearwater; White-faced Storm-Petrel *Pelagodroma marina*; Kelp Gull; Kaka. On **South East I., Chatham Is** (obs.; Fleming 1939; Young 1978; G.A. Taylor): Birds: Little Penguins *Eudyptula minor*; Common Diving-Petrel; Black-winged Petrel *Pterodroma nigripennis*; Broad-billed Prion; Sooty Shearwater; Grey-backed Storm-Petrel *Garrodia nereis*; White-faced Storm-Petrel; Kelp Gull chicks; Mammals: remains of sheep.

**Other records** (Species already mentioned in detailed studies above not repeated here; references to incidental records of those items are listed at the end of this paragraph.) **Plants** Algae (FAB). **Animals** Molluscs (Werth 1925): polyplacophorans: Mopaliidae: *Plaxiphora aurea*; gastropods: Haliotidae: *Haliotis virginea* (Hemmings 1990a); Trochidae: *Cantharidus (Plumbelenchus) coruscans* (Simpson 1965); cephalopods: cuttlefish (Storr 1964) and squid (G.A. Taylor). Crustaceans: barnacles: Lepadidae: *Lepas australis* (Simpson 1965; Hemmings 1990a; CSN 37). Arachnids: spiders (FAB). Insects: Diptera: Coelopidae pupae. Fish (Osborne 1985; Cooper *et al.* 1986; Murphy; CSN 22): Exocoetidae (Falla 1930). Birds: land birds (CSN 19 Suppl.); Snares Penguin *E. robustus* (Warham 1967); chicks (Wilson 1959); Erect-crested Penguin *Eudyptes sclateri* eggs (Moors 1980); Wandering Albatross eggs (Hall 1900); Shy Albatross chick (Fleming 1939); Buller's Albatross *D. bulleri* chicks (Hornig & Hornig 1974); Cape Petrel eggs (Parmelee & Rimmer 1985); Mottled Petrels *Pterodroma inexpectata* (Wilson 1959; Warham 1967; CSN 24); cormorant eggs and chicks (G.A. Taylor); Pacific Black Duck *Anas superciliosa* ads, juv. (Simpson 1965); Chatham Island Oystercatcher *Haematopus chathamensis*; Shore Plover *Thinornis novaeseelandiae* (Young 1976); Subantarctic Skua injured ads and chicks (Hall 1900; Murphy); White-fronted Tern (Hamel 1966): eggs and ads (CSN 22); New Zealand Pigeon; Kaka (Oliver). Mammals (Johnston 1973): Southern Elephant Seal carrion of ads, pups (Westerskov 1960; Simpson 1965; Johnston 1973; Jones & Skira 1979; FAB); sea lion excreta (Bailey & Sorensen 1962); New Zealand Sea Lion *Phocarctos hookeri* regurgitations (G.A. Taylor). Also, dog food (CSN 26); offal (Milledge 1977; Sinclair 1978); whaling and sealing offal (Waite 1909; Bailey & Sorensen 1962; Murphy). Pumice (Simpson 1965). Additional references to food items already listed as part of detailed studies: Bailey & Sorensen (1962); Cooper *et al.* (1986); Crawford (1952); Despin *et al.* (1972); Downes (1955); Downes *et al.* (1959); Hall (1900); Hemmings (1990a); Johnston (1973); Jones & Skira (1979); Merilees (1971); Moors (1980); Osborne (1985); Parmelee & Pietz (1987); Payne & Prince (1979); Pietz (1987); Rand (1954); Richdale (1943, 1944); Robertson *et al.* (1980); Simpson (1965); Stead (1932); Tickell (1962); Trivelpiece *et al.* (1980); Waite (1909); Warham & Bell (1979); Warham (1967); Westerskov (1960); Wilson (1959); Young (1976, 1978); CSN 19, 22, 24; Murphy; FAB.

**Young** First fed within 24 h of hatching. Food not predigested, even though chicks not always fed straight after return of parent (Burton 1968a). Up to 10 days old, chicks fed prion carcasses piece by piece (Osborne 1985), though Murphy said that adults invariably disgorge food to young. On Anvers

I., fed only on penguin remains (Pietz 1987). On Signy I., in 1981–82 and 1982–83, only avian material was recovered in samples regurgitated by chicks (Hemmings 1984).

**Intake** On South East I., average 0.7–3.3 prions killed in territories per night (maximum 6) and up to seven diving-petrels but unknown number of storm-petrels also taken (Young 1978). On Ile de la Possession, Iles Crozet estimated  $\geq 11,787$  kg of biomass used by Skuas per season; at Ile aux Cochons, 37,284 kg (Barré 1976).

**SOCIAL ORGANIZATION** Well known during breeding season. Major studies on South East I., Chatham Grp (Young 1978; Hemmings 1989), Signy I. (Burton 1968a,b), S. Georgia (Stonehouse 1956), Pt Thomas, King George Sound, S. Shetland Is (particularly on feeding territories; Trivelpiece *et al.* 1980; Trivelpiece & Volkman 1982), and Anvers I. (Pietz 1984, 1986, 1987; Parmelee & Pietz 1987). Little known outside breeding season except for study on South East I. (Hemmings 1990a). Account includes material from original contribution by K. Green.

On arrival at breeding areas, birds settle in small groups; breeding birds become territorial almost immediately and, during breeding season, breeding pairs are solitary when on territories. Non-breeding birds, including those returning to natal area for first time, more social; on breeding islands, non-breeders gather in **Clubs** where some hostile and, apparently, pairing behaviour occurs; birds in Club bathe, preen and roost together in particular areas (Falla 1937; Stonehouse 1956; Downes *et al.* 1959; Burton 1968a). On Signy I., up to 70 birds in Club at one time (Burton 1968a,b); on S. Shetland Is, one Club had c. 35 Subantarctic and 15 South Polar Skuas (Trivelpiece & Volkman 1982) and, at Fildes Pen., King George I., a maximum of 136 non-breeding birds in Club (Hans-Ulrich *et al.* 1990); on South East I., records of 10–20 resident non-breeders (Young 1978) and c. 30 in Club (Hemmings 1990a). Breeding birds never seen in Clubs (Burton 1968a). On Heard I., flocks (status of members not stated) reached maximum size in Oct., when Southern Elephant Seals bred; flocks on one beach averaged c. 50 birds in early Oct., 120 in mid-Oct., and 200 by end of month; numbers in flocks on beaches started to decrease Feb.–Mar. (Downes *et al.* 1959). At end of breeding season, at least some leave breeding area in groups consisting mainly of juveniles. On S. Georgia, some flocking Apr. (Stonehouse 1956). Outside breeding season, little known, especially away from breeding grounds. On Chatham Is, in July, and apparently through winter, some stay as pairs on territories, and up to eight birds seen in Club area (Hemmings 1990a). On Heard I., May to early June, occur in groups of three or four, sometimes up to 24 (Downes *et al.* 1959). During winter, singles often seen at sea (e.g. Barton 1982; K. Bartram); in waters off s. Aust., from Nov. to Apr. most records of single birds (Aust. Seabird Atlas). Sometimes form large flocks when feeding (e.g. Bailey & Sorensen 1962) and hierarchies may form (see Agonistic behaviour). Sometimes hunt, and often feed, co-operatively, especially as pairs (Stonehouse 1956; Downes *et al.* 1959; Moors 1980; Osborne 1985; see Food); trios also recorded sharing food (Stead 1932).

**Bonds** Monogamous, though some communal breeding recorded (see below). Generally, pairs faithful to mate and site from year to year. On Anvers I., over 9 years, of nine males, six had only one mate and three had two; of ten females, three had one mate, and five had two mates; longest recorded residency at one site by individual at least 9 (probably 11) years and by same pair at least 5 (probably 7) years; on South East I., some

pairs together 16 years; on Campbell I., one pair together on same site for at least five seasons (Hemmings 1989; Pietz & Parmelee 1994; E.C. Young; G.A. Taylor). Changes of mates or sites rarely preceded by reproductive failure (Parmelee & Pietz 1987). In some areas, pair-bond not maintained during non-breeding periods (e.g. Parmelee 1992); on Chatham Is, some pairs remain together through winter (Hemmings 1990a). Obtain new mate if partner dies, does not return for the year, or disappears; may find new mate immediately (e.g. Hemmings 1990a) or may take more than 1 year (Parmelee & Pietz 1987). On Anvers I., change of mate did not usually lead to change of territory (though change of territory usually involved change of mate); males more likely not to return for 1 year; during outbreak of avian cholera, twice as many males as females disappeared or found dead (Parmelee & Pietz 1987; Pietz & Parmelee 1994). Males generally arrive on breeding grounds before females (Neilson 1983). First member of established pair to arrive at breeding site often associates with one or more temporary partners and, if mate of previous year does not return, will then breed with temporary partner. Temporary mate displaced even if permanent partner returns in next year (Burton 1968a; Stonehouse 1956). Some known breeding birds return after longer absences (Parmelee & Pietz 1987). Throughout breeding season, a Skua may be joined by another when mate away foraging (Burton 1968a). Burton (1968a) observed instances of permanent changes of mate (not related to mate dying) when opposite partners of two neighbouring pairs did not return for 1 year; in these cases the deserted mates paired and nested in one of their territories; twice, missing birds returned 1 year later, formed new pair, and used vacant territory. Do not breed till several years old; youngest breeding age on Anvers I., 6 years old (Parmelee & Pietz 1987). On Chatham Is, most do not occupy breeding territories before c. 8 years old (Hemmings 1989); age of first breeding: females, 7.44 years (1.45; 29), males, 8.92 (2.48; 26), combined 8.21 (2.09; 5–14; 56) (E.C. Young). On Signy I., birds usually return to natal area when 3–4 years old; 7-year-olds recorded holding territories for 2 years but not laying (Burton 1968a).

**TIMING OF PAIR-FORMATION: GENERAL:** On Signy I., pair-formation takes place from about early Oct. to early Nov., with laying c. 3 weeks after pair-formation (Burton 1968a); on Macquarie I., start arriving early to mid-Aug., pairs formed by late Sept., and have nests and eggs by late Oct. (Falla 1937); on Bird I., S. Georgia, first birds arrived 7 Sept., and pairs held territories by 19 Sept. (Osborne 1985); on Campbell I., arrive on territories over Sept., and most have laid by third week of Nov. (Bailey & Sorensen 1962). Timing of laying related to variety of factors, such as latitude and availability of food (see Breeding).

**ESTABLISHED PAIRS:** In populations that leave breeding sites during winter, members of pairs may return to breeding area on same day, or one may arrive up to a fortnight before the other, and defend territory (see above) (Burton 1968a). On Bird I., S. Georgia, pairs usually formed within 1–2 weeks of one partner arriving on territory (Bonner 1964). Once reunited, takes a few days before birds behave as co-ordinated pair. On S. Georgia, one record of c. 8 weeks between return of pair and laying, but sexual behaviour occurred only in last 3.5 weeks of this period (Stonehouse 1956).

**NEW PAIRS:** Newly formed pairs often do not lay in first, and sometimes second, season; if they lay, often do so later than established pairs (Burton 1968a; Parmelee & Pietz 1987). Once, member of established pair whose partner did not return took series of temporary partners between arrival on territory in late Sept. and obtaining new partner in late Oct. Another bird, unpaired,

recorded: defending deserted territory, alone, from mid-Oct.; taking temporary partner in mid-Nov.; changing to another new partner in late Nov.; then courting and nest-building immediately, eggs being laid 5 days later (Stonehouse 1956). On Chatham Is, pair once formed in winter, when female bonded with new partner, seemingly within 2 days of death of established partner; pair bred successfully next breeding season (Hemmings 1990a). Subantarctic and South Polar Skuas sometimes interbreed and produce viable offspring (Parmelee *et al.* 1977; Neilson 1983; Hemmings 1984; Pietz 1984; Parmelee & Pietz 1987), e.g. Anvers I., at least one mixed pair each year, and on Signy I., three mixed pairs in 1981–82. Usually pair found, or believed, to consist of male South Polar Skua and female Subantarctic Skua (Trivelpiece & Volkman 1982; Hemmings 1984; Pietz 1986, 1987; Furness 1987). For further details on mixed pairs, see Pietz (1984, 1986, 1987).

**Co-operative breeding** Trios (usually of adults) and sometimes even larger groups (up to seven) (Hemmings 1989) occur on territories. Trios recorded at many sites but comprise <1% of breeding territories overall. Possibly more common at n. breeding sites (Snares, Stewart and Chatham Is) than s. breeding sites (Hemmings 1989). Trios or groups recorded: on islands round Stewart I. (e.g. Fleming 1939; Stonehouse 1956); on one island, trios occurred at 8 of 12 nests (Richdale 1965); on another, in 2 of 9 nests; on others, in about half of the nests (Stead 1932); Guthrie-Smith (1925) considered trios to be the norm for this area. On South East I., trios or groups recorded in one-third of territories (Hemmings 1989); in 5 of 11 territories (Young 1978). On Snares Is, in one year, on 3 of 27 territories (Young 1978). On Bird I., S. Georgia, in 1976, 1–2 trios noted in c. 500 pairs (Bonner 1964; Young 1978; Osborne 1985). On Marion I., 3 recorded, and more probably present (Williams 1980a,b). On Signy I., of c. 100 breeding pairs over 7 years, one trio lasted at least several years (though two original members replaced) and another formed for one season (Burton 1968a). On Anvers I., trios rare (Parmelee & Pietz 1987). Also recorded Iles Crozet (Barré 1976; Dernenne *et al.* 1976) but not on Heard I. (Downes *et al.* 1959) or Antipodes Is (Hemmings 1989). Trios usually consist of two males and a female (though see Bonner 1964) and larger groups seem to have only one female; in trios, both males copulate with female (Hemmings 1989). Trios said to be usually all adults (Bonner 1964; Young 1978), though younger birds may be involved (Stead 1932; Fleming 1939). On South East I., no evidence for retention of young or that birds are more related within trios than within whole population. Little aggression within trios or groups and associations as stable and long-lasting as those within pairs (Hemmings 1989). On South East I., number of chicks produced per adult generally lower for trios than pairs, with no significant differences in clutch-size, size of eggs, or growth and condition of chicks (Hemmings 1989); less detailed studies have noted no apparent difference in reproductive success between pairs and trios (Young 1978; Brown 1987). On Marion I., chicks raised by trios, rather than pairs, grew faster and probably fledged with greater reserves of fat, though hatching success and chick survival same (Williams 1980a). More recent studies of pattern of reproductive success and sex-ratios in communally breeding Skuas determined by DNA methods in Millar *et al.* (1992, 1994). For role of members of trios in breeding attempt, see Parental care. On South East I., breeding trios reduced to pairs for 1 or more weeks from mid-Jan., before territorial behaviour lapsed (Young 1978).

**Parental care** Both members of pair build nest, defend territory and incubate; and brood, feed and guard young (Stonehouse

1956; Richdale 1965; Burton 1968a,b; Pietz 1986). Females less active before laying, and fed mostly by males (courtship feeding); when laying, often less active in defence; may incubate more (Stonehouse 1956); brood chicks more often and, when not brooding, usually stand near chicks, whereas males often stand on roosting site (Burton 1968a). Males contribute more to hunting and defence (Trivelpiece *et al.* 1980). Also see Breeding. In trios or groups, all adults defend territory, copulate and rear offspring (Hemmings 1989); others have also noted shared defence of territories, incubation and feeding and care of young (Guthrie-Smith 1925; Bonner 1964; Richdale 1965; Young 1978). Once able to fly, young cared for and guarded for some time (e.g. Richdale 1965; Young 1978). On S. Georgia, proficient at take-off and landing c. 2 weeks after first flights, and parental interest then wanes (e.g. attack intruders less vigorously); once able to fly, young stay on territory for 3–4 weeks, usually leaving second or third week of Mar. (Stonehouse 1956). On Heard I., stay on territories and cared for by parents for considerable time after moult into juvenile plumage (Downes *et al.* 1959). On Antarctic Pen., chicks fed by parents well after fledging, as late as Mar. and sometimes Apr. (Neilson 1983). Both parents do not abandon juveniles on same day: one stays with young till it leaves, or for 1–2 days after; other leaves a few days before them (Stonehouse 1956); in one trio, second adult left 11 days after first, then third left a few days later, and chick left same afternoon. Time between hatching and departure of young >65 days (Richdale 1965). At sites where juveniles move out to sea, not known when they start to forage for themselves (Burton 1968a).

**Breeding dispersion** Solitary, but seldom far from other Skuas (e.g. Stonehouse 1956; Richdale 1965). Nests widely dispersed (e.g. South East I.) or concentrated round colonies of breeding petrels (e.g. Bird I., S. Georgia) or penguins (e.g. Signy I., Macquarie I.) (Falla 1937; Burton 1968a; Young 1978); dispersion sometimes related to local topography (e.g. Burton 1968a). Often before laying, pairs build more than one scoop (see Breeding). Distance between nests: South East I., 100–625 m (Young 1978); mean distance between nests on different parts of island, 97–284 m (n=36 territories); on Mangere I., c. 135 m (n=23 territories) (E.C. Young). In other areas: Big South Cape I., NZ, c. 50+ m apart (Stead 1932); Campbell I., closest 20–30 m apart (G.A. Taylor); Bird I., S. Georgia, some nests a few metres apart (Bonner 1964); Signy I., once widely spaced, 60–700 m (Burton 1968b); more recently, with increases in population, minimum distance between nests <50 m, especially in areas near penguin colonies (A.D. Hemmings); Anvers I., partly depends on type of territory; closest nest of Subantarctic or South Polar Skua, 49 m; in earlier years, when higher densities recorded, nearest nests still often >30 m apart (Pietz 1987), though in 1974–75, not uncommon to find nests 15–20 m apart (Parmelee *et al.* 1977). On Signy I., usually return to natal area when 3–4 years old (Burton 1968a); at Anvers I., three banded chicks returned as adults, one nesting at natal nest-site and another c. 15 km from natal nest; two others returned as pre-breeders (Parmelee & Pietz 1987; also see Pietz & Parmelee 1994).

**Territories** Generally return to same territory each year (see Bonds). Single bird (of either sex) that has lost mate is able to defend territory (Parmelee & Pietz 1987). Breeding birds vigorously defend territories against other Skuas, including neighbours. Birds flying over territory always challenged and birds seldom take off over neighbouring territories. Boundary disputes rare (Stonehouse 1956; Burton 1968b). See also Agonistic behaviour. **TIMING OF TERRITORIAL BEHAVIOUR:**

Territories defended soon after arrival at breeding grounds (Stonehouse 1956; Downes *et al.* 1959; Young 1978). Arrive breeding territories on Anvers I., late Oct. to mid-Nov. (Parmelee 1992); on S. Shetland Is, mid- to late Oct. (Trivelpiece & Volkman 1982). On Signy I., territories defended from Oct. till departure in Mar.; young birds that establish territories only 1 year earlier take up territories later than more experienced birds; defended till departure in Mar. (Burton 1968a,b). Defence more vigorous when territories first established; weaker at end of season when young flying (Burton 1968b). On S. Georgia, boundaries break down Feb.–Mar.; when one member of pair leaves, the other defends territory less vigorously (Stonehouse 1956). On South East I., 65% of summer adult population present in July, and 82% of Skuas present on territories during breeding season were still on territories, though defence was less intense (Hemmings 1990a) (some earlier studies assumed territories defended only mid-Aug. to early Feb., e.g. Young 1976, 1978). Territorial behaviour possibly occurs throughout year in areas where birds remain during winter. **ESTABLISHMENT OF TERRITORY:** Abandoned territories usually quickly occupied by new pairs (Burton 1968a). One deserted territory defended for 1–2 days by unpaired bird, which seldom came into conflict with neighbours and soon obtained temporary partner (Stonehouse 1956). New pairs can form territories by occupying neutral zones or outer parts of large established territories, sometimes with little protest from original owners (Burton 1968a). **BASIC PHYSICAL CHARACTERISTICS:** Territory primarily consists of breeding and resting places, centred on high point; usually includes one or more roosting sites that overlook nest and where off-duty bird, visible to other Skuas, loafs during day; also places for chicks to rest and feed lower down slope. If roosting site changes between years, nesting site also changes (Stonehouse 1956; Burton 1968a,b; Young 1978). Estimated size of territories varies greatly: South East I., 5600–37,500 m<sup>2</sup> (Young 1978); Signy I., may be >10,000 m<sup>2</sup> (Burton 1968a); Heard I., c.  $\leq$ 400 m<sup>2</sup> (Downes *et al.* 1959); estimate of 10.0–81.3 m<sup>2</sup> on S. Georgia (Stonehouse 1956) seems unusually small. Breeding activities and defence concentrated in small area round nest and roosting sites; on Signy I., this area c. 30–50 m, regardless of overall size of territory (Burton 1968a,b). Outlying parts of territory not defended vigorously, unless part of feeding territory (see below); often only visited if intruders land, or if food available (Stonehouse 1956; Burton 1968a,b). When core-areas widely spaced, neutral zones exist between territories (Burton 1968a) and bird will not enter neutral zones in view of its neighbours (Stonehouse 1956). On South East I., much of each territory densely covered in tall plants and, on ground, birds mainly use roosting sites, shore platform, and clear areas in long grass; no boundaries run through open ground; little contact between neighbours at territorial boundaries; ground-based displays not used (Young 1978). On S. Georgia, boundaries usually coincide with obvious landmarks, such as a cliff, stream or side of pond; boundaries extend to edge of sea but not beyond (Stonehouse 1956). Territories appear stable, with boundaries rarely affected by changes in roosting and nesting sites (Stonehouse 1956; Burton 1968a; Trivelpiece *et al.* 1980; Hemmings 1990a). On Anvers I., where depend almost entirely on Adelie Penguins for food (Parmelee & Pietz 1987), numbers of breeding pairs more or less adjust to numbers of Penguins and to availability of territories near colonies (Parmelee *et al.* 1978). **TYPES OF TERRITORIES AND FEEDING AREAS:** May defend: breeding-only territory (feeding area, very often nearby, not defended); separate breed-

ing and feeding territories, which are sometimes very near each other; or single all-purpose territory. All-purpose territories, and feeding areas and territories usually include parts of breeding colonies of other seabirds, such as penguins and petrels. All-purpose territories defended against Skuas, and other birds such as South Polar Skuas, Kelp Gulls and Pale-faced Sheathbills *Chionis alba* (Richdale 1965; Trivelpiece *et al.* 1980; Pietz 1984, 1985, 1987); at Pt Thomas, have more aggressive interactions with aggressive but non-territorial Subantarctic Skuas and Kelp Gulls than with territorial Subantarctic Skuas (Trivelpiece *et al.* 1980); on Chatham Is, Young (1978) found Kelp Gulls, nesting near Skuas, generally not attacked on ground, nor in flight. Territories that temporarily contain large amounts of food sometimes invaded by large numbers of Skuas, probably mainly non-breeders without territories, and overwhelmed owners return to roost to watch (Stonehouse 1956). At Pt Thomas, birds with all-purpose territories fed exclusively at penguin colonies once eggs available late Oct.; territories contained an average of 1028 (90–2011) penguin nests and some included two or more species of penguin; suboptimal territories contained 90–260 nests, optimal territories contained 766–2011 nests; those with large feeding territories bred earlier and fledged more chicks per pair than those with small or no feeding areas (Trivelpiece *et al.* 1980; Trivelpiece & Volkman 1982), but this not always so (Parmelee 1992) (see also Breeding). On Anvers I., four feeding territories contained c. 700–2300 penguin nests and two had  $\leq$ 300 nests; pairs with feeding territories spent more time chasing other birds than those without (Pietz 1984, 1986, 1987). On Signy I., apparently two types of territories: small breeding territories next to penguin colonies (where Skuas forage), and larger territories used for feeding and breeding away from colonies (where Skuas prey on small petrels) (Hemmings 1984). On South East I., on barren coast, birds forage completely away from territories; in other areas, forage on territories (Young 1978; Young *et al.* 1989). On Antipodes I., pair mainly hunts in territory and rarely seen outside territory (Moors 1980). Birds sometimes return to territories with prey (Hemmings 1990a), and birds with feeding territories often take food back to nesting site (Trivelpiece *et al.* 1980). In areas of sympatry, Subantarctic Skuas feed in penguin colonies and South Polar Skuas feed at sea (e.g. Trivelpiece *et al.* 1980; Trivelpiece & Volkman 1982; Pietz 1987). Trivelpiece & Volkman (1982) found no penguin remains on territories of hybrid pairs, but Pietz (1987) recorded a mixed pair where Subantarctic Skua brought only penguin food to chick and South Polar Skua brought only fish. **OTHER ACTIVITIES IN TERRITORIES:** During breeding season in some locations, both members of pair rarely leave nest territory at same time (Pietz 1986). From just before laying until clutch complete, female less active, rarely leaving centre of territory (though Burton [1968a] saw no sign of this); during period when copulations occur, female not seen to feed directly at all (Stonehouse 1956). During incubation, off-duty bird mostly stands or sits at roosting site (Burton 1968a). After hatching, at South East I., both parents forage at night, leaving territories and chicks; as chicks fledge, pairs away from territory for most of day as well (Young 1978; Young *et al.* 1989). Some chicks stay near nest, while others move away to another part of territory (Stonehouse 1956; Burton 1968a). Late in breeding season, juveniles or pairs with chicks often cross into neighbours' territories causing aggressive encounters if neighbours have not left (Stonehouse 1956). However, fledgelings sometimes fly onto neighbours' territories when disturbed, with no obvious an-

tagonism (Young 1978); may even stay in neighbouring territories until departure from breeding grounds (Burton 1968a). Birds holding territories during winter do not necessarily stay on territories all day (Hemmings 1990a). **Home-range** If no feeding territories: on S. Georgia seldom take food from sea (Stonehouse 1956); on Anvers I., forage at least part of time on another island <1 km away; after penguins have left, pairs with territories supplement feeding, possibly by searching for penguins on more distant islands, but some foraging at sea (Pietz 1987).

**Roosting** Roost-site an important part of breeding territory (see above); may be on knoll, small rock (Burton 1968a) or rocky outcrop; sometimes commands wide view of coast (Young 1978); generally overlooks important parts of territory, such as nesting and feeding sites (Stonehouse 1956). During breeding season on South East I., birds mostly inactive on roost-sites during day; when chicks first hatch, breeding birds feed at night, then, as chicks fledge, also during day (Young 1978; Young *et al.* 1989). On Heard I., feeding restricted to dusk when Fulmar Prion *Pachyptila crassirostris* and Antarctic Prions began returning to burrows; flocks of non-breeders scavenged by day and rested in flocks on sand flat at night (Falla 1937). Study of time-budgets on Anvers I. found: (1) resting and foraging not related to time of day; (2) no differences between sexes in pattern of daily resting and foraging; (3) patterns of resting and foraging in Subantarctic Skuas appeared to be more random than in South Polar Skuas (Pietz 1984, 1986). When brooding finished, chicks ignore nest and rest in natural depressions on ground or against rocks; these roosts become very conspicuous with droppings. Some pairs make extra scoops, which may be used as resting places by chicks but not apparently in preference to natural ones (Burton 1968a). On Chatham Is in winter, use same loafing sites in territories as in breeding season (Hemmings 1990a). During breeding season rarely settle on open water (Stonehouse 1956).

**SOCIAL BEHAVIOUR** Well known during breeding season, with major studies on S. Georgia (Stonehouse 1956); Signy I. (mainly agonistic behaviour) (Burton 1968b); and Anvers I. (Long Call Complex) (Pietz 1984, 1985); account includes material from original contribution by K. Green. General comparative studies with other Stercorariinae by Devillers (1978), Stonehouse (1956), and Burton (1968b); comparative studies with South Polar Skua by Spellerberg (1971a), Young (1978) and Pietz (1987). On Anvers I., no difference in behavioural repertoires of Subantarctic and South Polar Skuas, and both species call and display to the other (Pietz 1985); for further details in relation to Long Call Complex (where there are slight differences), see account for South Polar Skua. Anxiety Upright display of Chilean Skua *C. chilensis* and nominate subspecies of Great Skuas (Moynihan 1962; Perdeck 1960) absent in Subantarctic Skua (Burton 1968b). Fearless and curious; easy to trap and observe (e.g. Stonehouse 1956; Murphy), though in some areas dense vegetation may make observation difficult (Young 1978). **Comfort behaviour** Wash in freshwater pools and streams (Stonehouse 1956; Hemmings 1989); sometimes make bathing depressions (Bailey & Sorensen 1962).

**Agonistic behaviour** Varies with circumstances of interaction (e.g. in breeding territories, feeding groups, or Clubs). In Clubs, birds usually ignore each other, but hostile at times; defend individual space 2–3 m diameter. In feeding groups, individual space often smaller. At a carcass, several birds may feed together with little aggression (Burton 1968b), or with

frequent short quarrels (Stonehouse 1956); all birds may give Obliques (see below), but often without effect; such groups may be dominated by one or two birds, often occupants of nearby territory, that may become so preoccupied with aggression that they feed little; frequency of display increases with arrival of newcomers (Stonehouse 1956; Burton 1968b). Disputes over food usually settled by threat displays on ground. At Signy I. at breeding sites, aggression between Subantarctic Skuas probably related to spacing of birds rather than defence of eggs and young, as intraspecific predation on broods slight (Burton 1968b). On Anvers I., aggressive behaviour occurs throughout day during summer (Pietz 1986). Territorial behaviour in winter recorded by Hemmings (1990a), see above. **Territorial advertising** Often use Obliques, Bent Neck, and Long Call Complex (see below). Both members of pair advertise to strangers flying overhead (Stonehouse 1956). Hemmings (1990a) recorded **TERRITORY CIRCUITS** performed in association with formation of new pairs. **Threat** The following agonistic displays and postures from Burton (1968b) unless stated. **UPRIGHT** (Challenge-walk of Stonehouse 1956) (Fig. 2): Adopted by challenging bird; often difficult to distinguish from alert posture with neck stretched up, but bird has rounded



Figure 2 Upright

breast and stiff-legged gait; if challenged bird stays, it may adopt same attitude and the two may circle one another before one becomes submissive (**CIRCULAR PARADING**). Variations in posture sometimes occur and are less aggressive: neck bent sideways or withdrawn so that head held away from opponent; bill pointed down (though also pointed down before attack if using downward jabbing). Stonehouse (1956) noted wings held slightly out; Burton (1968b) only recorded this near nest. When Upright used by defending pair in boundary disputes, intruding pair may retire immediately (Stonehouse 1956; Burton 1968b). **OBLIQUE** (Fig. 3): has distinct variations of position of neck: high, normal, low and very low, and all may be given with or without wing-raising. Low Obliques least aggressive; often adopt normal Oblique when threatened, which

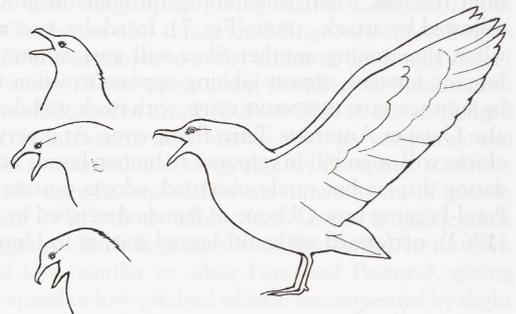


Figure 3 Oblique

changes to low or very low Oblique as bird retreats. Oblique often adopted by birds in feeding groups. **LONG CALL COMPLEX** (Oblique with Long Call of Burton 1968b; Challenge Display of Stonehouse 1956): Bird extends wings obliquely up and back, showing white on under-surface (Fig. 4); calls with body erect, chest out and bill wide open (Stonehouse 1956). Similar

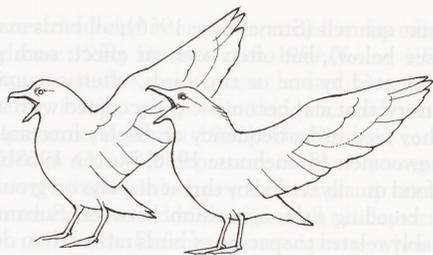


Figure 4 Long Call Complex

to Long Call Complex of South Polar Skua (q.v.), but tend not to lean as far back during display. Also like that of Chilean Skua (Moynihan 1962) but tail is raised and lowered in time with call (Burton 1968b). Figure 5 shows Long Call Complex displays of individual Subantarctic Skuas (Pietz 1985). One of most common, visible, and audible displays; varies greatly.

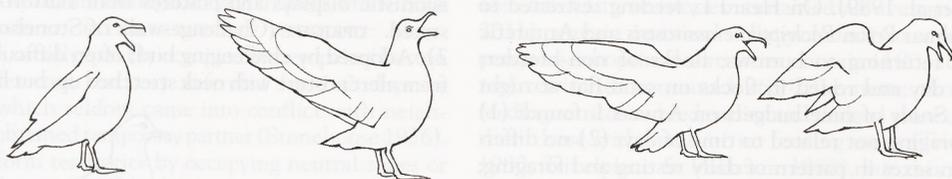


Figure 5 Long Call Complex

Occurs both in and out of breeding colonies and often related to ownership of territory, temporary or permanent: often used for territorial advertising; given on landing in territory, when other Skuas enter territory or pass overhead, between attacks from other Skuas, after boundary disputes, and between battles over carcasses. Members of pair may display together (Stonehouse 1956; Trivelpiece *et al.* 1980; Pietz 1985). **BENT NECK** (Fig. 6): Bird stretches neck up, bringing bill down to touch breast, where it may make preening movements; sometimes neck stretched horizontally rather than vertically, so that neck and body in straight line with bill pressed against breast and pointing backwards; posture occasionally preceded by several downward flicks of bill but flicks sometimes made without full posture; posture held for short time but may be quickly repeated several times and stifled Long Call may be given, where bill moved away from neck as each note given. Occurs when another Skua comes too close or often by territorial resident when threatening intruder on ground; rarely followed by attack. **GAPE** (Fig. 7): In adults, two main types: when threatening another Skua will give **AGGRESSIVE GAPE**, lunging forward, almost jabbing opponent; when threatened by another, give **DEFENSIVE GAPE**, with neck withdrawn. Skuas also Gape at Antarctic Terns flying over. At a very early age, chicks will open bill in response to human hand. **BOW**: Intimidating display but rarely observed; adopts posture similar to Food-begging Low Oblique of female described by Moynihan (1962); performed with stiff-legged gait, as in Upright, when

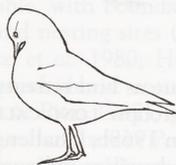


Figure 6 Bent Neck



Figure 7 Gape

approaching or circling another Skua; sometimes hold head away from opponent as in Upright. **QUACK**: Quiet call; said to show unease (Stonehouse 1956); most often heard when person in territory, but not near enough to nest to provoke Alarm Calls; also given by Skuas who appear to want to join feeding group but are hesitant. **GAKKING** (Short Call; see Voice): Recorded a few times; given by one pursuing another in air. Two other rarely seen threatening displays, Pecking at the Ground and Bill Down, are considered to be a mixture of attack and fleeing. **PECKING AT THE GROUND**: Often peck at ground or snow; rarely, tear lumps of moss with bill and flick them sideways over shoulder. **BILL DOWN**: Momentary threatening posture, which can be quickly repeated several times; possibly intention movement of Pecking at the Ground; typically seen when one bird displayed at another that failed to retreat, or by Skua standing near food from which it has been driven away. **GRASS-PULLING**: Recorded by Stonehouse (1956)

at S. Georgia, but not seen at Signy I. (Burton 1968b). Generally, Upright display and Gaping directed at Skuas close by; Bent Neck display directed at Skuas flying over or those > 10 m away on ground; Obliques used as long-distance advertisement by owner in its territory and also in disputes over food (Burton 1968b). Trivelpiece *et al.* (1980) found defence of feeding territory consisted of hierarchy of agonistic responses, from low-level Long Call display, given from ground by one or both members of territorial pair, to aerial chases or attacks or both, which were generally confined to within their territorial boundaries. On South East I., where vegetation reduces contact between neighbours on ground, most territorial defence by aerial display and attack, and territorial advertising using Long Call Complex and Bent Neck (Young 1978). In Clubs, two main types of agonistic behaviour. One involves response of individual whose space is violated. Second more complicated: Skua walks towards another in Upright posture, then often stops and relaxes, or other retreats a few metres; but sometimes circle each other in Upright (Circular Parading), then sit side by side; overt fighting rare and brief; Circular Parading similar to that seen in meeting ceremonies of mated birds described by Moynihan (1962), so possibly preliminary behaviour to mating (Burton 1968b), see Sexual behaviour. **Attack, Fighting SWOOP AND SOAR**: Swooping acts as threat and for physical attack. Generally, single resident, or members of resident pair approaching from different directions, swoop at intruder in long arcs, starting and ending 30 m in air, and usually give Alarm Calls as they rise and turn to make next swoop; at low intensity, target missed by 1–2 m; at higher intensity, birds lower feet and strike; sometimes intruder surprised and knocked over in first pass. Swooping attacks most frequent in boundary disputes, when residents spot intruder from roosting site; may chase intruder as it flies off, sometimes continuing aggression into neighbour's territory. Normally, if both members of pair unoccupied, they both defend, but single member of pair capable of driving off intruding pair. Also see Parental anti-predator behaviour. Owner will chase intruder trying to steal

prey from within its feeding territory; after chase, owner usually flies over penguin nests within its territory and occasionally obtains food exactly where intruder had been feeding (Trivelpiece *et al.* 1980). When fighting on ground, attacking Skua rushes and pecks opponent, often grabbing feathers of wing and tail; if attacking bird fights back, both throw themselves forward and, jumping up, attempt to get on top of one another, thrusting feet forward when in air; talons used for gripping but fighting birds more often seen with interlocked bills; wings beat continuously, but not used as weapons (Stonehouse 1956; Burton 1968b). Fights short (Burton 1968b), though Clarke *et al.* (1913) reported one lasting 1 h. Fighting occurs often when chicks start to wander (Stonehouse 1956).

**Escape, Appeasement HUNCHED POSTURE (Fig. 8):** Appears to be appeasement posture, with head lowered and neck withdrawn; often accompanied by Quacks or soft call, especially if being chased. Seen when one approaches another at carcass, if about to be attacked from air, or by chicks and females begging for food (Burton 1968b). Skua attacked on ground by swooping, crouches low with head and neck extended along ground,



Figure 8 Hunched Posture

then rises as attacker passes, and gives Long Call with raised wings; crouches again at next swoop (Stonehouse 1956). When challenged, submissive bird may rapidly walk or fly off; more often settles on ground digging tip of bill repeatedly into surface with sideways movements of head and, if originally standing by food, gradually forced away (often giving chattering call), keeping distance of c. 1 m between itself and aggressor (Stonehouse 1956); if caught by attacker, emits harsh calls; Defensive Gape may be given to prevent attack and pursuit after attack. In feeding group, attacked bird may redirect attack to a third bird (Burton 1968b). Often mobbed by other species of birds, e.g. giant-petrels, Wilson's Storm-Petrels, Antarctic Prions, Snow Petrels, and Antarctic Terns (Stonehouse 1956). At carcasses, give way to giant-petrels (Bailey & Sorensen 1962). Richdale (1965) reported play-type behaviour between Silver Gulls and Skuas, in which birds swoop at each other.

**Sexual behaviour** Not so well documented as other behaviours. **Pair-formation, Courtship** On S. Georgia, at start of season, Stonehouse (1956) observed new bird settled on deserted territory and after c. 1 month took temporary then permanent partner and immediately started courtship and nest-building. Another bird returned to territory and kept company with new bird; in early stages, birds shared territory but behaviour not co-operative, with new bird taking no part in defence and owner often engaging in low-intensity threat (Challenge-walking) to which new bird responded submissively; eventually pair roosted close together and behaved as well-established pair. Burton (1968a) stated pair-formation at territory simple: Skua lands by solitary territory-owner, both give Long Call Complex displays and stand side by side; no hostility between birds at this time; new bird does not seem to defend territory for a few days. Hemmings (1990a) observed pair-formation in winter: each time female (surviving member of established pair) moved to different part of territory, new bird followed and alighted nearby; female adopted an Aggres-

sive Upright posture (Perdeck 1960) and gave Long Call but without raising wings; the next day, both defended territory. In one pair, sexual behaviour not seen until pair established for c. 5 weeks (Stonehouse 1956). Burton (1968a) considered Circular Parading, described above and often seen in Clubs, to be preliminary of pairing; Circular Parading not given by owners of territories; Territory Circuits (see above) also associated with pair-formation. When members of previously established pair return to territory, seem to be wary of each other at first but, usually, soon stay together, combining in defence, advertising and feeding (Stonehouse 1956). **Greeting Long Call Complex** used for greeting mates (Burton 1968a; Pietz 1985). Little ceremony at change-over: incubating bird rises on approach of mate and steps quietly off nest if ready for relief; one bird, on relief, often walked immediately to pond to drink (Stonehouse 1956). Sideways nest-building, almost invariably seen in relieved birds (E.C. Young). **Courtship feeding** Female adopts Hunched Posture and begs, with neck lowered and bill raised. On S. Georgia, female not seen to feed directly at all round time when copulation occurring; courtship feeding twice preceded copulation; male also regurgitated if female came across him feeding (Stonehouse 1956). Rarely seen by Burton (1968a), possibly because most females fed themselves at nearby penguin colonies. Apparently similar to courtship feeding of other species of skua (Burton 1968a). **Copulation** Pair may copulate many times before laying (Osborne 1985). In one recorded copulation: male called and tried to flutter onto partner's back but she moved away; then female begged, giving soft piping call; male regurgitated food, which female ate; male fluttered onto partner's back; she settled then shifted rapidly as male brought his tail to side and downwards; male fluttered off, landing 2 m away and trod with feet while moving tail rapidly with sideways movements; pair stood for some minutes making small head-flagging movements then flew off; when again seen copulating, female occasionally pecked upwards at fluttering partner. Male sometimes tries to copulate unsuccessfully: he calls, then tries to mount by fluttering onto female's back but she ignores him or flies off (Stonehouse 1956). Burton (1968a) noted copulation appeared to be same as in other species of skua, though he observed it only once.

**Relations within family groups** Chicks brooded until 2 weeks old (see Breeding). To begin brooding, parent walks to and stands over nest till chick runs underneath parent; one adult stood with wings open, giving Alarm Calls, till chicks ran to it. Chick can also solicit brooding: runs Squealing to sitting adult and attempts to crawl under it; adult may object and lunge with bill and move away; if willing to brood, adult walks to nest followed by chick (Burton 1968a). Newly fledged young has characteristic walk: moves furtively with neck and body almost horizontal and wings slightly drooping; contrasts sharply with upright and deliberate movements of parent (Stonehouse 1956). Both adults feed chicks (e.g. Richdale 1965). **Begging:** Chick begs with body horizontal, head withdrawn and low (similar to adult Hunched Posture), giving persistent squeal or low-pitched whistle accompanied by slight upward movements of bill (Stonehouse 1956; Burton 1968a). Not always fed immediately adult returns from foraging and, often, some time later. Parents or chick can take initiative in feeding; parent may walk up to chicks without any call and regurgitate, or chick may run squealing to parent in Begging posture and peck at parent's bill, often so violently that parent has to run away from chick to regurgitate. Begging by chick may initiate foraging by parent; occasionally chick ignores

parent's attempt to regurgitate or parent drives soliciting chick away. In earlier stages of chick-rearing, parent leads chick away from nest, regurgitates food (apparently not predigested) onto ground, and then picks and holds pieces in tip of bill for chick to peck; other parent often assists in tearing food, but sometimes feeds itself and not the chick, sometimes even taking food from bill of partner. When chick 2 weeks old, takes food directly from ground (Stonehouse 1956; Burton 1968a). Stonehouse (1956) noticed when food present, chicks seemed aggressive to parents; also recorded parents leaving food when chicks approached whistling, though this not seen by Burton (1968a), who heard chicks whistling near nest but parents apparently ignored them. Sibling rivalry, as recorded for South Polar Skua, not a feature of this species (see Richdale 1965; Burton 1968a); on South East I., Young (1978) found two chicks from same brood seemed to be reared and fed together throughout development. **Anti-predator responses of young** In response to Alarm Calls of parents, run a few metres then crouch motionless or hide, under rocks or vegetation (Falla 1937; Stonehouse 1956; Downes *et al.* 1959; Richdale 1965); if in tussock-grass can be difficult to find (Osborne 1985). When handled, peck and give Alarm Calls, which stimulate parents to attack (Stonehouse 1956; Burton 1968b); will fight viciously with bill and claws when 10 days old (Stead 1932). Both adults and chicks disgorge food when agitated, returning to swallow it when alarm passed (Stonehouse 1956). When chicks c. 1 month old, appear able to defend themselves, and parents spend more time away from territory, sometimes both adults being away at same time; will rush squealing at intruding Skua but never attack own parents. Though start to fly when c. 60 days old, young still run from danger till fully proficient at take-off and landing c. 2 weeks later (Downes *et al.* 1959; Burton 1968a). Williams (1980b) noted youngest chicks to escape capture by flying were 50 days old. **Parental anti-predator strategies** Nest always covered by either parent unless both birds actively defending site (Stonehouse 1956); pair seldom off nesting territory at same time (Pietz 1986); on South East I., chicks often left unattended, first at night, then also during day (Young 1978). Observations by Stonehouse (1956) and Burton (1968b) suggest conspecifics present territorial rather than predatory threat. Responses to people: Birds may give alarm-type calls or attack for entire period intruder on territory. Generally, reaction increases as nest or brood approached. As person enters territory Skua performs BUZZ: flies down from roosting site, glides overhead and flies back; may be repeated 2–3 times, and can be seen at least 1 week before laying. As intruder approaches brood, reaction intensifies: Buzzing replaced by Swooping and Soaring (see Agonistic behaviour), often with landing between attacks; often hit intruder; less aggressive Skuas often HOVER just above and behind intruder rather than Swooping and Soaring; away from brood, Skuas circle intruder between each Swoop and Soar but, as brood approached, circling omitted and birds 'stall turn' at top of each Soar. When nest approached, bird leaves nest to attack, Alarm Call changing to Attack Call; near nest, Swoops become more vigorous and Attack Calls more frenzied. If person close to nest, Skuas may stand nearby with wings held out slightly; at slightest movement, will attack aerially (Burton 1968b). If person stays in area, calls lessen to Quacks as birds stalk round; birds often settle to face observer, sometimes pulling fiercely at vegetation in front of them. Birds handled on nest Quack, sometimes pecking gently at observer, but not so violent as when handled elsewhere in territory (Stonehouse 1956). Richdale (1965) also described Skuas Swooping, then

standing on tussocks or similar, calling with wings outstretched. Reactions vary individually, and affected by weather, age of eggs or young, whether parent on or off duty, and presence or absence of mate. Just after laying, attacks absent or weak; in some, remain weak till chicks hatch, when attacks intensify; usually most aggressive before chicks start to fly, after which drops off again. Seasonal pattern of Alarm Calls similar to that of attacks, though Alarm Calls usually heard as soon as eggs laid (Burton 1968b); Young (1978) found birds rarely gave Alarm Call at night, even if chicks handled. If mate absent, on-duty bird has lower threshold for Alarm Calls, which recall mate immediately if within hearing range; it also has increased tendency to sit on nest and to attack (Burton 1968b). In winter, Hemmings (1990a) recorded following: LOW PASSES, less intense form of Swoop, and Quack Calls, in response to person entering territory. If penguin or seal enters territory, parent runs over and stands between it and chicks; if come too close to chicks, parent utters Alarm Calls, Hovers, and may Swoop (Burton 1968b; P.J. Pietz). Stonehouse (1956) also noted that threats on ground subjected to diving attacks; also recorded instance where Skua pulled at vegetation in manner similar to described above for human intrusion. On South East I., breeding areas shared with other species of bird, including some that hold territories, but Skuas only seen to chase Swamp Harrier when it was close to ground near Skua chicks (Young 1978; Hemmings 1990a); elsewhere Harriers recorded being attacked (Stead 1932). Trios holding territory recorded attacking Kelp Gulls savagely; after repeated diving, one Gull fell from sky (Richdale 1965).

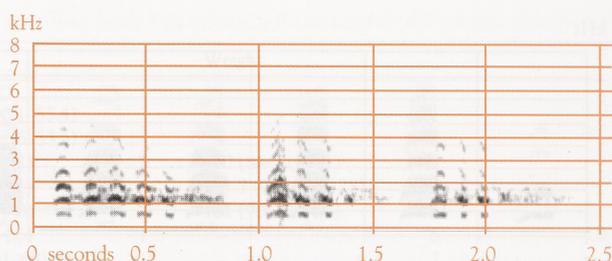
**VOICE** Well known from studies of Stonehouse (1956), Burton (1968b) and Brunton (1982); Pietz (1985) studied Long Call; Brunton (1982) and Pietz (1985) give sonagrams. Generally silent and seldom call in flight, but utter persistent raucous calls when defending nest (Stonehouse 1956); on Chatham Is, heard constantly at night while hunting prions (Campbell), though said rarely to utter Alarm Calls at night, even if chicks handled (Young 1978). Many calls, ranging from ear-splitting screams to soft piping. On Chatham Is, where territories are defended out of breeding season, Quack and Long Call heard July (Hemmings 1990a). No sexual differences reported in calls given by both sexes; no differences between sexes in structure or duration of Quack, Alarm Call, or Long Call (Brunton 1982); Begging Call given only by female, Copulation Call only by male. Little variation in Alarm Calls of an individual, but differences between frequency patterns in sonagrams can identify individuals (Brunton 1982); individual differences apparent in Long Call (Brunton 1982), most obviously in rate of repetition of notes, pitch, and number of harmonics (Pietz 1985). Possible regional differences in Long Call (see below). All calls very similar to those of South Polar Skua. For Long Call, wide overlap between the two species in all characteristics measured: Great Skua has significantly slower rate of repetition of notes, higher pitch (despite generally larger size), and fewer harmonics; no significant differences in number of notes per call, duration of calls and duration of notes; temporal splitting of notes only in South Polar Skua (Pietz 1985). Alarm Call analagous to Charge Call of Kelp Gull; the Alarm Call of Kelp Gull has no analogue in Subantarctic Skua (Brunton 1982).

**Adult QUACK:** Quiet low-pitched call of single syllable, typically 0.1 s long; double voicing (i.e. simultaneous utterance of two independent sounds by a single bird) sometimes obvious (Brunton 1982). Sonagram A shows four Quacks



A T. Howard; Macquarie I., Dec. 1991; priv. MI8B

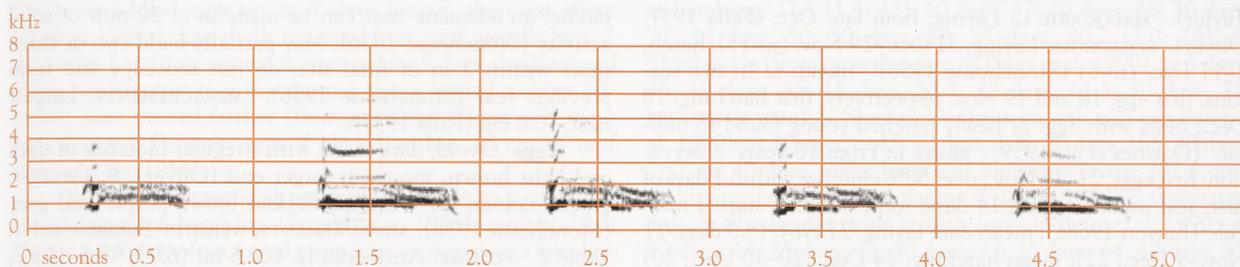
made at different times by members of a single pair. Described as bark, similar to but shorter than single note of Long Call (Brunton 1982). Denotes uneasiness. Uttered: at change-over; when Skua in another territory gives Long Call; when an intruding bird flies over nest; when person enters territory but is still distant from nest (if intrusion persists, Alarm Calls given, then Quacks continue antiphonally with mate); and when handled on nest (Stonehouse 1956; Burton 1968b; Brunton 1982). When begging for food, often accompanies submissive posture, whether by adult or by younger bird not stated (Brunton 1982). **ALARM CALL:** Single note, drawn out and plaintive in comparison to notes of Long Call (Burton 1968b) (sonogram B); may be uttered once or many times in succession (Brunton 1982). Double voicing, if present (as in sonogram B), makes call harsher, and usually occurs towards end of call; occurrence consistent in Alarm Calls of an individual (Brunton 1982). Mean duration 0.48 s (0.12; 0.3–0.7; 30), about twice that of single note of Long Call (Brunton 1982). Varies from high-pitched intermittent raucous screams of bird swooping in attack to repeated warbling plaintive calls of incubating bird, increasing in rate of repetition and intensity with approach of intruder, and changing to aggressive scream when leaving nest to attack (Stonehouse 1956; Brunton 1982). Uttered while defending territory against people, Skuas or other large birds, both from ground and from air, in conjunction with swooping attacks (Stonehouse 1956; Brunton 1982); also uttered when potential predator approaches brood, or mate trapped or shot (Burton 1968b). Heard in territory from time eggs laid. Heard once outside territory, from bird standing near group feeding on seal carcass; bird called several times for no apparent reason, causing alertness in some birds but no other reaction (Burton 1968b). Rarely given at night, even if chicks handled (Young 1978). Brings partner to nest (Stonehouse 1956). **ANXIETY CALL:** 4–6 hoarse notes, rapidly repeated; quieter than Alarm Call; sonogram C shows three calls made at different times by the same bird; double voicing evident in each. Similar in structure to Anxiety Call of Kelp Gull. Uttered when intruder near nest but threat insufficient to stimulate Alarm Call (T. Howard). **GAKKING** (Short Call): Series of rapidly repeated, short, emphatic notes made



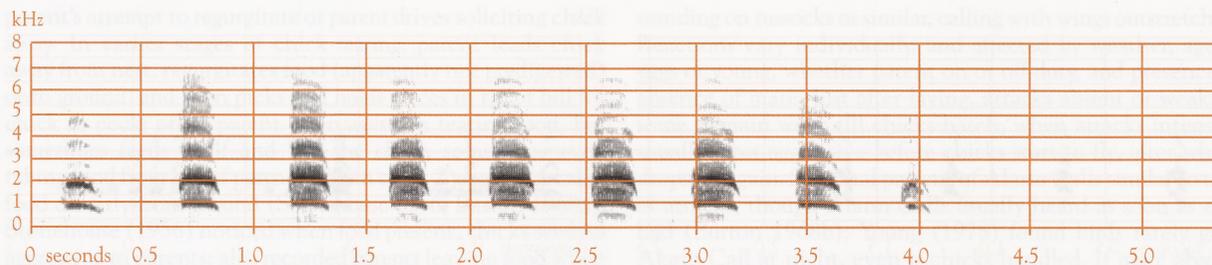
C T. Howard; Macquarie I., Dec. 1991; priv. MI8B

when in aerial pursuit of another Skua; heard infrequently (Burton 1968b). **LONG CALL:** Raucous full-throated yells (Stonehouse 1956); see sonogram D. On Anvers I., for 27 calls of 11 individuals, mean duration 4.7 s (2.6–8), mean number of notes 11.1 (6–19); only calls accompanied by wing-raising included in analysis, excluding less intense calling, when notes fewer, shorter and of lower pitch (Pietz 1985). On Chatham Is, calls typically 5–9 notes, lasting 2–4 s (Pietz 1985), and may include calls where wings not raised (Pietz 1985). Within pair or trio each member gives Long Call equally often (Brunton 1982). Infectious; often given simultaneously by neighbouring pairs or trios (Brunton 1982). For full discussion of Long Call Complex, see Social Behaviour: Agonistic behaviour. In less intense display, with Bent Neck (see Social Behaviour), when in fear of bird to which display made, call stifled, probably from constriction caused by position of head and neck (Stonehouse 1956; Burton 1968b). **YELL:** Loud and intermittent, given by aggressor in dispute over food (Stonehouse 1956). **SQUEAL:** Given by bird being attacked (Burton 1968b; Brunton 1982). Probably same as agitated chattering of weaker bird in dispute over food, described by Stonehouse (1956). **SQUAWK:** Harsh squawk; given if caught by opponent; similar to squeals of chick when handled (Burton 1968b). **SQUEAKING:** High-pitched notes uttered with bill wide open; preceded by Quacks. Given by both members of pair when selecting nest-site (Brunton 1982). **BEGGING CALL:** Soft piping by female to elicit courtship feeding; sometimes continued during copulation (Stonehouse 1956; Brunton 1982). **COPULATION CALL:** Short and continuously repeated call; 3–5 calls/s; call similar in structure to note of Long Call, but less harsh and softer (Brunton 1982). Given by male only; after courtship feeding and before and during copulation or attempted copulation (Stonehouse 1956; Brunton 1982). **REGURGITATION CALL:** Short and harsh; only heard sometimes, just before regurgitation when feeding chick (Brunton 1982).

**Young** Calls before and from time of hatching. Brunton (1982) recognized three calls. **CONTACT CALL:** High-pitched whistle, up to 1.5 s long; given almost continuously by chicks >8–10 days old. With increased hunger or prospect of feeding, call changes to **FOOD-BEGGING CALL:** lower-pitched and with



B T. Howard; Macquarie I., Dec. 1991; priv. MI8B



D T. Howard; Macquarie I., Dec. 1991; priv. M18B

frequency modulation. During feeding and when highly excited (e.g. when about to be brooded by adult), changes to **EXCITEMENT CALL**: call divided into series of shorter calls, somewhat similar in structure to Long Call of adult. **Other calls** **SQUEALS**: Given by young chicks attempting to crawl under parent; to attract attention of parents; used by 1-month-old chicks when driving off intruding adult while parents absent (Burton 1968a). Shrill call or squeal given when approached or attacked by other Skuas, stimulating parents to attack intruders (Stonehouse 1956; Burton 1968b). **WHISTLES**: Persistent low-pitched whistle, first heard at about 3 weeks old, used to elicit regurgitation from parent returning with food; also uttered when hungry to induce parents to forage, and when parents away; often given while roaming round nesting area, with parents taking no notice (Stonehouse 1956; Burton 1968a). Whistling call given by flying young to maintain contact with parents (Murphy).

**BREEDING** Well known; studied on S. Georgia (Stonehouse 1956), Heard I. (Downes *et al.* 1959), Signy I. (Burton 1968a; Rootes 1988), Marion I. (Rand 1954; Williams 1980b), Antipodes Is (Moors 1980) and Palmer Stn, Anvers I., Antarctica (Pietz 1987). Usually breed in simple pairs; trios recorded (Bonner 1964; Burton 1968a; Young 1978; Williams 1980a; Hemmings 1989), usually of two males and one female (see Social Organization). Close interaction between breeding cycles of Skuas and penguins (Trivelpiece & Volkman 1982). Hybridize with South Polar Skua (Pietz 1986).

**Season** Laying starts later at higher latitudes: from mid-Sept. at Chatham Is (44°S) to mid- and late Nov. at S. Orkney (60°S) and S. Shetland (62°S) Is (Young 1977; Jablonski 1986). Eggs laid c. 3 weeks after formation of pair (Burton 1968a); on Campbell I., possibly up to 2 months after arrival of pair on territory (G.A. Taylor). **SOUTH EAST I., CHATHAM IS**: Laying period, 15 Sept.–25 Oct. (mean laying date, c. 10 Oct.); mean hatching date, c. 10 Nov. (Young 1978). **MARION I.**: Laying, 23 Oct.–19 Dec.; in two seasons, 70% eggs laid 2–14 Nov.; hatch, 24 Nov.–16 Jan., 51% (n=43 chicks) hatched by 8 Dec.; fledge, late Jan. and Feb. (Williams 1980b). **CAMPBELL I.**: First eggs, 22 and 24 Oct.; hatch in first half of Dec. (Oliver); in 1986, first eggs 1 Nov.; hatch from 3 Dec. (G.A. Taylor). **MACQUARIE I.**: Laying, from late Oct. (Falla 1937; Oliver). **S. GEORGIA**: Laying, 31 Oct.–29 Nov. (n=15); hatch, 2–17 Dec. (n=6) (Stonehouse 1956). **HEARD I.**: In two seasons, first egg, 18 and 19 Nov. respectively; first hatching, 18 Dec.; nests with eggs or newly hatched young found to mid-Jan. (Downes *et al.* 1959). **SIGNY I.**: From 10 years' observation: first eggs, 21–29 Nov.; over 50% clutches within 7 days of first, rest usually within 14 days; some clutches started mid-Feb. (Burton 1968a); mean date laying, 27 Nov. (5.0 days; 21 Nov.–9 Dec.; 22); mean hatching, 24 Dec. (20–30 Dec.; 20) (Rootes 1988). **S. SHETLAND IS**: Main period of laying, 18–27

Nov.; eggs still being incubated, Feb.; hatch from 24 Dec. (Jablonski 1986); laying 23 Nov.–30 Dec. (Peter *et al.* 1990); mean date first egg, 2 Dec. (8.9 days; 17 Nov.–21 Dec.; 15); pairs with large feeding territories began laying earlier, 29 Nov. (8.8 days; 17 Nov.–13 Dec.; 9), than pairs with small or no feeding territories, 8 Dec. (6.9 days; 4–21 Dec.; 6) (Trivelpiece & Volkman 1982). **PALMER STN**: Earliest recorded laying date, 29 Nov., though evidence of earlier. Over three seasons, mean laying period 30 Nov.–5 Dec. (Parmelee 1992). For two seasons, median dates of hatching, 30 Dec. (16.1 days; 28 Dec.–7 Feb.; 6) and 27 Dec. (14.9 days; 24 Dec.–29 Jan.; 5) (Pietz 1987).

**Site** Flat or sloping areas; never hollows, in which snow can accumulate; often sheltered by a rock or vegetation; on elevated grasslands, *Azorella* slopes, in ledges of grass, grassy patches or open moss-covered ground, on *Pleurophyllum* flat adjoining a penguin colony, mound riddled with prion burrows (Falla 1937; Rand 1954; Stonehouse 1956; Downes *et al.* 1959). Some nests on Marion I. sited in lush vegetation growing round old nests of Wandering Albatrosses (Rand 1954). Nest usually placed in centre of territory (Downes *et al.* 1959), near roosting site that forms focal point of territory (Burton 1968a). Nests aggregated round penguin colonies; sites traditional, varying by a few metres between years; occasionally both roosting site and nesting site changed within territory (Burton 1968a); site may be used by same bird for up to 11 seasons, individuals averaging one territory during nine seasons (Parmelee & Pietz 1987).

**Nest, Materials** Scoop or hollow in vegetation, e.g. grass, *Azorella*, moss, lichen; scratched or torn out then pressed down by repeated stamping and settling to form scoop, sometimes lined with vegetation plucked from nearby; usually raised slightly above ground; sometimes made in more barren areas; sometimes made through a few centimetres of snow; one pair on Heard I. built small mound of moss on bare rock; another nested in hollow of sand near edge of vegetation (Falla 1937; Stonehouse 1956; Downes *et al.* 1959; Burton 1968a; Parmelee 1992). Both sexes build, usually with one bird, probably female, sitting on nest for most of time (Stonehouse 1956); female spends much time constructing nest or incubating early in season (Trivelpiece *et al.* 1980). Building intense and spasmodic; an adequate nest can be made in c. 20 min of solid activity (Stonehouse 1956). May partially build two or three nests within 2 m of final site; do not reoccupy site from previous year (Stonehouse 1956). **MEASUREMENTS**: Largest nest, 50.8 cm (Falla 1937).

**Eggs** Ovoid; dark stone with irregular blotches of dark and light brown, mostly at larger end (Oliver). S. Georgia: ground-colour, olive-brown, flecked brown-purple and grey (Stonehouse 1956). **MEASUREMENTS, WEIGHTS**: Summarized in Table 2. **VOLUME**: Antipodes Is: 100.6 ml (6.93; 95.6–103.7; 20) (Moors 1980); Palmer Stn: 99.9 ml (9.27; 82.8–112.1; 16)

Table 2

Location	Length	Breadth	Weight	
Anvers I.	73.6 (3.18; 68.6–79.5; 16)	53.1 (1.66; 50.1–55.4)	–	1
Antipodes Is	74.8 (2.55; 73.3–77.0; 20)	53.0 (1.57; 52.6–53.5)	–	2
Marion I.	76.6 (72.2–84.2; 43)	52.6 (50.1–60.2)	100 (84–119; 21)	3
	76.4 (71.0–81.9; 136)	52.7 (50.1–56.2)	111.7 (92–134; 128)	4
Iles Crozet	76.5 (72.0–85.0; 20)	52.9 (45.0–59.0)	101 (90–120; 20)	5
Iles Kerguelen	75.2 (70.8–80.0; 17)	53.3 (50.4–54.6)	–	6
S. Georgia	75.5 (3.40; 71–82; 20)	53.2 (2.26; 51–58)	–	7
S. Shetland Is	73.1 (69.8–76.5; 31)	52.2 (49.9–58.9)	93.9 (82.0–115.0; 31)	8
	74.2 (2.9; 68.7–80.1; 80)	52.0 (1.4; 48.5–55.3)	–	9

(1) P.J. Pietz; (2) Moors (1980); (3) Rand (1954); (4) Williams (1980b); (5) Barré (1976); (6) Paulian (1953); (7) Stonehouse (1956); (8) Jablonski (1986); (9) Peter *et al.* (1990).

(Parmelee 1988). First laid eggs significantly longer, and with greater volume, than second laid eggs (Hemmings 1989).

**Clutch-size** Usually two eggs; occasionally, one; nests with four eggs a result of two females laying in same nest (Downes *et al.* 1959; Burton 1968a). Oliver says two or three eggs per clutch; records of a pair, a trio and a group of seven birds laying three eggs (Hemmings 1989).

**Laying** First egg laid 2 days after scoop made; second egg, 2 days later (Burton 1968a). Laying interval 2–3 days (Stonehouse 1956); at 15 nests, 2 (n=3) or 3 (n=12) days (Williams 1980b). If first egg lost, will re-lay two more; if egg lost because not incubated, new nest made and clutch re-laid after a few days; will not re-lay if complete clutch lost (Burton 1968a), though Bailey & Sorensen (1962) said second clutch laid if first clutch removed from nest; continue to incubate remaining egg if other removed from nest. Neither removal of first egg, nor adding egg to nest already containing one, inhibited laying of a second egg (Stonehouse 1956). Two clutches of two eggs hatched 48 and 72 h apart (Moors 1980).

**Incubation** Begins when clutch complete. Stints average 115 min (60–150; 9) (Burton 1968a). Sitting bird only leaves nest during change-over, to defecate or to be fed (Burton 1968a). Female incubates more than male (Downes *et al.* 1959). As incubation progresses, one or both of pair often leave eggs on warm sunny days (Stonehouse 1956). Eggs that roll out of, or are removed from, nest, not retrieved but eaten; it is possible to stimulate parent to roll egg back to nest but only if both eggs removed and placed <10 cm from edge of nest (Burton 1968a). **INCUBATION PERIOD:** 28–29 days (Downes *et al.* 1959); 32 days (n=3) (Stonehouse 1956); from laying to hatching, 30.5 days (29–31; 16) (Burton 1968a); from last egg laid to hatching, 29 days (0.7; 28–30; 10); laying to hatching interval of ten first eggs, 30 days (0.3; 30–31) (Williams 1980b); at one nest, 29–32 days (G.A. Taylor). Hatching interval of ten clutches, 2.1 days (0.7; 1–3) (Williams 1980b). Eggs usually start to chip 2–3 days before chick emerges (Stonehouse 1956; Burton 1968a; G.A. Taylor). Incubate infertile or addled eggs up to 7 days longer, then eat them (Burton 1968a). Egg-shells removed from nest, usually by c. 2 days after hatching; once not removed for 9 days; shells moved a few centimetres to a few metres; those moved a short distance, later moved farther (Burton 1968a). Skuas will incubate Gentoo Penguin eggs if placed within 10 cm of nest (Stonehouse 1956).

**Young** Semi-precocial; ptilopaedic. May leave nest within a few hours of hatching (Stonehouse 1956); within 24 h (Burton 1968a); often found away from nest within a few days of hatching (Downes *et al.* 1959). In some areas, nest loses all

significance to chicks and parents within 24 h of second chick hatching; roam near nest for first few days, later moving to other parts of territory (Stonehouse 1956). Become more active when 3 weeks old, wandering round nesting area, up to 91 m away, usually toward a roosting site where rocky ground provides more cover (Burton 1968a). Feathers begin to appear at c. 10 days (Barré 1976); primaries visible at 13–15 days, fully grown at c. 55 days (Stonehouse 1956; Williams 1980b); contour feathers appear at 19–21 days (n=1); down still visible for up to 4 weeks (Stonehouse 1956). **Growth** No significant difference between growth rate of first and second hatched chicks, or between chicks in pairs and in trios (Hemmings 1989). **WEIGHT:** Mean weight at hatching: Antipodes Is, 74.3 g (65–87; 7) (Moors 1980); S. Shetland Is, 76.2 (71.0–81.0; 12); Marion I., within 24 h hatching, 76.9 (6.6; 63–92) (Williams 1980b). Weight of yolk sacs of two chicks collected within 24 h of hatching, 6.1 and 4.4 g (Williams 1980b). Gain of weight of chicks in first 4 days small and some may even lose weight; after 4 days, gain of weight rapid, up to 40.4 g/day (Moors 1980). On S. Shetland Is (from growth curves in Peter *et al.* 1990): at 10 days, 330; 20 days, 740; 30 days, 1150; 40 days 1410. On S. Georgia (one chick): at 4 days, 100; 8 days, 180; 13 days, 315; 21 days, 660; 30 days, 1200; 44 days, 1600; 55 days, 1700 (Stonehouse 1956). On Campbell I. (one chick): on Day 1, 71.5; Day 3, 110; Day 6, 182; Day 9, 281; Day 17, 625; Day 24, 1005; Day 28, 1220; Day 33, 1170 (G.A. Taylor). Chicks of trios significantly heavier than chicks from pairs at between 10 and 50 days after hatching (Williams 1980a) *cf.* Hemmings (1989) found no significant difference. **LENGTH OF BILL:** Antipodes Is: at hatching, 17.8 mm (17.3–18.2; 4); little increase in first 4–5 days; average daily growth after 4 days, 1.0 mm (0.7–1.2; 6) (Moors 1980). **LENGTH OF CULMEN:** Marion I. (from growth curves and Table 3 in Williams 1980b): at hatching, 18.2 (0.6; 42); 10 days, 28; 20 days, 37; 30 days, 46; 40 days, 50; 50 days, 52; 55 days, 52.1 (2.2; 15); growth most rapid during first 30 days (Williams 1980b). **LENGTH OF TARSUS:** Marion I. (from growth curve and Table 3 in Williams 1980b): at hatching, 27.1 (1.4; 42); 10 days, 47; 20 days, 66; 30 days, 77; 40 days, 80; 50 days, 80; 55 days, 80.2 (2.0; 14). S. Shetland Is (from growth curve in Peter *et al.* 1990): at 5 days, 35; 10 days, 45; 15 days, 53.5; 20 days, 61.5; 30 days, 72. **LENGTH OF WING:** S. Shetland Is (from growth curve in Peter *et al.* 1990): at 10 days, c. 45; 20 days, 108; 30 days, 185; 40 days, 260. At 40 days, mean length of longest primary, 202.6 mm; maximum daily growth, 6.8 mm (Williams 1980b). **LENGTH OF TAIL:** S. Shetland Is (from growth curve in Peter *et al.* 1990): at 20 days, 14; 25 days, 25; 30 days, 43; 35 days, 64; 40 days, 87; 45 days, 106. **Parental care, Role of sexes** Brooded almost

constantly during first 24 h; brooded less up to 7 days, and only sporadically up to 14 days old; in some areas, chicks always return to nest to be brooded; females brood more than males (Burton 1968a). Brooding not correlated with weather (Burton 1968a). On Heard I., young may be brooded by either parent in squats or unlined nests in grass (Downes *et al.* 1959). When brooding ends, nests ignored, chicks rest in natural hollows or against rocks (Burton 1968a). Chicks c. 1 month old defend themselves, driving away intruding Skuas by rushing forward, squealing (Burton 1968a). First fed within 24 h of hatching (Burton 1968a; Williams 1980b). Both parents take equal share in feeding; chicks led away from nest to be fed, parent regurgitates food onto ground, picks up pieces in tip of bill for chick to peck, other parent often helping. At 2 weeks, chick takes food directly from ground; chick or parents may initiate feeding (Burton 1968a). By 50 days, start feeding themselves from carcasses on beach (Stonehouse 1956). Lack of droppings round nest indicate chicks defecate away from nest (Burton 1968a).

Weight of chicks according to hatching order and brood size given in Table 3 (Williams 1980b):

Table 3

AGE (days)	1	2	3	4
0	81 (7.2; 5)	79 (7.3; 6)	81 (7.0; 11)	75 (4.3; 12)
10	326 (41.8; 6)	327 (34.6; 5)	327 (36.8; 11)	323 (57.3; 12)
20	780 (145; 5)	714 (81.9; 4)	750 (119; 9)	812 (136; 13)
30	1214 (137; 5)	1162 (87; 4)	1191 (114; 9)	1208 (143; 6)
40	1442 (162; 4)	1486 (52; 4)	1461 (121; 8)	1462 (155; 10)
50	1460 (14; 5)	1488 (88; 4)	1476 (64; 9)	1566 (137; 8)

(1) First hatched of brood of two chicks; (2) Second hatched of brood of two; (3) Combined average; and (4) Broods of one chick.

**Fledging to maturity** FLEDGING PERIOD: Start to fly at c. 60 days, but continue to run from danger until fully proficient at take-off and landing, c. 2 weeks later (Burton 1968a); most chicks able to fly at 55–60 days (Hemmings 1989); youngest chicks flew at 50 days, oldest at 65 days, most between 55 and 60 days (Williams 1980b). Timing of first flight governed by development of chick and suitability of site for practice; on Chatham Is, fledge after mean 9.3 weeks (1.0; 7–10.5) (Young 1978). Stay in territory of parents after fledging, for 3–4 weeks after flying (Downes *et al.* 1959; Burton 1968a). One parent stays with young till they leave territory, or 1–2 days after; the other parent leaves a few days before (female in eight pairs studied; Burton 1968a).

**Success** Antipodes I.: from 13 eggs, 7 (53.8%) hatched (Moors 1980). Chatham Is: fledging success for 11 nests, 1.55 young/nest (Young 1978). On Mangere I., mean number of chicks fledged each season per occupied territory, 1.10 (0.19; 0.74–1.42; 14 seasons); on South East I., 1.19 (0.19; 1.00–1.39; 14 seasons) (E.C. Young). On South East I., over three seasons: hatching success of pairs, 73–85%; fledging success from eggs laid, 65–85%; hatching success of trios, 55–80%; fledging success from eggs laid, 55–80%; number of fledgelings produced by trios significantly lower than by pairs (Hemmings 1989). On Marion I. from 57 eggs from 29 pairs, 45 (78.9%) hatched and 28 (49.1%) fledged (= 0.966 young fledged per pair) (Williams 1980b; though note data in Williams' Table 3 not consistent with data in text); two-egg clutches have higher hatching success (88%) than single-egg clutches (75%) (Williams 1980b). On Heard I.: from 30 pairs and 60 eggs, 35

(58.3%) young fledged (= 1.17 young per pair) (Downes *et al.* 1959). On S. Georgia: from 20 eggs, 12 (60%) hatched, nine (45%) fledged; four young removed by researcher (Stonehouse 1956). On Signy I.: from 128 eggs, 85 (66.4%) hatched, 77 (60.2% [not 59%]) fledged (= 1.18 young fledged per breeding pair); annual variation in study area (n=3 years): hatching success, 57–72%; fledging success, 45.9–69.8%; young per pair, 0.89–1.36; fledging success at other localities, 53–71% (n=7 years); main causes of loss of eggs were: failure to incubate after laying (30.4%), followed by failure to hatch (23.9%), accidentally lifted out of nest (19.6%), broken (8.7%), and unknown (17.4%); no record of abandoning eggs once incubation begun (Burton 1968a). On S. Shetland Is, from 56 eggs in 31 nests, 38 (67.9%) young fledged (= 1.2 young fledged per breeding pair) (Jablonski 1986); pairs that defend optimal feeding territories fledged significantly more young than those without, 1.15 young per pair (0.19; 13); pairs with suboptimal territories fledged no young (n=3); and pairs with no territory fledged 0.38 young per pair (0.26; 8) (Trivelpiece *et al.* 1980). On Anvers I.: hatching success, 90% (10.8; 73–100); fledging success, 1.4 young per pair (0.4; 0.7–1.8) (Pietz 1987); 9-year summary for nine males and nine females banded as breeding adults: males fledged 4.6 young (2.2; 1–7); females fledged 6.1 young (3.2; 1–12) (P.J. Pietz); similar data in Parmelee & Pietz (1987) included hybrid pair; pairs with territories had no advantage over those without (Parmelee 1992). On Signy I., 1958–65, success rate decreased as total number of pairs increased, possibly through increase in number of inexperienced pairs; experienced pairs (both members have been paired in previous years) have higher fledging success (71%; n=113 pairs) than inexperienced pairs (52%; n=115 pairs); success of 20 pairs in their second season 17% higher than first, and only further 2% (19% higher than first) in their third (Burton 1968a).

**PLUMAGES** Prepared by D.J. James. Begin pre-juvenile moult at c. 13 days and fledge at 50–63 days (Stonehouse 1956; Osborne 1985; Burton 1968a). Undergo complete post-juvenile moult to immature non-breeding plumage in first year, followed by partial pre-breeding moult to immature breeding plumage (these two plumages poorly known; see Ageing). Thereafter, undergo complete post-breeding and partial pre-breeding moults each cycle, producing alternating non-breeding and breeding plumages with little or no seasonal change in appearance. Transition to adult plumage gradual, and immatures (possibly up to third year) differ only slightly from older birds (see Ageing). Minimum age of first breeding probably 4 years (Furness 1987) but not recorded breeding until 6–8 years old; see Social Organization. Sexes similar in plumage, though females slightly larger than males. Seasonal variation slight. Considerable individual and geographical variation but no morphs. Four allopatric subspecies; only *lonnbergi* recorded in HANZAB region. Some hybridization with South Polar and Chilean Skuas (see Geographical Variation and introduction to Stercorariinae). Subspecies *lonnbergi* described below.

**Adult** (Definitive basic and alternate). Sexes similar; in mated pairs on S. Shetland Is, males often darker (36%) than mates; rarely paler (2%) (Peter *et al.* 1990). Feathers of head and body have concealed pale-grey (dirty 86) bases, about one-quarter or less of feather. Much individual variation, apparently resulting from: (1) ground-colour of plumage of head and body; and (2) amount of pale streaking and blotching on feathers. Darkest birds almost uniform, very dark brown with no contrast between upperparts and underparts; palest show

some contrast between lighter brown underparts and dark upperparts. Both dark and light birds can show much or little pale mottling, especially on upperparts. Brown colours in plumage characteristically have red or tawny tone. **Head and neck** In darkest birds, uniform dark brown (219–121) without marked contrast between crown and cheeks (and without strongly capped effect). Pale birds show some contrast between dark-brown (219) cap and brown (123) sides of head; some are grey-brown (c28) round base of bill, especially round interramal area (though never so prominently as in South Polar Skua). Palest birds have untidy light grey-brown (c119C) fringes to scattered feathers of forehead and crown, which are most prominent when worn. Nape slightly to distinctly paler brown, tinged yellow (c121C), forming half-collar; feathers have profuse to sparse, fine straw-yellow (56) to yellow-brown (123C) or light-brown (123A) shaft-streaks; half-collar more obvious when shaft-streaks palest and profuse; streaks extend variously and untidily, but less profusely, to ear-coverts, hindneck and sides of neck and, sometimes, sparsely to foreneck; anterior edge of area of streaking somewhat well defined (though less so than in subspecies *antarctica*) but rear edge ill-defined. Prominence of streaks affected by following: (1) streaks become much paler with wear, while ground-colour changes little; (2) streaks become paler and more profuse with age, at least over first few years (juveniles and probably first-year birds have no streaks); and (3) some have darker napes than others, apparently throughout life. It has been suggested that streaks are a feature of breeding plumage. However, they are found on skins from all months, though they may be slightly duller in non-breeding plumage (no skins in moult show obvious difference between old and new shaft-streaks). Some birds have white flecks on head, which are usually asymmetrical and independent of darkness of plumage, suggesting leucism, possibly increasing with age. **Upperparts** Dark brown, varying greatly from almost uniform to heavily mottled white and rufous-brown. In darkest birds (with inconspicuous streaks on nape), mantle, dark brown (219–121), not contrasting with head, and with occasional light-brown (123A) shaft-streaks. In palest birds, mantle, grey-brown (c91) with scattered straw-yellow (56) shaft-streaks; mantle contrasts slightly with darker crown and is more affected by wear than head so that contrast increases slightly with wear. Scapulars, back, rump and uppertail-coverts mainly black-brown (119) when fresh, dark brown (121–21) when worn; some feathers have irregular, white to off-white tips or distal edges (flecked dark brown [121]), forming pale mottling and streaking; some birds have large irregular white blotches on scattered feathers. Whitish markings can comprise up to c. 20% of surface of scapulars; tend to be more frequent on birds with paler underparts; apparently number and size of blotches increases with age, though some adults remain rather uniform. Markings more common on scapulars and back, decreasing to rear and only a few birds have markings on tail-coverts. Some birds have a small number of feathers (usually <10%) with rufous-brown (136–37) to light rufous-brown (139) blotches or streaks, which vary from small to quite large, elongate to rounded and give impression of sparse rufous splotching over scapulars. **Underparts** **DARKEST BIRDS:** Uniform dark brown (121) when fresh, showing little contrast with head, upperparts or wing-coverts. Most birds slightly paler, tawny brown (c33), becoming grey-brown (91) when worn, and showing slight to moderate contrast with head, upperparts and underwing-coverts. **PALEST BIRDS:** Have some irregular straw-yellow (56) tips to feathers of upper breast, forming pale mottling; and sparse

irregular brown (123) tips to feathers of rest of underparts, forming faint brown mottling; very occasionally, a few straw-yellow (56) tips found on feathers of belly. Some birds have faint reddish tinge to ground-colour of underparts, but others greyer (very much like dark-morph South Polar Skua). Slight tendency to become paler from front to back but never abrupt. Axillaries, dark-brown (219) always matching wing-lining but sometimes contrasting slightly with body in pale birds. **Tail** Rather uniform, black-brown (119) to dark brown (219); can fade to greyish brown (28) with wear. Shafts, white, grading to brown (219A) at bases. Rectrices sometimes have white peppering or mottling on fringes, edges or tips (matching same on remiges). **Upperwing** Coverts like scapulars, black-brown (119) to dark brown (219) when fresh. Most birds have white speckling or mottling at tips on scattered coverts (like scapulars but less conspicuous). Narrow white bases to greater primary coverts sometimes partly visible during moult of lesser primary coverts. Tertiaries and humerals, black-brown (119) to dark brown (219), occasionally with white streaks or blotches along edges or tips. Remiges, black-brown (119), fading to dark brown (121) with wear, with white bases to inner web of p10 and both webs of p9 to p7 or p6 (and rarely inner web p5); white bases generally 15 mm (10–30) longer on inner web than outer and longer on outer feathers, decreasing inwards (amount of white visible beyond greater coverts on outer web of p9, 10–50 mm; of p6, 5–10 mm); also often mottled or speckled distally, not sharply demarcated from dark tips. White bases form white crescent across basal third of outer primaries, visible when wing spread and sometimes when wing folded. Secondaries have similar white bases but these normally concealed by greater coverts. Shafts of remiges, white, grading to dark brown (219A) near tip of primaries and about half-way along secondaries. **Underwing** Lesser and median coverts and subhumerals, black-brown (119) to dark brown (219) when fresh; no pale markings on lining. Remiges and greater coverts, dark brown (219) with reflective sheen that gives slight contrast (depending on light) with rest of coverts. White basal patch to primaries appears broader on underwing because white patch longer on inner webs. Remiges sometimes have off-white or light grey-brown (119C) markings along edges; markings asymmetrical, irregular, uncommon, and independent of ground-colour but correlated with amount of white streaking on upperparts.

**Downy young** Down, dense, woolly and moderately long. Upperparts, rather uniform light brown (c26–223C) to brown (223B) with an unevenly distributed rich tone (red and yellow pigments). Underparts, usually greyer, light grey-brown (119C) with no pattern.

**Juvenile** Concealed pale bases to feathers of head and body larger than in adult, up to two-thirds of feather. Individuals vary greatly, from uniformly very dark brown to slightly paler brown with rufous scalloping on upperparts. **Head and neck** Uniform dark brown (121–221); slightly richer and warmer than most adults; some have distinct rufous tinge to tips of feathers. On many, throat and ear-coverts, greyish brown (28), slightly paler than crown, producing impression of dark cap. With wear, fringes on nape and crown may become slightly paler but in general nape does not contrast with rest; never have yellow shaft-streaks. **Upperparts** Mantle, scapulars and upper back, dark brown (219–121), usually with tips or fringes mottled with red-brown (32), though sometimes unmarked; occasionally have narrow red-brown (32) shaft-streaks; red-brown may wear and fade to rufous-brown (37) or light brown (123A). Prominence of rufous marks decreases to

rear, so anterior scapulars more strongly marked than posterior ones. However, mantle sometimes uniformly dark brown (121), darker than scapulars; with wear, tips of feathers become much paler, almost light brown (c123A). Lower back to uppertail-coverts, uniformly dark brown (121) and probably never have rufous markings. **Underparts** Vary. Breast, belly and flanks, uniform dark brown (223) (darkest birds) to brown (219A) (paler birds); have more of a reddish tinge than most adults. Some have faint mottled tips to feathers at side of breast near bend of folded wing. Undertail-coverts, dark brown (121–219), usually slightly darker and browner than belly. Axillaries, dark brown (219) matching wing-lining and contrasting slightly with underbody. **Tail** Like adult. **Upperwing** Lesser secondary coverts like scapulars, with rufous markings in some birds. Rest of coverts, uniform dark brown (219–121). Marginal coverts, slightly paler and redder, dark brown (22) (rather like underparts). Primaries like adult but show much less white at bases (rarely more than 10 mm visible on outer webs and white not visible when wing folded [Jehl *et al.* 1978]). Secondaries, tertials and humerals like those of adult but without irregular pale markings. **Underwing** Like that of adult except white on primaries, narrower.

**Hybrids** *C.s. lonnbergi* hybridizes with *C. maccormicki*, probably wherever sympatric (see Geographical Variation). At least two hybrids (possibly from pale or intermediate *C. maccormicki* parents) were examined, collected Balleny Is, where both probably breed (NMNZ 11604), and Davis Stn, where only *C. maccormicki* breeds (MV B 17737). Hybrid plumages are poorly known and pose identification problems. These skins identified as hybrids by measurements (matching those of *C.s. lonnbergi*) and plumages. (1) Specimen from Balleny Is, a worn female. Head mostly dark brown, with no contrast between crown, ear-coverts and throat, giving hooded rather than capped effect. Prominent fine yellow shaft-streaks on paler nape. Mantle, greyish brown (28), contrasting somewhat with dark brown rest of upperparts and upperwing-coverts; white blotches on scapulars, uppertail-coverts and humerals, more prominent and irregular than usual in *C. maccormicki*, and more like *C.s. lonnbergi*. Underparts, light grey-brown (119C–27), like intermediate morph *C. maccormicki*, contrasting very strongly with dark brown underwing-coverts (normally diagnostic of *C. maccormicki*). Breast contrasts with throat (not known in *C. maccormicki*). A second skin from Balleny Is (NMNZ 11518) is similar but identity not certain. (2) Specimen from Davis Stn, a male. Similar to specimen from Balleny Is in having cold, light grey-brown underparts contrasting with blackish underwing-coverts, mantle contrasting with rest of upperparts, and scapulars with prominent irregular white blotches. Has capped rather than hooded appearance (throat does not contrast with breast). Fringes to feathers of sides of breast, washed yellow and suggest *C. maccormicki*.

Parmelee (1988) and Peter *et al.* (1990) describe hybridization involving dark-morph *C. maccormicki*, but details of plumages are scarce. On the Antarctic Pen., adults resembled small *C.s. lonnbergi* with 'somewhat rufous underparts and prominent yellow to white tipped' upperparts, and juveniles looked more like *C.s. lonnbergi* than *C. maccormicki* (Parmelee 1988).

**BARE PARTS** Based on photos (Pringle 1987; NZ DOC Slide Library; unpubl.: D.J. James; T. Howard). **Adult** Bill, uniform dull black. Mouth, pale pink to white. Eye, black. Narrow orbital ring, black. Legs, dull black. **Downy young**

Bill, black, with white egg-tooth at first. Mouth, dull pink. Iris, black. Narrow orbital ring, grey-black (83). **Juvenile** Bill, black on ridge of culmen and tip of both mandibles in front of gonys; sides of bill behind gonys, dull grey, with pink or blue-grey tinge giving subtle two-toned effect, which is useful in ageing, but duration uncertain. Iris, black. Narrow orbital ring, grey-black (83). Legs, dull, dark grey (c83), sometimes with blue tinge at tarsal joint; possibly have pale patches on tarsus (D.W. Eades). **Immatures** As adults.

**MOULTS** Based on about 85 skins with dates (AIM, CM, MV, NMNZ), 50 observations at sea from se. Aust. and between Tas., Heard I. and Antarctica (D.W. Eades, D.J. James), and some data from Anvers I. (Neilson 1983). Poorly understood; moult takes place mostly away from colonies; patterns complicated by difficulty in ageing birds and large geographical and individual variation. **Adult post-breeding** (Pre-basic). Complete, primaries outwards. One or two primaries moulted at a time. Rest of plumage moulted with primaries, but secondaries and head sometimes begin up to 1 month earlier. Secondaries centrifugal, usually with two active feathers, one at each front. On Anvers I., begin moult of body and inner primaries before leaving breeding colonies; moult of body begins early Jan., on belly, then breast and throat, then back and, by mid-Feb., nape and head; moult of primaries begins early Feb., with p1, followed quickly by p2 and p3 (leaving conspicuous gap in wing); one bird had new p1 when last seen 4 Apr. (Neilson 1983). On subantarctic islands of Atlantic Ocean, primaries often begin Feb., before adults leave colonies. In Pacific and Indian Oceans, primaries start mainly Mar.–May and finish by Oct., but pattern not properly known; many (possibly non-breeders or immatures) do not moult during this time: Oct.–Feb., none of 30 moulting; in Mar, 8/16; in Apr., 2/15; in June, 3/4; in July, 3/3; in Aug., 0/8; in Sept., 4/4. Skins from South Africa mostly in active primary-moult, July–Sept. (Brooke 1978). **Adult pre-breeding** (Pre-alternate). Partial moult of head and neck (particularly nape), but usually not body. Most adults actively moulting, Sept., when post-breeding moult of primaries nearly finished. **Pre-juvenile** From two chicks at S. Georgia (Stonehouse 1965): remiges appeared at Day 13–15, contour feathers on Day 19–21; by Day 40 contour feathers, though still growing, covered chicks; remiges fully grown by Day 55 and birds flew before Day 60. **Post-juvenile** (First pre-basic). Complete, primaries outwards. Timing uncertain but probably later than adults; single beachcast birds from NI, NZ, and Vic. in Apr. not yet moulting; birds in early stages of primary-moult at sea in Sept. (when adults would be finishing) tentatively identified as juveniles or immatures.

**MEASUREMENTS** Variation complex (see Geographical Variation). Skins measured (AIM, CM, MV, NMNZ) mostly from Indian Ocean and subantarctic islands of NZ; sex based on label data (referred to as 'from skins' throughout). Raw data from literature from various locations are here combined and analysed, but caution required in interpreting these statistics since data were collected by numerous investigators, probably using slightly different methods (especially for wing), and include both fresh and dried measurements (referred to as 'from literature' throughout); sources are Bailey & Sorensen (1962), Elliot (1957), Hagen (1945, 1952), Holgersen (1957), le Morvan *et al.* (1967), Lowe & Kinnear (1930), and Westerskov (1960). Data from Falla (1937) not used because most of these specimens were measured again.

Subspecies *lonnbergi*. (1–5) Adults and immatures, skins and literature combined. (1) Throughout much of range (no data for Antarctic Pen.). (2–4) As (1) but separated geographically: (2) NZ region, including Chatham and subantarctic islands; (3) Macquarie I.; (4) Subantarctic islands of Indian Ocean (Heard I., Iles Kerguelen et Crozet); (5) Subantarctic islands of Atlantic Ocean (S. Georgia, S. Orkney and S. Shetland Is).

	MALES	FEMALES	
WING	(1) 411.9 (13.9; 375–447; 78)	420.6 (17.6; 381–475; 77)	**
	(2) 424.6 (12.7; 404–447; 25)	431.6 (18.2; 406–475; 24)	ns
	(3) 416.5 (6.1; 404–424; 13)	421.9 (14.4; 400–453; 22)	ns
	(4) 400.2 (6.4; 390–410; 10)	419.5 (12.3; 430–437; 6)	**
	(5) 402.7 (9.0; 375–415; 24)	404.7 (13.7; 381–425; 13)	ns
TAIL	(1) 156.8 (11.2; 138–193; 35)	159.5 (10.2; 143–183; 22)	ns
BILL	(1) 54.7 (3.17; 43.5–61.5; 79)	55.3 (3.2; 44.0–62.0; 79)	ns
	(2) 56.5 (1.81; 53.0–61.5; 26)	55.4 (3.07; 47.5–60.0; 26)	ns
	(3) 55.5 (2.24; 51.0–57.5; 13)	56.9 (1.80; 53.9–62.0; 22)	*
	(4) 53.9 (4.89; 43.5–59.0; 10)	57.4 (0.38; 57.0–57.9; 5)	ns
	(5) 52.6 (2.81; 47.0–58.5; 24)	51.7 (3.57; 44.0–55.0; 13)	ns
TARSUS	(1) 74.4 (4.98; 62.3–95.0; 70)	77.1 (4.45; 64.0–92.0; 82)	**
	(2) 77.2 (3.97; 68.5–82.1; 18)	78.9 (4.9; 69.0–92.0; 26)	ns
	(3) 77.9 (5.60; 73.3–95.0; 13)	77.7 (2.97; 71.1–82.7; 22)	ns
	(4) 71.2 (2.19; 68.0–75.0; 10)	75.1 (2.77; 70.2–77.8; 6)	**
	(5) 71.2 (3.33; 62.3–76.0; 23)	71.5 (3.53; 64.0–77.0; 13)	ns
TOE	(1) 66.6 (2.89; 61.9–72.9; 31)	68.1 (3.15; 62.5–75.2; 22)	ns

Sexual dimorphism weak; females slightly larger than males in some measurements and some samples only; Furness (1987) reported similar observations. However, in mated pairs, females usually larger and heavier (Barré 1976; Furness 1987; Peter *et al.* 1990; P.J. Pietz; E.C. Young) and data from studies using sex-specific DNA marker show that this is so (Millar *et al.* 1992).

When sexes combined, significant differences ( $P < 0.01$  unless stated) found between samples

WING	(2) >(3) [ $P < 0.05$ ]	>(4)	>(5)
BILL	(2), >(3), (4)	>(5); (3)	>(4)
TARSUS	(2), (3)	>(4), (5)	

Size decreases gradually from NZ region W to subantarctic islands of Atlantic Ocean; birds from Atlantic Ocean have smaller bills than those from Indian Ocean but do not differ in length of wing and tail; birds from Macquarie I. smaller than birds from NZ region, but closer to NZ birds than to birds from Heard I. Data in Hamilton (1934), Barré (1976), Brooke (1978), Clancy (1981), Furness (1987), Rand (1954), Swales (1965), Weimerskirch *et al.* (1989) and Murphy also show cline in size from E to W. Unsexed data for Aust. waters in HASB.

**WEIGHTS** Subspecies *lonnbergi*. (1) Chatham Is, adults, 1–10 Dec. 1994 (E.C. Young). (2) Stewart and Chatham Is and NZ subantarctic islands, label data (NMNZ). (3) Macquarie I., label data (MV). (4) Iles Crozet (Barré 1976).

	MALES	FEMALES	
(1)	1735 (75.37; 1610–1960; 30)	1935 (129.5; 1660–2180; 32)	–
(2)	1735 (291; 1300–2108; 5)	1432, 1665, 1924	
(3)	1761 (318; 1415–2150; 4)	1837 (160; 1670–2180; 13)	
(4)	1536 (1250–1650; 8)	1735 (1560–1800; 6)	*

Subspecies *lonnbergi*. (5) Iles Kerguelen, live, Nov.–Feb. (Weimerskirch *et al.* 1989). (6) Iles Crozet, live (Barré 1976). (7) King George I., S. Shetland Is, breeding adults (Peter *et al.* 1990). (8) Anvers I. (P.J. Pietz). (9) Anvers I. (Neilson 1983).

UNSEXED	
(5)	1922 (163; 1670–2130; 15)
(6)	1630 (1250–1800; 44)
(7)	1683 (176; 1400–2150; 77)
(8)	1768 (1550–2050; 14)
(9)	1802 (1381–2212; 47)

**STRUCTURE** Wing, pointed and long but broader and more rounded than in *Stercorarius*. Eleven primaries; p10 longest; p9 2–14 mm shorter, p8 17–28, p7 32–47, p6 55–72, p5 78–95, p4 100–113, p3 128–145, p2 149–173, p1 170–191; p11 minute, c. 10 mm long. Eighteen to 20 secondaries, including four tertials. Twelve rectrices, with broad rounded tips; tail, fairly short, slightly wedge-shaped to rounded (t2 12–24 mm longer than t6); central rectrices usually project 14–25 beyond t2 but often broken off level with t2; in juveniles and some older birds, central rectrices do not project; variation in projection of t1 renders length of tail a poor measurement for comparison. Bill, heavy and strong; straight, short, deeper than wide but quite wide at base; inconspicuous horny cere at base, slightly wrinkled in adults, less so in juveniles; sutures between bill-plates prominent; upper and lower ridges nearly parallel from base to gonys; reinforced ridge along tomium; tip of culmen, bulbous with strongly hooked nail; steep, prominent gonydeal angle; nostril elongate, slit-like. Depth of bill at gonys: 21.3 mm (20.5–22.5; 30) (Neilson 1983); 21.0 mm (19.4–22.3; 14) (P.J. Pietz). Tibia mostly feathered, bare distally. Tarsus, longest of skuas, heavy, laterally flattened; single column of heavy scutes on front of tarsus; small reticulate scales elsewhere. Middle and outer toes quite long; outer 91–95% of middle, inner 59–72%, hind 11–13%, raised. Full webbing between inner, middle and outer toes. Claws moderately long, strong, laterally compressed, strongly hooked and sharp.

**AGEING** Juveniles readily separated from immature and adult plumages by: uniform, rich dark-brown plumage without contrasting pale nape and shaft-streaks; often, rufous tinge or fringes at tips of feathers, especially on scapulars and breast; smaller white patch at base of primaries, which is not visible when wing folded; and bill bicoloured (see Bare Parts). After post-juvenile moult, immatures cannot be separated reliably from adults on current knowledge. White mottling and streaks in plumage apparently increase with age, so heavily marked birds are probably at least several years old. However, there is too much individual variation and insufficient information to use this accurately. Immatures may lack pale streaks on nape or have only faint ones (there is no conclusive evidence of this), but many dark adults also have faint streaks.

**GEOGRAPHICAL VARIATION** For discussion of relationships within *Catharacta*, see introduction to Subfamily Stercorariinae. Here, we treat *skua*, *antarctica*, *lonnbergi* and *hamiltoni* as four subspecies of *Catharacta skua* (which has nomenclatural priority) (Devillers 1977, 1978; Brooke 1978; Furness 1987; cf. Murphy; Aust CL.; BWP).

Plumages are of little use in taxonomy because there is

much complex variation within taxa compared with between taxa, and measurements have been relied upon. However, in discussing taxonomy, Furness (1987) advocated caution in interpreting relationships from measurements; he described correlations between length of tarsus and height of vegetation on breeding grounds, and between wing-loading and amount of aerial foraging undertaken during breeding.

The subantarctic group (*lonnbergi*, *hamiltoni*, *antarctica*) is characterized by dark-brown plumage with slight rufous tinge and numerous whitish blotches. Subspecies *lonnbergi* most widespread of these forms, with circumpolar subantarctic breeding distribution. Formerly, different subspecies have been recognized in each ocean (Lowe & Kinnear 1930; Mathews; Peters), but Hamilton (1934), Murphy, and Falla (1937) concluded that these could not be distinguished on plumages nor measurements. Differences in plumage between oceans or islands outweighed by great individual variation within populations, and confused by poorly understood variation associated with wear, age and season. There is a w. cline in diminishing size from NZ to islands of Atlantic Ocean, with significant differences between oceans (see Measurements), but differences do not justify subspecific division (Hamilton 1934). Lowe & Kinnear (1930) suggested NZ populations darker with less yellow on nape than other populations. Birds from Campbell I. are slightly larger and darker than those from other NZ islands (skins, NMNZ).

**Subspecies *antarctica*** (the smallest *Catharacta*) is distinctly smaller than *lonnbergi* (see below) with stocky appearance, square-looking head and prominent supra-orbital ridges (Devillers 1978). Plumage differs from that of *lonnbergi* by: adults often have rather capped appearance and sometimes have straw-yellow mottling on breast; juveniles usually have more rufous tone (Devillers 1977). Measurements from Falkland Is given in Table 4. When sexes combined, birds from Falkland Is have significantly smaller ( $P < 0.01$ ) wing, bill, and tarsus than those of *lonnbergi* from subantarctic islands of Atlantic Ocean (see sample 5, Measurements).

**Table 4.** Subspecies *antarctica*. Falkland Is: (1) Adults and immatures, skins and literature combined; (2) from Hamilton (1934).

	MALES	FEMALES	
WING	(1) 354.8 (36.6; 300–377; 4) (2) 375.5 (9.8; 360–390; 13)	383.2 (10.6; 368–398; 6) 383.6 (7.7; 368–400; 20)	* *
BILL	(1) 45.0 (4.6; 41–49; 4) (2) 46.4 (1.9; 44–51; 13)	49.0 (2.0; 47.0–52; 6) 48.0 (1.9; 45–52; 20)	ns *
TARSUS	(1) 66.1 (4.1; 60.0–69.0; 4) (2) 65.8 (2.0; 63–69; 13)	69.1 (0.8; 68.0–70.5; 6) 67.7 (1.9; 64–70; 20)	n *

**Subspecies *hamiltoni*** poorly marked, intermediate in size between *lonnbergi* and *antarctica*, but with wing and bill closer to that of *lonnbergi* and tarsus closer to that of *antarctica* (see below); head rather square, like that of *antarctica* (Devillers 1978). Compared with *lonnbergi*, adults often have somewhat capped appearance and more rufous and straw-coloured streaking on upperparts; juveniles similar to *antarctica* (Devillers 1978). However, Furness (1987) described juveniles as rather uniform dark brown with few streaks and little yellow and rufous tone in plumage. Subspecies *hamiltoni* accepted by most authors since described (Hagen 1952; Elliot 1957; Swales 1967; Devillers 1977, 1978; Clancey 1981; Furness 1987) but often tentatively, and Richardson (1984) argued that it is not subspecifically distinct from *lonnbergi*. Measurements given in

Table 5. When sexes combined: length of wing of sample 1 greater ( $P < 0.01$ ) than that of subantarctic Atlantic *lonnbergi* (see sample 5 Measurements); bill of subantarctic Atlantic *lonnbergi* greater ( $P < 0.05$ ) than bill of sample 1; and tail and tarsus do not differ; further, wing, bill and tarsus of sample 1 greater ( $P < 0.01$ ) than those of birds from Falkland Is (sample 1 of subspecies *antarctica*; see above). Weights of live breeding adults from Gough I. during breeding season (Furness 1987): males: 1429 (100; 1300–1600; 9); females 1649 (1550–1800; 9).

**Table 5.** Subspecies *hamiltoni*. (1) Tristan Grp and Gough I., data combined from Hagen (1945, 1952) and Elliot (1957). (2) Gough I., live birds (Furness 1987). (3) Gough I., live (Swales 1965). (4) Tristan da Cunha and Gough Is, skins (BMNH, Royal Scottish Museum, Edinburgh) (Richardson 1984).

	MALE	FEMALE	
WING	(1) 386.3 (7.4; 373–400; 14) (2) 397.9 (6.0; 388–409; 9)	390.8 (9.0; 378–402; 11) 412.4 (9.0; 398–423; 9)	ns **
TAIL	(1) 146.1 (6.3; 140–161; 8) (2) 154 (2.1; 152–158; 9)	148.6 (9.3; 134–161; 7) 151 (2.4; 148–154; 9)	ns *
BILL	(1) 53.0 (2.0; 50.5–56.8; 11) (2) 54.8 (1.3; 52–56; 9)	53.7 (1.2; 51.0–55.0; 10) 54.4 (1.3; 53–57; 9)	ns ns
TARSUS	(1) 71.0 (2.1; 69.0–74.8; 10) (2) 74.2 (1.8; 72–77; 9)	72.5 (1.6; 71.0–75.5; 9) 75.9 (2.3; 72–79; 9)	ns ns
UNSEXED			
WING	(3) 400.3 (381–419; 115) (4) 392 (8; 372–408; 15)		
TAIL	(3) 158.9 (4.47; 141–176; 115) (4) 158 (8; 142–172; 15)		
BILL	(3) 53.3 (50–56; 115) (4) 55 (2; 52–58; 15)		
BILL D	(3) 22.2 (20–25; 115)		
TARSUS	(3) 65.4 (78–94; 115) (4) 73 (2; 70–78; 15)		

Birds breeding Iles Amsterdam and St Paul similar in size to subspecies *hamiltoni* rather than to Indian Ocean *lonnbergi* (though bill is shorter); measurements given in Table 6. When sexes combined, birds from Iles Amsterdam and St Paul have shorter bills ( $P < 0.05$ ) than those from Gough I.; and have shorter wings and bills ( $P < 0.01$ ), and tails ( $P < 0.05$ ) than those from subantarctic Indian Ocean. Data on plumages lacking. Population at Tristan Grp and Gough I. undergo post-breeding moult during summer, coinciding with breeding (Hagen 1952; Swales 1965; Furness 1987) whereas birds on Iles Amsterdam and St Paul do not (Jouanin 1953). Jouanin treated these as *lonnbergi* despite differences in size, but this might be inconsistent with recognition of *hamiltoni* as a subspecies. Segonzac (1972) treated Amsterdam birds as *hamiltoni* based on measurements, and similarity of other species (*Eudyptes* penguins and *Sterna* terns) between these islands. However,

**Table 6.** Subspecies not certain. (1) Iles Amsterdam and St Paul; data from Jouanin (1953) and le Morvan *et al.* (1967) combined.

	MALE	FEMALE	
WING	(1) 387.5 (5.0; 385–395; 4)	399.2 (6.9; 390–409; 5)	ns
TAIL	(1) 146.0 (7.3; 135–150; 4)	149.2 (10.5; 134–160; 5)	ns
BILL F	(1) 52.3 (1.3; 51–54; 4)	51.6 (1.7; 49–54; 5)	ns
TARSUS	(1) 71.3 (1.3; 70–73; 4)	72.8 (1.8; 70–74; 5)	ns

morphological similarity between oceans may be convergence.

For description of nominate *skua*, see BWP.

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Volume 3, Plate 24

Great Skua *Catharacta skua* (page 388)

1 Adult on breeding grounds, austral summer; 2 Downy young; 3 Juvenile

South Polar Skua *Catharacta macconnicki* (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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Volume 3, 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