

Order ANSERIFORMES

Medium-sized to large aquatic, marine and terrestrial birds. Three families: (1) Anhimidae (screamers), (2) Anseranatidae (Magpie Goose) and (3) Anatidae (true wildfowl); Screamers confined to South America, Magpie Goose confined to Aust. and New Guinea, and rest cosmopolitan. Suggestion that the order is distantly related to Phoenicopteriformes and Ciconiiformes (see Sibley & Ahlquist 1972) now seems unlikely. Claims for some anatomical similarities with gamebirds such as Cracidae, suggesting distant affinity with Galliformes via Anhimidae and Anseranatidae (Simonetta 1963; Johnsgard 1968; Bock 1969), strongly rejected by Olson & Feduccia (1980).

All members of the Anseriformes are web-footed (in some semi-palmate) swimming (some now almost terrestrial) and diving birds that are filter-feeders or are derived from aquatic filter-feeders. They differ from Galliformes in almost every anatomical feature (see Olson & Feduccia 1980). The unique filter-feeding mechanism is diagnostic of the order. Two groups of filter-feeding birds probably evolved from some charadriiform origin; in one, the specialized mechanisms for filtering evolved in the lower mandible (flamingoes); in the other, the upper mandible housed the specialized tongue used to provide the pump-action for filtering. The complex structure of the bill and its operation during filter-feeding in a typical duck has been investigated recently (Zweers 1974; Zweers *et al.* 1977; Kooloos 1986; Kooloos & Zweers 1989; Kooloos *et al.* 1989). Sensory apparatus of the bill associated with this filtering function is likewise complex (Berkhoudt 1980). The typical bill, representing the fundamental apparatus unique to the order, acts as a double-action suction-pump in which fluid is drawn in at the tip and expelled past filter plates at the sides and rear. The tongue and internal shape of the bill provide the elaborate piston effects and the lamellae or fine plates, common to all members of the order, act as the sieves. Lamellae trap the food, which is then brushed free and swallowed by the combined actions of tongue and lamellae. Vestigial lamellae occur in screamers (Olson & Feduccia 1980). Filtering is the original feeding method and departures from it towards adaptations for grazing in geese, serrated edges for catching fish in 'saw-billed' ducks (mergansers and allies) or superficially fowl-like bill of screamers, are all derived features (Olson & Feduccia 1980). Anhimidae, however, being extralimital, are not considered further.

The innovative modern classification of the ducks, geese and swans, and the systematic order proposed by Delacour & Mayr (1945, 1946) and Delacour (1954-64), was modified by Johnsgard (e.g. 1965a, 1968) in the light of further studies, particularly on behaviour and social signals, and new information on little known species. Woolfenden (1961) and Livezey (1986) have prepared phylogenetic analyses of the order based on morphological characters, and the classification by Livezey has been followed by some recent works (e.g. Madge & Burn 1988). Madsen *et al.* (1988) provide important additional information from DNA studies and give a partial classification of the order. We have adopted the classification of Johnsgard in Peters with some modification concerning only those species within our area. Our reasons for these changes are as follows but the arrangement of species fits closely the proposed classification of the order given by Sibley *et al.* (1988) and Madsen *et al.* (1988). The arrangement is consistent with the persuasive argument presented by Olson & Feduccia (1980) concerning the origin and evolution of the order. The fossil *Presbyornis* (Eocene; North America) and the endemic *Stictonetta* (Freckled Duck) and *Malacorhynchus* (Pink-eared Duck) of Aust. have special significance in this respect (see Olson & Feduccia 1980).

Special features of *Stictonetta* are: reticulated anterior face of tarsus; lack of a syringeal bulla; no speculum; unpatterned downy young (see Frith 1964a,b). Structure of the trachea and syrinx described by Ramsey (1878) and in more detail by Campbell (1889) and in Campbell demonstrate the lack of any development of a swollen bulla in drake. Claim by Frith (1964a, 1965, 1967, 1982) that tracheal loop occurs in mature drake is unconfirmed in many hundreds of birds examined (G.F. van Tets). Long neck. Uropygeal wax esters like those of some swans (Edkins & Hansen 1972) but chemotaxonomy difficult to interpret because similarities also shown with *Cereopsis*, *Branta*, *Cairina*, *Tadorna*, *Mergus* and *Melanitta* (Jacob & Glaser 1975). Brush (1976) has shown that the feather-proteins are unique. Verheyen (1953) on skeletal characters (cranial & post-cranial) concluded that it was sufficiently distinct to be separated from other waterfowl. Clearly it shows a large number of 'primitive' characters. Olson & Feduccia (1980) emphasize several features of the cranium that are unique in living ducks: the markedly recurved rostrum and mandible and the expanded lachrymal. Livezey (1986), largely from osteological characters, supports traditional conclusions that it is the last branch of the waterfowl with reticulate tarsi and places it after the geese and swans. Faith (1989) has shown that many of these skeletal characters might be explained on divergence between diving, dabbling and grazing adaptations. Recent DNA studies (Madsen *et al.* 1988) lend some support to an earlier suggestion, based on behaviour and some morphological features, of possible similarity with Oxyurinae (Johnsgard 1965b). Fullagar *et al.* (in press) add support to idea that *Stictonetta* has several behavioural similarities with stiff-tails. The uniqueness of this species has been widely supported, but in the past the absence of information about its behaviour and ecology ensured that it remained doubtful to which other group of

wildfowl it was most closely related. Many of these deficiencies have now been resolved (see text elsewhere) and the argument for a link with stiff-tails has become more compelling. Plumages, social signals and vocalizations are all in some way most readily comparable to *Oxyura* and *Biziura* but specially to *Heteronetta*. A seasonally colourful bill in the male most closely matches the condition found in *Heteronetta* but also in most stiff-tails; sequence of moults follow unusual pattern found in at least some, if not all, stiff-tails but not known in other wildfowl, notably the presence of a post-juvenile moult including wings. Many characteristics of breeding biology (nest-construction and choice of site; small clutch-size; predisposition to dump laying; appearance and quantity of down used in lining nest; unpatterned ducklings) are features shared with most stiff-tails. In particular the unusual copulation involving greatly elongated pseudopenis is most closely comparable with features shown only by stiff-tails.

Major recommended works of reference are: **Comprehensive accounts:** Delacour (1954-64); Todd (1979); Phillips (1922-26) [ducks]; Scott (1972) [swans]; Owen (1980) [geese]. **Regional accounts:** Palmer (1976) [Nearctic]; BWP [w. Palaearctic]; Bauer & Glutz von Blotzheim (1968-69) [Europe]; Frith (1982) [Aust.]. **Field guides:** Scott (1988); Madge & Burn (1988). **Special studies:** Hochbaum (1955, 1973) and SOWLS (1955) [migration and habits]; Johnsgard (1965a) [complete review of behaviour]; Hochbaum (1944); Driver (1974) and Kear & Berger (1980) [species monographs].

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Family ANATIDAE wildfowl

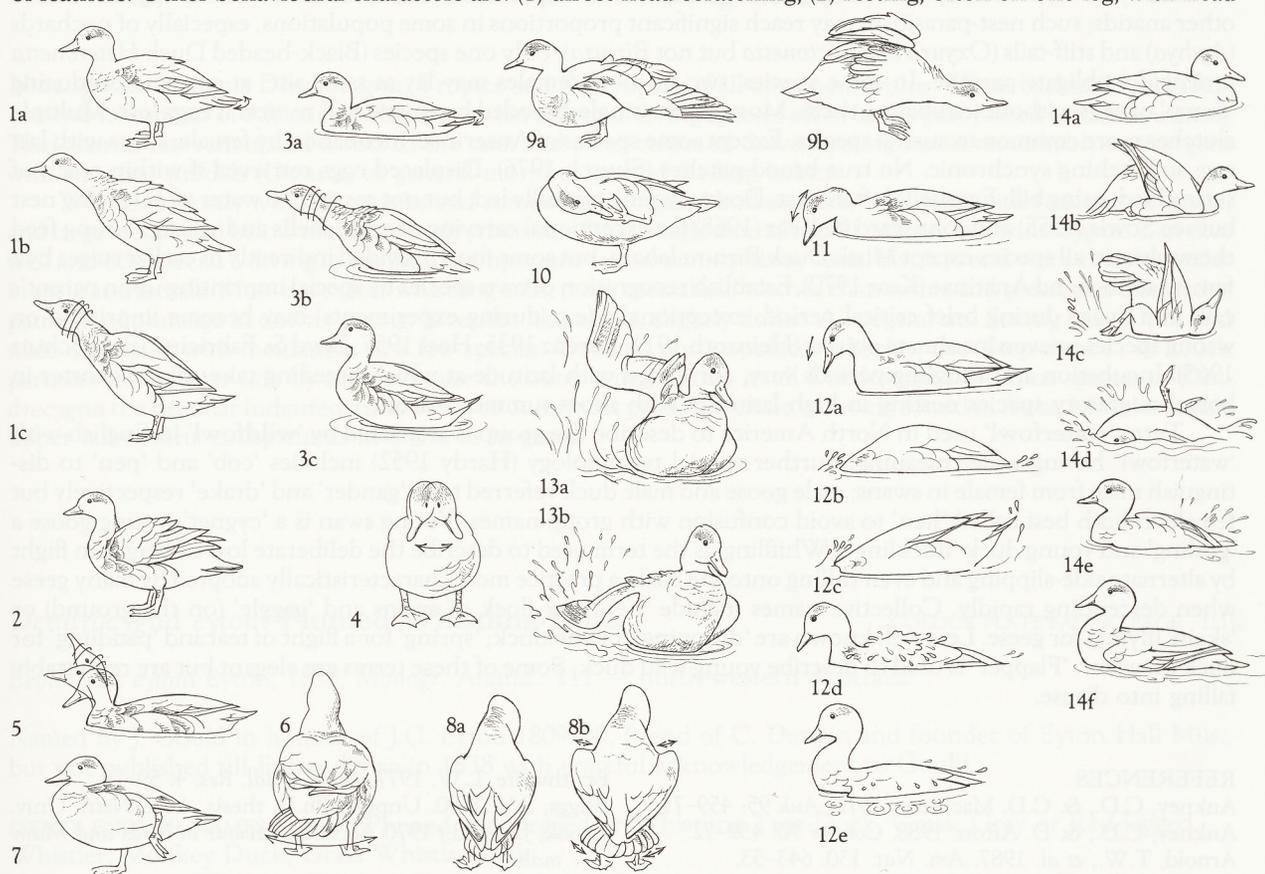
Waterbirds (some more or less terrestrial) with rather short legs and front toes connected by webs; hallux elevated and reduced. Though considerable adaptive diversity in outward appearance, size, colours of plumage, behaviour, and ecology, homogeneous in many characters, as attested by numerous, often fertile, interspecific hybrids reported, chiefly in captivity (see Gray 1958). About 160 species in six sub-families: (1) Dendrocygninae (whistling-ducks); (2) Oxyurinae (stiff-tails and Freckled Duck); (3) Anserinae (swans and geese); (4) Tadorninae (shelducks, sheldgeese and steamer-ducks); (5) Anatinae (dabbling ducks and allies); (6) Merginae (eiders, scoters, mergansers and allies).

Body, broad and rather elongated in many, though more rotund in some, especially diving species. Plumage, thick and waterproof; contour-feathers distributed over distinct feather-tracts with underlying coat of down. Neck, medium to long. Wings generally rather small; mostly pointed, fairly broad in many, but narrower in some highly migratory species. Small claws on first and second digits occur in most. Spurs—horny sheathed bones—occur in several species as projections near carpal joint; attached either to radial carpal or the metacarpal. Wing-spurs are found in the Tadorninae and *Sarkidiornis*, *Plectopterus* and *Merganetta* in the Anatinae. Eleven primaries; p9 nearly always longest, p11 minute. Wide range in number of secondaries, from 12 to 24, innermost (tertiaries) often long and brightly coloured; diastatic. Many species, particularly in Tadorninae, Anatinae and Merginae have a specialized, contrastingly coloured patch (speculum) on upper surface of inner wing, important for sexual and social signalling. Most fly fast and have large, high-keeled sternum. Tail, short and square or slightly rounded in most; long in some diving species (serving as rudder), pointed or with elongated central feathers in some others. Tail-feathers, 14–24 but varying even in single species. Bills show much adaptive variation but typically of medium length, broad, often flattened centrally and distally but high at base, and rounded at tip with horny nail at tip, producing slight terminal hook; covered with soft skin. Edges of mandibles with rows of lamellae, showing different development in various ecological types and taxonomic groups; most highly specialized in surface plankton-feeders, least so in species (such as scoters *Melanitta*) that swallow molluscs whole. Tongue, thick and fleshy; epithelium covered with papillae and horny spines. Lower part of tibia and tarsus bare; front toes connected by webs (reduced in a few species), hind toe elevated. Gait, striding or waddling. Oil gland, feathered. Aftershaft, reduced or absent. Special intromittent copulatory organ present in males; vascularized sac everted from wall of cloaca, protruded by muscular action; facilitates sexing by examination (Hochbaum 1942), even of small young. Salt-secreting nasal glands subject to adaptive variation in size, even in same species; enlarged in forms inhabiting saltwater or brackish habitats, modifying profile of head considerably. In many species, males have remarkably lengthened, bent, or locally widened trachea forming resonating tubes; also syngo-bronchial sound-boxes (bullae), either fully ossified or with membranous fenestrae. These vocal structures highly characteristic of species or larger taxonomic units (see Eyton 1838 and, especially, Johnsgard 1961, 1971). Considerable diversity in types of plumage: male and female similar, nearly similar, or show extreme sexual dimorphism. In all species, except some sheldgeese, flight-feathers moulted simultaneously, producing period of flightlessness lasting 3–4 weeks. Two body-moult per cycle. Young precocial and nidifugous, covered with thick down; pattern often cryptic and characteristic of taxonomic groups within sub-families. Able to swim soon after hatching.

Cosmopolitan, but absent from continental Antarctica and some islands. Usually on or close to water. Highly vulnerable to human pressures on habitats. Labrador duck *Camptorhynchus labradorius* extinct during last century, and three more (Crested Shelduck *Tadorna cristata*, Pink-headed Duck *Rhodonessa caryophyllacea*, Auckland Merganser *Mergus australis*) probably so this century. A few species domesticated: Swan Goose *Anser cygnoides*, Greylag Goose *A. anser*, Muscovy Duck *Cairina moschata*, and Mallard *Anas platyrhynchos* (Goodwin 1965); some populations of a few more (Mute Swan *Cygnus olor*, Canada Goose *Branta canadensis*, Egyptian Goose *Alopochen aegyptiacus*) kept in semi-domesticated or feral conditions.

N. forms often highly migratory and tied to Arctic or high latitudes for breeding, exploiting brief but productive period each year to raise young; for many of these species autumn movements preceded by marked moult-migrations by males to special areas for period of flightlessness. More sedentary in warmer latitudes, specially in equatorial regions. The term 'boreal' for these n. wildfowl is useful to draw attention to the marked differences between the breeding ecology of n. high-latitude wildfowl compared with many s. hemisphere species for which the term 'austral' has been used (Fullagar *et al.* 1988). In general, most austral species are more sedentary and certainly lack spectacular migrations. Regular movements in most s. hemisphere species are at best only local. Occasional much wider dispersal is often initiated by factors such as flooding rains and drought (specially in Aust.). Many austral ducks exploit seasonally persistent or occasional, extremely propitious conditions by responding with an extended breeding season. In reality, most are seasonal breeders but productivity of some will vary greatly according to rainfall and flooding; most notable with many species in Aust. For further details see Fullagar *et al.* (1988).

Wide range in diet, from totally vegetable to totally animal, and in feeding habits, from terrestrial grazing to bottom diving; correlated with conspicuous adaptations in structure of bill, musculature of head, length of neck, and in general proportions of body. Terminology of feeding methods in species accounts mainly after Szijj (1965) and Bauer & Glutz (1968, 1969); see also Olney (1963). Typical filtering action of most members of the order, described earlier, best termed 'suzzling'. Most species gregarious, feeding, loafing, roosting, and travelling in cohesive flocks, integrated by calls and special pre-flight signals. Generally solitary breeders nesting in concealed sites, though some species colonial, either habitually or, more often, as alternative to dispersed nesting, usually in protected areas such as islands. Degree of territorialism when breeding and relation between territory and nest-site vary between species and larger taxa; some strictly territorial; others occupy wholly or largely undefended home-ranges. Monogamous pair-bond in most species but much variation between taxonomic groups in duration of bond and degree of male promiscuity (if any). Social systems and displays correlated with formation and maintenance of pairs; complex (see classic work of Lorenz 1951-53) and largely dissimilar in six sub-families (see below). Copulation on water in all species (except some Anserinae and Tadorninae), typically with male grasping female's nape in bill. Vocalizations varied but generally simple (mainly honks, grunts, quacks, coos, and whistles); often different between sexes when linked with anatomical differences in vocal apparatuses (syringeal bullae). Non-vocal sound-signals produced in some species. Calls of downy young are: (1) Contact or Greeting Call (also termed Pleasure and Contentment Call) and (2) Distress Call (see Kear 1968). Comfort-behaviour well known. Bathing frequent and elaborate. Typically performed while swimming in water too deep for standing; involves head-dipping, wing-thrashing, somersaulting, and diving. Followed by oiling (with use of bill and head) and preening. Full description of comfort movements, the behaviour patterns of shaking, stretching, preening, bathing and related activities given by McKinney (1965). The diagrams (Figs 1 to 14) based on those from McKinney illustrate most of these actions, all of which are common to all wildfowl. Some essentially aquatic species (genera *Thalassornis*, *Oxyura* and *Biziura*) have other, slightly specialized, preening and shaking actions peculiar to them because they are performed on water. No elaborate thermoregulatory responses except erection of feathers. Other behavioural characters are: (1) direct head-scratching; (2) resting, often on one leg, with head



Figs 1-14. Comfort movements of Anatidae (based on Grey Teal): (1a-c) Body-shake; (2) Wing-shake; (3a-c) Swimming-shake; (4) Head-shake; (5) Head-flick; (6) Tail-wag; (7) Foot-shake; (8a,b) Wing-shuffle and tail-fan; (9a) Wing-and-leg Stretch; (9b) Both-wing Stretch; (10) Foot-pecking; (11) Bill-cleaning; (12a-e) Head-dipping; (13a,b) Wing-thrashing (14a-f) Somersaulting.

turned back and bill inserted in scapulars on same side as lifted leg (Heinroth & Heinroth 1954), latter being characteristically stowed away in waterproof flank 'pocket'.

Breeding strictly seasonal in boreal, migratory species and populations; less so or opportunistic at warmer latitudes. For most wildfowl, censuses of breeding numbers extremely difficult. Although breeding habitat and nest-sites show considerable diversity, nests usually placed over water or on or near ground. Well hidden in vegetation or sometimes concealed in other dark places such as burrows and tree holes (or nest-boxes); some species also use old nests of other birds or cliff ledges. Often near water but some species may at times nest far away from it. Nests made only of vegetation, or other materials, within reach of sitting bird, using side-building method (see Harrison 1967). In spite of limited scope of this method materials are often collected from large area by repeated movements of this form. Nest usually lined with down plucked from female's belly (often cryptic and grown specially for this purpose). Value of down for insulation and for concealing nest examined for arctic geese by Thompson & Raveling (1988). Eggs, large, immaculate; surfaces greasy. Clutches often large. Regulation of clutch-size in Anatidae has been the subject of much investigation in n. hemisphere (Rohwer 1984, 1988), but has received little attention in s. Proximate (physiological and psychological [Lack 1974]) factors that may regulate clutch-size include availability of food, condition of birds, weather, age or experience of the breeding birds, ability to incubate, and, of the female, to acquire resources for production of eggs, time of breeding, hormonal levels and interactions between two or more of these (Bengston 1971; Johnsgard 1973; Braithwaite 1977; Ankney & MacInnes 1978; Drent & Daan 1980; Duncan 1987; Ankney & Afton 1988; Kingsford 1989; Briggs 1990). Ultimate (evolutionary [Lack 1974]) factors that may regulate clutch-size are availability of food, condition of birds, length of breeding season, weather, predation and viability of eggs, ability to incubate and rear brood, time of breeding, trade-offs between annual reproductive effort and residual reproductive value, and interactions between two or more of these (Williams 1966; Lack 1967; Ryder 1970; Johnsgard 1973; Braithwaite 1977; Pellis & Pellis 1982; Toft *et al.* 1984; Lessells 1986; Arnold *et al.* 1987; Briggs 1990). Both proximate and ultimate factors can act together to influence clutch-size. Eggs laid at intervals of 24 h in most species but longer in some. Clutch covered by down in most species during recess of adult. Some species may lay some or all of their eggs in nests of other anatids; such nest-parasitism may reach significant proportions in some populations, especially of pochards (*Aythya*) and stiff-tails (*Oxyura* and *Stictonetta* but not *Biziura*); only one species (Black-headed Duck *Heteronetta atricapilla*) obligate parasite. In some species, two or more females may lay at same site, at extreme producing 'dump' of eggs without incubating them. Most species single-brooded but many will re-nest if eggs lost. Multiple clutches more common in austral species. Except some species of Anserinae, incubation by female; starts with last egg; so hatching synchronic. No true brood-patches (Skutch 1976). Displaced eggs retrieved if within reach of sitting bird, using bill. Eggshells left in nest. Downy young typically led, but not carried, to water after leaving nest but see SOWLS (1955) and Johnsgard & Kear (1968) for exceptional carrying of eggs, shells and young. Young feed themselves in all species except Musk Duck *Biziura lobata*, but some food provided indirectly in earlier stages by a few Anserinae and Anatinae (Kear 1970). Establish recognition of own species by special imprinting upon parent's calls and image during brief critical period; exceptionally (e.g. during experiments) may become imprinted on wrong species or even inanimate objects (Heinroth 1911; Lorenz 1935; Hess 1957; Boyd & Fabricius 1965; Schutz 1965). Incubation and fledgling periods vary, correlated with latitude at which breeding takes place; shorter in boreal migratory species nesting in high latitudes with short summer season.

Term 'waterfowl' used in North America to describe the group is restricted by 'wildfowl' in English with 'waterfowl' having wider meaning. Further special terminology (Hardy 1952) includes 'cob' and 'pen' to distinguish male from female in swans; male goose and male duck referred to as 'gander' and 'drake' respectively but female in both best called 'hen' to avoid confusion with group names. Young swan is a 'cygnet'; young goose a 'gosling' and young duck 'duckling'. 'Whiffling' is the term used to describe the deliberate loss of height in flight by alternate side-slipping and even rolling onto the back; a practice most characteristically adopted by many geese when descending rapidly. Collective names include 'herd' for flock of swans and 'gaggle' (on the ground) or 'skein' (flying) for geese. Less well known are 'dropping' for shelduck; 'spring' for a flight of teal and 'padding' for duck on water. 'Flapper' is used to describe young wild duck. Some of these terms are elegant but are regrettably falling into disuse.

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Sub-family **ANSERINAE** swans and geese

Largest wildfowl. Tarsi reticulated in front. Twenty-four species in three genera of swans: *Cygnus*; extralimital *Coscoroba* (South America); and *Olor* (tundra swans, Holarctic); most with all-white plumage. *Cygnus* includes: Mute Swan *C. olor* (introduced) and Black Swan *C. atratus* (Aust., introduced NZ) and Black-necked Swan *C. melanocoryphus* (extralimital South America). *Olor* includes four largely allopatric forms of n. Arctic swans. Two main genera of geese: 'grey' geese *Anser* (nine species); 'black' geese *Branta* (five species). Aberrant *Cereopsis* (Cape Barren Goose, Aust.).

Bills of swans and geese, strong; adapted for grazing, especially in more terrestrial geese in which lamellae take form of varying number of horny 'teeth' especially along edges of upper mandible. No iridescent plumage coloration, pied pattern on wing, or contrastingly coloured tertials. Plumages of geese combine mostly grey, brown, or black with white. Especially in *Anser*, neck feathers of geese arranged in vertical furrows. Vocal apparatus in both sexes a simple tympaniform membrane where bronchi join trachea; in some swans trachea convoluted inside sternum. Lores naked in adult *Cygnus* and *Olor*. Bill and feet, usually bright pink or orange-yellow in *Coscoroba* and *Anser*, dark slate or black in *Branta* and bi-coloured in *Cereopsis*; prominent yellow-green cere covering base of bill in *Cereopsis*; in *Cygnus* and *Olor*, bill usually black with orange, yellow or red; feet, dark. Webs between front toes reduced in terrestrial *Cereopsis* and Hawaiian Goose *B. sandvicensis*. During post-breeding moult, male and female of mated pair normally shed flight-feathers and become flightless at different times. In at least some *Cygnus* and *Olor*, male first to moult, followed by female when male flying again or nearly so (Kear 1970). Downy young simply patterned with varying shades of white, grey, olive-yellow or brown. *Cereopsis* shows most striking pattern of downy young.

Largely Holarctic; four species native in s. hemisphere (two in our region). Most prefer cool or cold regions but generally stop short at ice or deep snow. Large aquatic and terrestrial herbivores; no more than marginally marine (except Brent Goose *B. bernicla* notably) and avoid most deep or fast-flowing waters. Many attached to grasslands and other areas of low, non-woody vegetation in high to mid-latitudes, from tundra to steppe, stopping short at deserts and mountains and most avoiding dense tall vegetation. Vigilant and wary; when breeding, favour sites that are inaccessible (islands and cliff ledges) or eminences commanding wide views over open country. Strong fliers. Most boreal swans and geese highly migratory (in w. Palaearctic, *C. olor* partial exception). Moulting restricted to non-breeders (i.e. mainly immatures); breeding males remain with mates and families, moulting during breeding cycle. In *Olor*, non-breeders tend to unite near breeding areas; in *Anser* and *Branta*, move northwards; most Holarctic species to tundra and forest tundra. Normal migration often at high altitudes, day and night; traditional halting places used on way (Hochbaum 1955).

Essentially vegetarian, feeding in shallow water and on land, mainly on grasses (including grain in some species) and aquatic and marsh plants. *Cygnus* and *Olor* mainly underwater grazers, neck-dipping and up-ending with frequent foot-paddling (*O. cygnus*); will also graze on land. *Anser*, *Branta* and *Cereopsis* mainly specialized terrestrial grazers while walking, also probing and digging, sometimes in soft mud; will also feed in water by up-ending, etc. Except *C. olor* partly, often highly gregarious at all times when not breeding, typically in flocks composed of pairs and family parties. Pre-flight signals largely **Bill-lifting** (*C. olor*, *C. atratus*), **Head-bobbing** (*Olor*), lateral **Head-shaking** (*Anser*), or **Head-tossing** (some *Branta*); usually reinforced by vociferous calls. When breeding, often loosely colonial (at times with small territories) at protective sites, especially in *Anser* and *Branta*; *Cereopsis* typically on coastal islands. *Cygnus* and *Olor* mostly with well-dispersed nests (in large territories), though *C. atratus* often, and *C. olor* sometimes, colonial. Strong, strictly monogamous long-term pair-bonds, of indefinite duration. Also strong family bonds, between parents and young, and between siblings. No communal courtship. Most important display in formation and maintenance of pair-bond, mutual **Triumph Ceremony** usually with characteristic calls; especially in geese, often initiated by male after attack on rival. Also performed at times by members of same family group. Unlike most Anatinae, little ritualization of comfort-behaviour especially in heterosexual situations though some movements (e.g. **Body-shake**, **Wing-flap**) used in threat by some species. Copulation typically while swimming on water except in *Coscoroba* (in shallows) and *B. sandvicensis*, *Cereopsis* (on land). Pre-copulatory display consists of mutual **Head-dipping**, female eventually assuming **Prone-posture**. In mutual post-copulatory display, pair rise in water to greater or lesser extent in most species; posture and movements varying in *Cygnus* and *Olor*, similar in all *Anser* and *Branta*, ended by bathing and wing-flapping. Elaborate nest-relief ceremony claimed in *C. atratus*; needs confirming. Though varying degrees of reliance on visual displays, vocalizations generally play key role in most species for individual recognition and cohesion of flock. Voice considerably reduced in *C. olor*; used generally at close quarters and not for example for territorial advertisement as in *Olor* and some other *Cygnus*; far-carrying, non-vocal throbbing sound from wings replace flight-calls of others. Voice loud but rather unspecialized in rest; quite powerful, sonorous, and often musical in *Olor* (in which sometimes used in duet), and honking in *Coscoroba*, *Cereopsis*, *Anser*, and

Branta. Apparent greater noisiness of last two genera in part related to almost continuous vocal activity of larger, close-knit flocks outside breeding season; but vocabulary of calls also larger than in *Cygnus* and *Olor*, especially in *Anser*. Calls closely similar in both sexes, though sometimes differ in pitch. In addition to usual calls of most Anatidae, downy young also have distinctive **Sleepy-calls**, given when nestling down before sleeping, also at times while feeding (Kear 1970). When threatened at close quarters, all species hiss freely. Comfort-behaviour and other behavioural characters much as in other anatidae, but bathing often spectacular with somersaulting and kick-diving.

Seasonal breeding in most; in Arctic species, highly synchronized laying periods. Nests on ground in open or in vegetation, usually near water but can be distant. Lined with down, though considerably less in *Cygnus* and *Olor* than in *Anser* and *Branta* (and most other Anatidae). Built by both sexes in *Cygnus* and *Olor* though female does larger share. Eggs white, creamy white, or pale green; smooth or with chalky covering. Clutches usually 4–7 (1–14); smaller in high-latitude forms, which do not lay replacements. Sometimes multi-brooded in *C. atratus*. Eggs laid at intervals of 1–2 days. Incubation by both sexes in *C. atratus*; in others, male may cover eggs only during laying or recess of female. Male often mounts guard at various distances from nest, especially in *Anser* and *Branta*. Incubation periods 29–36 days (swans), 24–30 days (geese) (Kear 1970). Downy young tended by both parents, but brooded only by female. In *Cygnus* and *Olor*, adults indirectly provide some food in early stages (plucking underwater vegetation and foot-paddling), young taking it from surface; in all *Cygnus* small young also habitually carried on back. Brood aggressively defended from predators; deferment of wing moult by one of pair in most or all species (see above) ensures that one parent always able to protect young. Fledging periods relatively short in high arctic breeders, long in temperate species. Distraction-display by both sexes, in form of ‘injury-feigning’ or ‘injury-flight’ also recorded in some *Anser* and *Branta* and in *Cereopsis*, but apparently lacking in *Cygnus* and *Olor* (see Hebard 1960). Young stay with parents after fledging at least through first autumn, in most through first winter, and into spring migration in some, at least in n. species; may reunite with them at end of one or more subsequent breeding seasons. Mature at 2–3 years.

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Branta canadensis Canada Goose

COLOUR PLATE FACING PAGE 1197

Anas canadensis Linnaeus, 1758, *Syst. Nat.*, ed. 10, 1: 123; based on *The Canada Goose* of Edwards, 1750, *Nat. Hist. Birds*: 151, Pl. 151; Canada — City of Quebec suggested by Todd, 1938, *Auk* 55: 661.

The etymology of *brant* is doubtful. Gesner and Aldrovandis derived the word from Greek βρένθος, an unidentified waterbird mentioned by Aristotle, but others have suggested a Swedish or Icelandic origin.

POLYTYPIC Peters recognizes 12 subspecies including *maxima* and *moffitti*, stating that birds introduced to NZ were mostly *maxima*; Palmer (1976) combined *maxima* with *moffitti*.

FIELD IDENTIFICATION Length 55–100 cm; wingspan 122–183 cm; weight 3–6 kg. Large, distinctive brown and white goose with black head and neck and conspicuous white facial patch extending from ear-coverts in a band beneath chin. Unmistakeable in A'sian region. Sexes similar; females slightly smaller. Juveniles similar to adults but can be distinguished in the field.

DESCRIPTION **ADULT.** Head and neck, black with distinctive white band extending from ear-coverts (level with eye) across cheek and broadening beneath chin (between base of bill and upper throat). Black of neck merges into brown plumage of mantle, back and scapulars; these feathers edged with buff give finely barred appearance in close view; rump, black. Tail, black; upper tail-coverts, white, forming prominent V between rump and tail visible in flight. In flight,

upperwing appears uniformly dark; upper wing-coverts, brown (like back) finely fringed with buff; secondaries, brown; primaries, dark brown to black. Ventrally: upper breast, cream to pale grey-brown, contrasting sharply with black base of neck; flank feathers, brown edged with buff extending to thighs; more finely marked over breast and extending towards mid-line as faint wash; abdomen and under tail-coverts, white contrasting with black undertail. Underwing, uniform brown. In flight, shows dark brown upperwings and back, black neck, rump and tail and prominent white V on upper tail-coverts; ventrally white with brown flanks and underwings and black undertail; white facial patch on otherwise black head and neck obvious. Iris, dark brown. Bill, black. Legs and feet, dark grey to grey. **DOWNY YOUNG.** At hatching, crown olive; rest of head and neck, bright yellow; upperparts

olive brown; underparts yellow. Second down, dirty grey. **JUVENILE.** Like adult but plumage tinged grey, fringing to feathers less distinct and cheek patch often washed brownish.

SIMILAR SPECIES Unmistakable in our area; large size and contrasting white and black head distinctive. Loud distinctive honking call frequently draws attention to presence. Even at distance, readily distinguished from **Black Swan** *Cygnus atratus* by that species's longer, more curved neck, all black plumage and red bill. **Canada Goose x Greylag Goose hybrids** are stockier, tend to have essentially muted Canada plumage; bills and feet, orange-pink. **Cape Barren Geese** *Cereopsis novaehollandiae* reported as vagrant to NZ and easily distinguished by extensive green cere covering most of bill, predominantly grey plumage lacking contrasting black and white features of Canada Goose and with legs, flesh to reddish.

Seen in pairs, in small groups and huge flocks on estuarine and freshwater lakes, open grazing lands and high country grasslands. Also mudflats and saltmarshes. Feed on water by dabbling and upending, on land by grazing and seed-pulling. Often swim, especially when breeding. Fly fast with deep regular wing-beats in V-formation, diagonals or single file; vocal in flight; hiss in threat or combat; in territorial defence, alarm or flight utter a trumpeted guttural *uh whong*. Call of male loud, sustained; of female, short and staccato.

HABITAT Inhabit grasslands, terrestrial wetlands and estuarine waters, where graze close to water in open grasslands, pasture and crops, or take aquatic plants from water. Stronghold on e. slopes of Southern Alps, NZ, on river flats and beside mountain lakes in high-country tussock grasslands; in Otago, remain in highlands all year, but Canterbury birds spend non-breeding season in lowlands, on lakes, coastal lagoons, estuarine mudflats, saltmarsh; birds increasingly overwinter in high-country as area of improved pasture increases, especially where winter snowfalls light (Williams 1981). SI habitat similar to that used by subspecies *maxima* in

North America; grasslands with complexes of lakes and marshes situated along margins of alpine country (Hanson 1965); most SI breeding grounds have mean Jan. temperature of 17 °C and average 110 frost-free days each year, which falls within range reported for North America (Imber 1971a).

Breed mainly in high-country grassland to c. 1800 m asl, choosing sites with unobstructed view not necessarily close to water. Small numbers nest beside coastal lagoons. Breeding adults moult in nesting areas in highlands; large concentrations of young and non-breeding birds form for moult, at coastal lagoons, particularly L. Ellesmere, but inland lakes increasingly used as area of improved pasture inland increased (Williams 1981).

Heights reached in flight not described; in North America, migrating birds fly at >100 m (Palmer 1976), although subspecies *maxima* reported to fly normally lower than other subspecies (Delacour 1954-64). Walk and swim well; use of underwater habitat limited to depths that can be reached by upending.

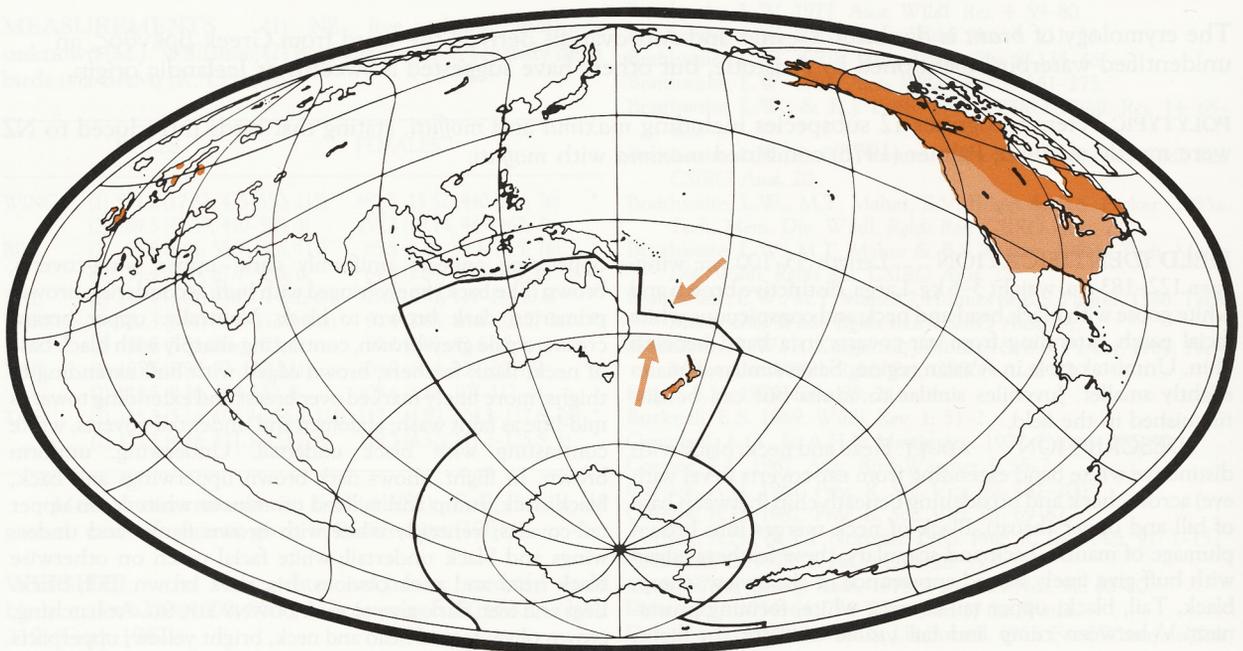
Damage to pasture and crops brings birds into conflict with farmers; increasingly so in high country as area of improved pasture increases and more birds remain to moult and overwinter (Williams 1981).

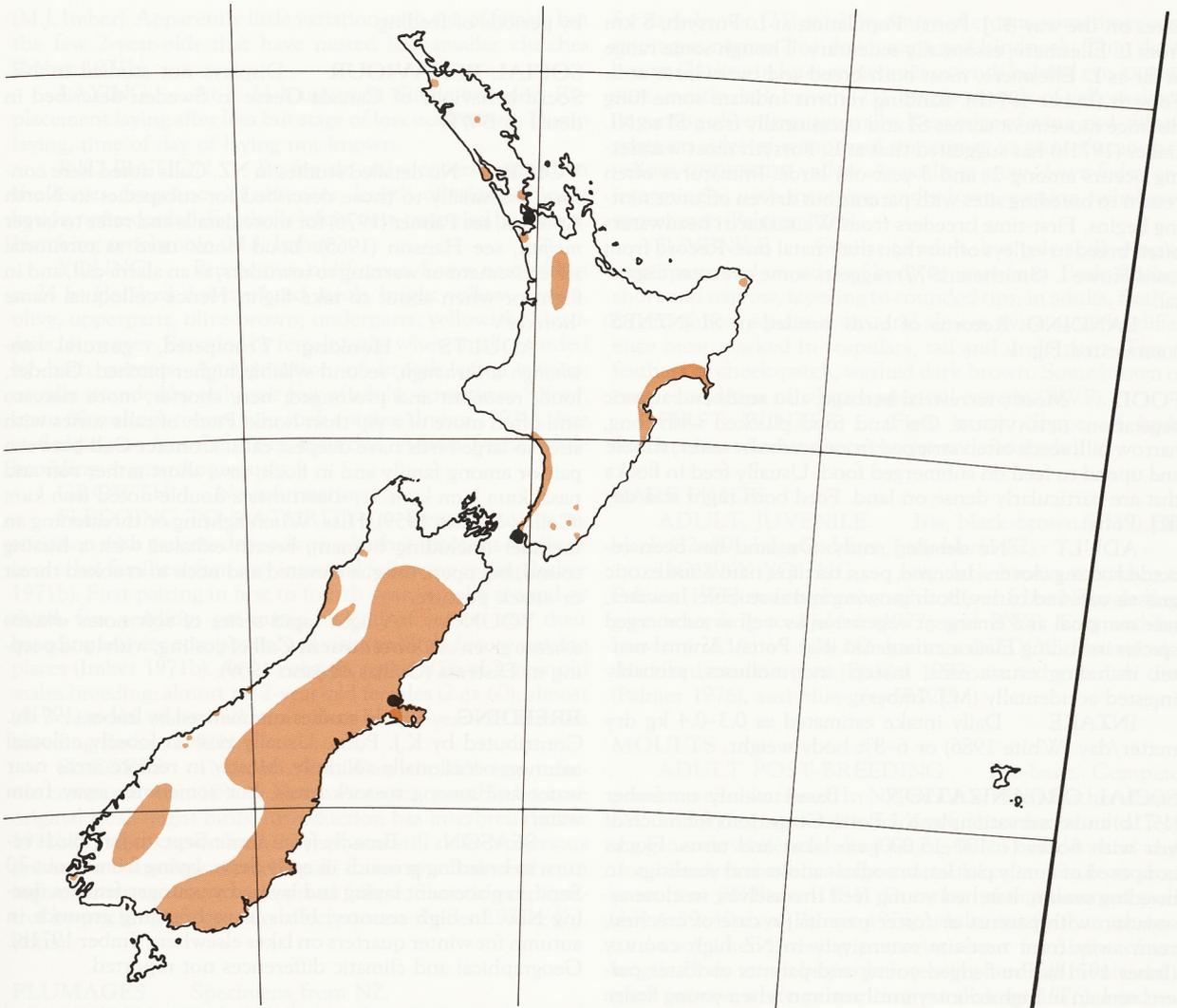
DISTRIBUTION AND POPULATION North America, Mexico; introduced nw. Europe, NZ and Aust. (unsuccessfully); vagrants reported from Tas., Lord Howe I. and New Caledonia.

AUST. Some birds liberated sw. Aust. between 1912 and 1920, and also later. No record of provenance or subspecies introduced. None survived (Long 1981). **Vic.** Unsuccessful release of birds at Sale, 1920s, with small numbers observed 1935 (Sharland 1981). **Tas.** Vagrant; two at Grimes Lagoon, near Tunbridge, Dec. 1927, assumed to have wandered from release area in Vic. (Sharland 1981).

LORD HOWE I. Vagrant: one at Johnson's Beach, 3-8 Feb. 1977 (Smithers 1977).

NZ. Introductions in 1876 (three birds) and 1879 (15) soon





failed (Thomson 1922). Several introductions (3-50 birds) from 1905 to 1920, released widely. Present population regarded as derived from 50 birds liberated SI in 1905 but racial origin uncertain (NZ Atlas). Subspecies *tavernii* probably released in 1920; nominate *canadensis* introduced at Canterbury in 1950; present population may therefore be mixed. Subspecies *moffitti* and *maxima* have also been suggested as origins (NZ Atlas; Delacour 1954-64; Imber 1971b; Palmer 1976; Long 1981). By 1930, had disappeared from NI but well established in SI (Otago, Canterbury areas). At present widespread in SI, mostly in central inland areas; sparse records throughout NI in recent years are of birds recently liberated, perhaps not yet with established feral populations, mostly as Whakaki Lagoon, Wairoa (Williams 1981; NZ Atlas).

POPULATION Estimates in 1987: NI at least 5000; SI 32 000 from aerial count in winter, thus actual figure probably 35-40 000 and possibly higher (K.J. Potts).

MOVEMENTS Partial migrant, some populations moving regularly between breeding grounds and overwintering areas, others breeding and overwintering in same place. Almost entire population of 10 000-15 000 (K.J. Potts) departs L. Ellesmere, coastal central SI, late Aug.-early Sept., most flying

to high country lakes in n. SI (Imber 1971b). Failed and non-breeders return early Dec. and then moult. Successful breeders and young return Mar.-May, adults having completed moult at about time young fledge. Sometimes stages at other

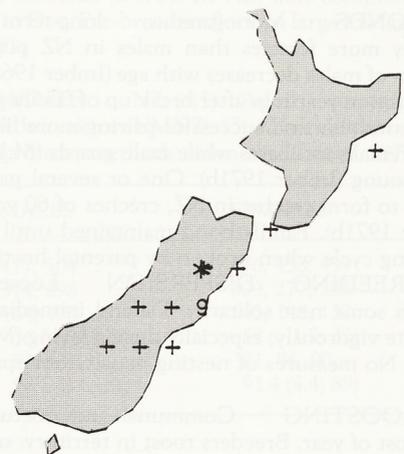


Fig. 1. 42S 172E 1X1 % NZNBS

lakes on the way (K.J. Potts). Population at L. Forsyth, 8 km from L. Ellesmere, essentially sedentary. Though some range as far as L. Ellesmere, most both breed and overwinter at L. Forsyth (Imber 1971b). Banding returns indicate some long distance movement across SI and occasionally from SI to NI. Imber (1971b) has suggested that at L. Forsyth most wandering occurs among 2- and 3-year-old birds. Immatures often return to breeding sites with parents but driven off once nesting begins. First-time breeders from Waimakariri headwaters often breed in valleys other than their natal one. Record from Lord Howe I. (Smithers 1977) suggests some overseas dispersal.

BANDING. Returns of birds banded n. SI (NZNBS) summarized Fig. 1.

FOOD Mostly terrestrial herbage, also seeds and aquatic vegetation. **BEHAVIOUR.** On land food plucked with long, narrow bill; seeds often stripped from heads. In water, dabble and upend to feed on submerged food. Usually feed in flocks that are particularly dense on land. Feed both night and day (K.J. Potts).

ADULT No detailed study. On land has been recorded taking clovers, lucerne, peas, turnips, native and exotic grasses, oats and barley, both growing and as stubble. In water, take marginal and emergent vegetation as well as submerged species including *Elodea canadensis* (K.J. Potts). Animal matter, including crustaceans, insects and molluscs, probably ingested accidentally (M.J. Imber).

INTAKE Daily intake estimated as 0.3–0.4 kg dry matter/day (White 1986) or 6–8% body weight.

SOCIAL ORGANIZATION Based mainly on Imber (1971b) and observations by K.J. Potts. Gregarious for much of year with flocks (<100–15 000) on lakes and tarns. Flocks composed of family parties, broodless adults and yearlings. In breeding season, hatched young feed themselves, in close association with parents or foster parents (in case of crèches); roam away from nest-site extensively in NZ high country (Imber 1971b). Pre-fledged young and parents or foster parents remain in high country until autumn when young fledge and fly with breeding adults to coastal L. Ellesmere (some to L. Forsyth). Non-breeders (mainly 1–2 year olds) and failed breeders return to coast earlier than breeders and yearlings, to moult in flocks. Feed in lakes and round margins. Unfledged young often walk down to lake edge and mix with birds of all ages.

BONDS Monogamous; long-term pair-bond. Slightly more females than males in NZ population; proportion of males decreases with age (Imber 1968). Pair-formation starts in yearlings after break up of family group, but first bonds unstable and successful pairing more likely in second year. Female incubates while male guards (M.J. Imber); both tend young (Imber 1971b). One or several pairs may foster young to form crèche; in NZ, crèches of 60 young common (Imber 1971b). Family-bond maintained until onset of new breeding cycle when broken by parental hostility.

BREEDING DISPERSION Loosely colonial, though some nest solitarily. Defend immediate area round nest-site vigorously, especially during laying (M.J. Imber; K.J. Potts). No measures of nesting density nor spacing between nests.

ROOSTING Communal and nocturnal throughout most of year. Breeders roost in territory, others on lakes and tarns. Sometimes roost on lakes during day, interrupted

by periods of feeding.

SOCIAL BEHAVIOUR Displays not studied in NZ. Social behaviour of Canada Geese in Sweden described in detail in BWP.

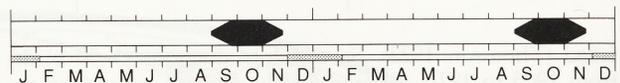
VOICE No detailed studies in NZ. Calls noted here conform essentially to those described for subspecies in North America, see Palmer (1976) for more details and refer to larger *moffitti*, see Hanson (1965). Loud honk used as territorial advertisement or warning to intruders, as an alarm call, and in flight or when about to take flight. Hence colloquial name 'honker'.

ADULTS **Honking:** Trumpeted, guttural *uh-whongh un-whongh*, second syllable higher pitched. Gander, loud, resonant and prolonged; hen, shorter, more staccato and often more of a yip than honk. Pitch of calls varies with size, so large birds have deepest calls. **Contact Call** between pair or among family and in flock; low, short rather soft and nasal *kum kum kum* . . .; sometimes a double-noted *wah kum* (Collias & Jahn 1959). **Hiss.** When fighting or threatening an intruder (including human); breath exhaled with a hissing sound, bill open, tongue elevated and neck in crooked threat or attack posture.

YOUNG A light rapid series of soft notes *wheoo wheoo* given as **Contentment Call** of gosling; with loud peeping in **Distress** (Collias & Jahn 1959).

BREEDING Field studies summarized by Imber (1971b). Contributed by K.J. Potts. Usually nest in loosely colonial manner; occasionally solitarily. Mostly in remote areas near water and among tussock grass, but sometimes away from water.

SEASON Broadly from about Sept. to Jan. Birds return to breeding grounds in early Sept.; laying from about 20 Sept.; replacement laying and laying by younger females during Nov. In high country, birds leave breeding grounds in autumn for winter quarters on lakes elsewhere (Imber 1971b). Geographical and climatic differences not reported.



SITE In high country, usually in tussock grasslands, sometimes on stony braids of river beds (K.J. Potts). On bare or stony ground or in low vegetation in pastures, usually with good view all round so that bird can detect intruders from afar (M.J. Imber). New sites used each year and for second layings; female selects site (M.J. Imber).

NEST, MATERIALS Shallow pile of grasses and plant material forming rough bowl, lined with down and feathers from female's breast. Female builds, collecting material within about 2 m of nest, plucking it with bill (M.J. Imber). Builds during laying period and completes nest with completion of clutch. Does not demolish used nest for second brood. Some birds may make building attempts before final choice of site (M.J. Imber).

EGGS Elliptical; smooth, mat, becoming glossy with incubation; white, becoming stained (M.J. Imber).

MEASUREMENTS: M.J. Imber (from L. Forsyth area): 88.3 (75.6–100.6; 101) x 58.3 (53.2–62.4).

CLUTCH-SIZE Two to ten. At L. Forsyth (coastal), average 4.4; at Nigger Ck (high country near Canterbury), 5.5

(M.J. Imber). Apparently little variation with age of female but the few 2-year-olds that have nested had smaller clutches (Imber 1971b).

LAYING At c. 24 h intervals. Single brooded. Replacement laying after loss but stage of loss not known. Dump laying, time of day of laying not known.

INCUBATION By female only; covers eggs when she leaves; frequency of absences, length of stints of incubation not recorded. Eggshells left in nest, trampled by female. Hatching synchronic (M.J. Imber).

YOUNG Precocious, nidifugous. Leave nest within c. 24 h. Hatched downy; head, neck, bright yellow; crown, olive; upperparts, olive-brown; underparts, yellowish. Mesoptile, dirty grey. Brooded by female only, when small; guarded by both parents. Amalgamation of broods often occurs; usually attended by only one pair of adults, sometimes 'a few'; up to 60 goslings common in such crèches (Imber 1971b). Age at fledging or first flight not recorded. Adults freeze while brooding or guarding young.

GROWTH No information.

FLEDGING TO MATURITY Dependence or association with parents depends on whether reared as family or in crèche; families often stay intact till following spring (Imber 1971b). First pairing in first to fourth year, usually second or third; few yearlings get mates by end of season and their breeding activity consists only of visits to likely future nesting places (Imber 1971b). At L. Forsyth, up to 20% of 2-year-old males breeding; almost no 2-year-old females (2 ex 60); almost all 3-year-old males and more than half 3-year-old females breeding (Imber 1971b).

SUCCESS No data. At L. Forsyth, 25% eggs infertile compared with 10% in North America, possibly because original small (eight birds) introduction has interbred (Imber 1971b). Oldest known bird: 27 years and still alive. No serious predators. Some eggs taken by gulls *Larus* spp. Bad weather in high country can cause widespread failure. Shooting and control by pricking of eggs may affect success (Imber 1971b; K.J. Potts).

PLUMAGES Specimens from NZ.

ADULT Definitive basic; assumed after first winter. Age of first breeding 3 years, occasionally 2 or 4 (BWP). **HEAD AND NECK**, black (82-89) with broad white patch on upper throat extending across cheeks and narrowing on ear-coverts. Feathers in centre of upper throat sometimes have grey-black (82) tips, bisecting white patch. Base of neck, light grey-brown (119D) to greyish white; feathers usually light grey-brown (119D) with horn-white (pale 92) tips, but sometimes brown tinge almost absent and feathers merge to white tips. **UPPER-PARTS**. Upper mantle as base of neck. Lower mantle, upper back and scapulars, dark brown (21) with scalloped or barred appearance caused by light grey-brown (c45) to whitish tips to feathers. Lower back, slightly darker with narrower light barring; feathers, black-brown (c19) with narrow light grey-brown (c45) to whitish tips. Rump, grey-black (c82). Upper-tail coverts, white forming curved band in front of tail. **TAIL**, grey-black (82). **UPPERWING**. Coverts as back. Remiges, black-brown. **UNDERPARTS**. Breast as base of neck. Flanks and sides of breast, dark brown with irregular paler barring; feathers, dark brown (21) with light grey-brown (c45) to off-white tips. Thigh-feathers, dark brown (121) with white fringes. Belly, vent and under tail-coverts, white. **UNDERWING**. Coverts, light greyish-brown (119C) with paler-brown (119D) tips.

DOWNY YOUNG **HEAD AND NECK**, yellow, save

for dark-brown (21) patch in centre of crown, sometimes continuing as narrow line down nape and hindneck. Thin dark-brown (21) line in lores sometimes extends behind eye. **UPPER-SIDE**, mostly dark brown (21), longer strands of yellow down imparting olive tinge generally. Rear edge of wing-pad, diffuse spots on sides of rump, and sometimes in area of scapulars, yellow. **UNDERSIDE**, yellow. As goslings grow, down fades, and intermingles with incoming underdown, causing soiled grey appearance (Palmer 1976).

JUVENILE Similar to adult, but pale scalloping on upperparts and on sides of body appears finer. Body-feathers short and narrow, tapering to rounded tips; in adults, feathers larger, almost square at tip, and almost twice as wide; difference most marked in scapulars, tail and underparts. Tips of feathers of cheek-patch, washed dark brown. Some brown on centres and tips of white upper tail-coverts (BWP).

FIRST WINTER (First basic). Shape of body-feathers intermediate between juvenile and adult.

BARE PARTS

ADULT, JUVENILE Iris, black-brown (c119). Bill, black (82-89). Legs and feet, grey-black (82).

DOWNY YOUNG Iris, dark brown according to Palmer (1976) and in photographs of four from NZ; pale blue-grey according to Fjeldså (1977) and BWP. Feet and legs brown (c223A) in two NZ goslings (NZDOC library); also described as olive-grey (Fjeldså 1977), muted greenish olive (Palmer 1976), and blue-grey (BWP).

MOULTS

ADULT POST-BREEDING Pre-basic. Complete, primaries simultaneous. In NZ, moult of flight-feathers begins Dec. and widespread in Jan. Successful breeders moult at nesting grounds while attending young; failed breeders and adult non-breeders move to large coastal lakes to moult at about same time (Williams 1981). Duration of flightlessness probably c. 39-40 days (Palmer 1976); adults can fly (but reluctant to do so) when growing primaries about five-sixths of final length. Body moult begins before wing- and tail-moult, and is most intense while primaries grow (Palmer 1976); head and body moult completed when wings full grown (BWP).

ADULT PRE-BREEDING Partial; head and neck, but not body moult, occurs in spring (Delacour 1954-64); Stead (1938) also recorded scapular moult at this time.

POST-JUVENILE Partial; head, body and tail from early autumn onwards (BWP). In NZ, first complete wing-moult begins in Dec. Pre-breeders flock in large lowland lakes (Williams 1981).

MEASUREMENTS NZ. (1) Adult, recently dead (NMNZ). (2) Adult, skins (NMNZ). (3) Adults and immatures combined, live birds; methods unknown (Imber 1971a).

	MALES	FEMALES	
WING	(1) 477, 504	476, 456, 459	
8TH P	(2) 314, 298	309, 277, 286	
TAIL	(1) 164, 136	143, 148, 152	
BILL	(3) 56.5 (2.1; 39)	52.6 (1.9; 32)	**
TARSUS	(1) 92, 101.3	81, 86, 90	
TOE	(3) 98.1 (3.6; 72)	91.4 (4.4; 89)	**

Males significantly larger than females. Great variation in

size between subspecies. For measurements outside NZ, see BWP, Palmer (1976), Imber (1971a) and references therein.

WEIGHTS All from Imber (1971a). Lightest when flightless during post-breeding moult; in Jan. adult males 4078 (268; 58), females 3320 (235; 45). Heavier in winter, when following weights taken in Canterbury, SI:

	MALES	FEMALES
ADULTS	4884 (354; 13)	4489 (327; 14)
YEARLINGS	4808 (332; 7)	4233 (160; 3)
JUVENILES	4261 (418; 20)	3821 (315; 15)

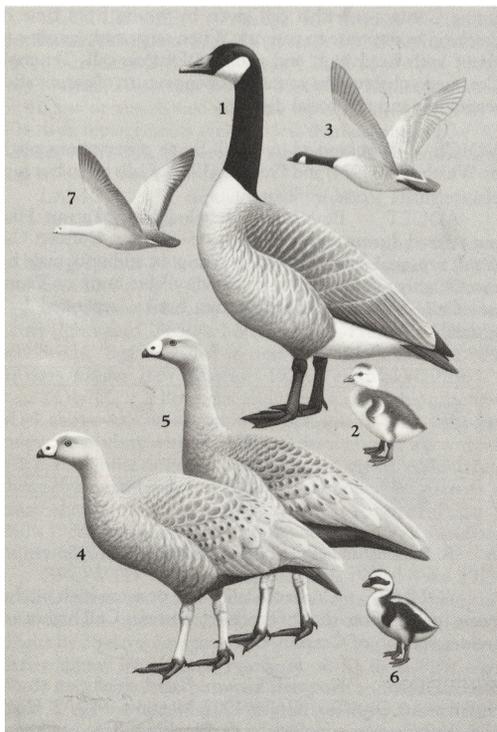
STRUCTURE NZ. Wing relatively long and pointed. Eleven primaries, p9 longest, p10 4-15 shorter, p8 2-7, p7 21-38, p6 56-73, p5 93-106, p4 124-139, p3 146-165, p2 168-191, p1 187-211; p11 minute. Outer web of p9-p7 and inner web of p10 emarginated; p8 and p9 slightly emarginated on inner web. Tail, short, rounded; 16-18 feathers; t1 to outer rectrix 20-30. Bill about as long as head, with broad nail; culmen slightly concave, lower mandible and tomia straight. Toes longer than tarsus, webbed; outer c. 93% length of middle, inner c. 78%, hind c. 29%.

GEOGRAPHICAL VARIATION Considerable; for full discussion see Palmer (1976). In original range in North America between eight and 12 subspecies have been recognized. Broadly, cline of increasing darkness westwards, and of

increasing size southwards; geographical variation in size more marked than in any other bird (Madge & Burn 1988). NZ stock possibly derived from the large, pale breasted birds in SE of range; Imber (1971a) ascribed NZ birds to race *maxima* from Great Plains region of USA. This subspecies has since been combined with race *moffitti* (Palmer 1976). Hybrids with Feral Goose *Anser anser* known from L. Ellesmere (O'Donnell 1985). Similar to Canada Goose, but stockier. Bill, feet and legs, pink (7). Dark areas of head and neck, dark brown (c20) with indistinct margins to mantle and breast. Some have pure white band across central throat. DIR

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Canada Goose *Branta canadensis*

- 1. Adult, subspecies *moffitti*
- 2. Downy young
- 3. Adult

Cape Barren Goose *Cereopsis novaehollandiae*

- 4. Adult, e. Aust. birds
- 5. Adult, WA birds
- 6. Downy young
- 7. Adult, e. Aust birds

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