

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

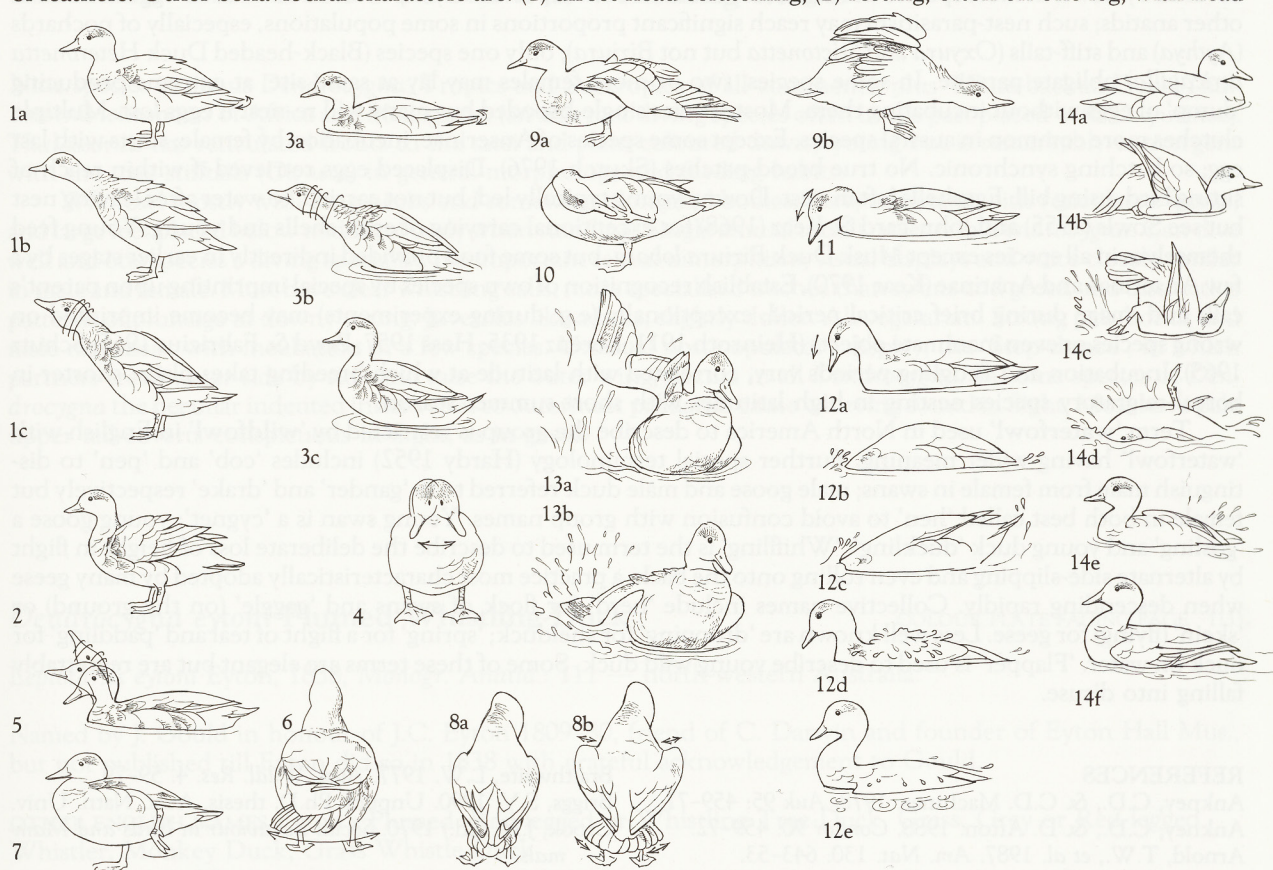
Waterbirds (some more or less terrestrial) with rather short legs and front toes connected by webs; hallux elevated and reduced. Though considerable adaptive diversity in outward appearance, size, colours of plumage, behaviour, and ecology, homogeneous in many characters, as attested by numerous, often fertile, interspecific hybrids reported, chiefly in captivity (see Gray 1958). About 160 species in six sub-families: (1) Dendrocygnae (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 (tertials) 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. Palearctic, *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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Anas atrata Latham, 1790, *Index orn.* 2: 834 — lakes of Australia.

Latin and English names clearly translate one another (*atratus* = made black).

MONOTYPIC.

FIELD IDENTIFICATION Length 110–140 cm of which head and neck about half; wingspan 160–200 cm; weight males 6 kg, females 5 kg. Very large, black, typically swan-like bird, with white remiges, most conspicuous in flight, and red bill. Sexes alike; females slightly smaller with proportionately shorter neck and bill. No seasonal changes in plumage. Juveniles mottled grey-brown.

DESCRIPTION **ADULT MALE.** Head, neck and upperparts, black, often with brown wash; fine, pale fringes visible only in close views. Usually, upper wing-coverts, black; primaries and outermost secondaries, white (usually visible only during flight and some displays); innermost secondaries (tertials), mostly black. Tips and outer webs of tertials and innermost greater coverts, upturned, giving characteristic curled appearance to feathers when wings folded. (There is much variation in extent of white and dark remiges and also white in coverts; some birds have only small number of flight feathers white, most black — see Plumages). In flight, white remiges contrast markedly with black upper wing-coverts, inner secondaries and body. Underparts, dark grey to black; feathers with fine pale fringes. Bill, orange to dark red with pale to white subterminal bar and nail. Iris, red, light red, pink or white (colour possibly related to sexual condition; see Braithwaite 1981a). Legs and feet, dark grey to black. **ADULT FEMALE.** Like male but bill and eye more often paler. **DOWNY YOUNG.** Uniform light grey. Bill, dark grey. Iris, grey-brown. Legs and feet, dark grey. **JUVENILE.** Dull grey-brown with paler margins to feathers. Primaries and most secondaries, white tipped black; dark tips to primaries, characteristic of juveniles. Bill, dull red with traces of grey; terminal bar and nail grey. Iris, as adult. Legs and feet, dark-grey. Pale (leucistic) individuals recorded, usually fawn, some pure white.

SIMILAR SPECIES Unmistakable on ground and in water. In flight, no likely confusion with Magpie Goose *Anseranas semipalmatus*, which has almost reverse pattern of white abdomen and underwing coverts and black remiges.

Seen in pairs, small groups to flocks of thousands on permanent, large, open, fresh, brackish and saline waters usually with emergent and subaquatic vegetation; occasionally on open sea; also tidal mudflats, flooded pasture, green crops, ornamental lakes. On water swim gracefully, often alert with neck erect or roosting with bill under scapulars. Feed by upending or plucking vegetation from below or on water surface. Take off with feet running across surface, needing 40–50

m to become airborne; cannot do so in thick vegetation, among timber or in rough water. In flight, neck outstretched, wing-beats slow, ponderous, white flight-feathers prominent; often call. On land, slow rolling gait; may graze on waterside pasture. Musical *bugle* or *trumpet*, longer and deeper in males. Usually heard in flight or on water.

HABITAT Widespread in temperate and tropical terrestrial wetlands, sheltered estuarine and maritime habitats. Terrestrial and aquatic; feed in shallow or deep open water, on wetland margins, exposed mudflats, or ashore, wherever floating or submerged aquatic plants, emergent vegetation or soft terrestrial herbage can be reached (Frith *et al.* 1969; Loyn 1975; Briggs 1979). Prefer large permanent waters; avoid those where fast flow, strong wave-action or turbidity prevent establishment of aquatic vegetation, or that are so overgrown or small that take-off is difficult; tall emergent vegetation (reeds, shrubs, trees) may be no impediment or deterrent, provided tracts of open water remain. Terrestrial habitats used especially when flooded or moist; dry ground usually avoided. Recorded often or in large numbers on shallow freshwater swamps, deep swamps vegetated with tall emergents (e.g. *Typha*, *Eleocharis*), fresh meadows, lakes, reservoirs, large sewage ponds, and wide slow-flowing rivers with sheltered margins (Corrick & Norman 1980; Gosper 1981; Fjeldså 1985; Peter 1989). Range of salinities tolerated from fresh to hypersaline, although usually limited to <60‰ which is threshold of tolerance of aquatic food plants, *Ruppia* and *Lepilaena* (Corrick 1982); fresh water needed for drinking (Frith 1982). Common on large salt lakes, coastal lagoons, estuaries, inlets, saltpans and saltmarshes (Corrick & Norman 1980; Gosper 1981; Jaensch *et al.* 1988; Peter 1989). Other habitats used include wooded lakes and swamps, flooded or irrigated pastures, large farm-dams, ornamental ponds and lakes, saltworks, and bays and other sheltered inshore waters (Cooper 1967; Crawford 1975; Corrick & Norman 1980; Frith 1982; Pescott 1983).

Habitats similar in NZ; large waterbodies with abundant aquatic vegetation (lakes, swamps, rivers, estuaries, harbours) and nearby pastures (Miers & Williams 1969; Williams 1980). L. Ellesmere, a brackish coastal lagoon, held huge numbers of birds until storm uprooted aquatic vegetation (*Myriophyllum*, *Ruppia*); food shortage caused breeding failure and serious long-term decline in numbers (Williams 1975).

Breed in fresh, brackish or saline (but not tidal) wetlands, with enough soft vegetation for nest-building and feeding young, tall vegetation or islands for shelter, support and security of nests, and open water for feeding (Guiler 1970; Lavery 1971b; Williams 1980; Braithwaite 1981a). Freely exploit ephemeral waters; at times of widespread flooding nest in any shallow water collected in depressions, swamps, low-lying pastures or roadside drains (Frith 1982; M. Cameron).

Moulting birds seek safety of large open bodies of water: lakes, lagoons, estuaries or sheltered marine areas (Williams 1977b, 1981a; Corrick 1982). Birds rise from water with difficulty, fly strongly; flocks in formation reach considerable heights (Frith 1982). Use of underwater habitat limited to depths reached by up-ending; c. 1 m (Frith *et al.* 1969).

Reservoirs, farm dams, other water storages, and irrigated crops and pastures have provided additional feeding habitat for Swans. However, many densely vegetated wetlands used for breeding and feeding have been affected by drainage, clearing, grazing and burning (Riggert 1966; Goodrick 1970; Corrick & Norman 1980; Corrick 1981, 1982). In agricultural districts, increased run-off and manipulation of water-levels cause losses of nests by flooding (Tingay *et al.* 1977) and eutrophication of wetlands drives birds onto pastures, where they come into conflict with farmers (Williams 1981a).

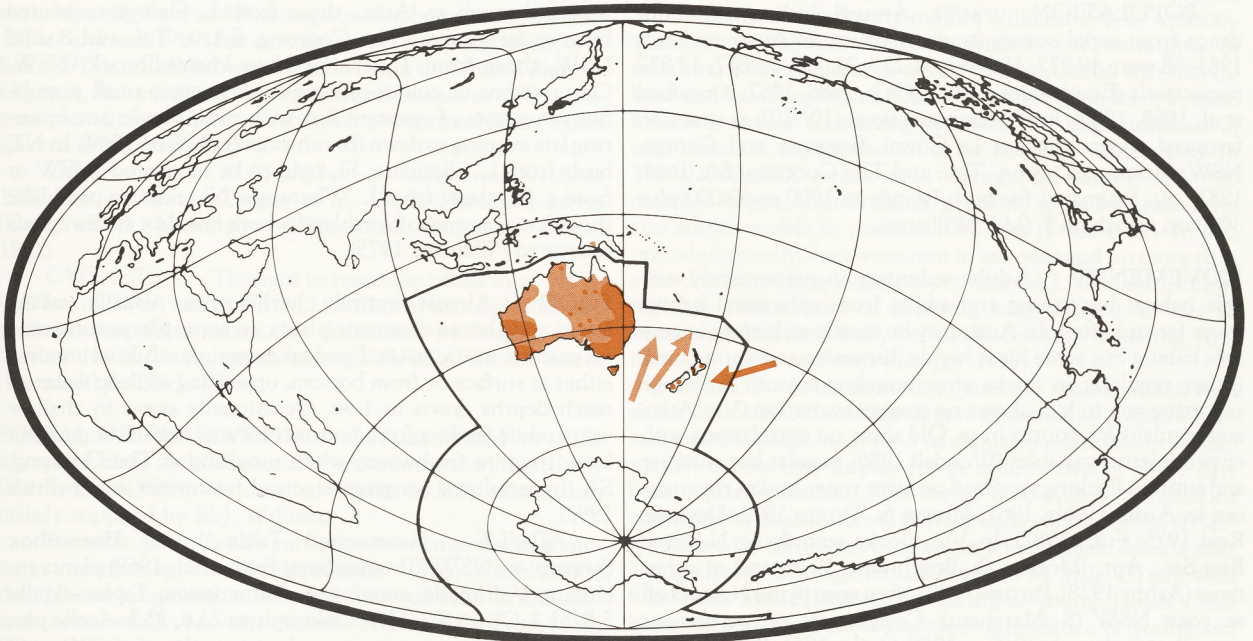
DISTRIBUTION AND POPULATION Endemic to Aust., introduced to NZ. Extraliminally, vagrant to New Guinea (Beehler 1980).

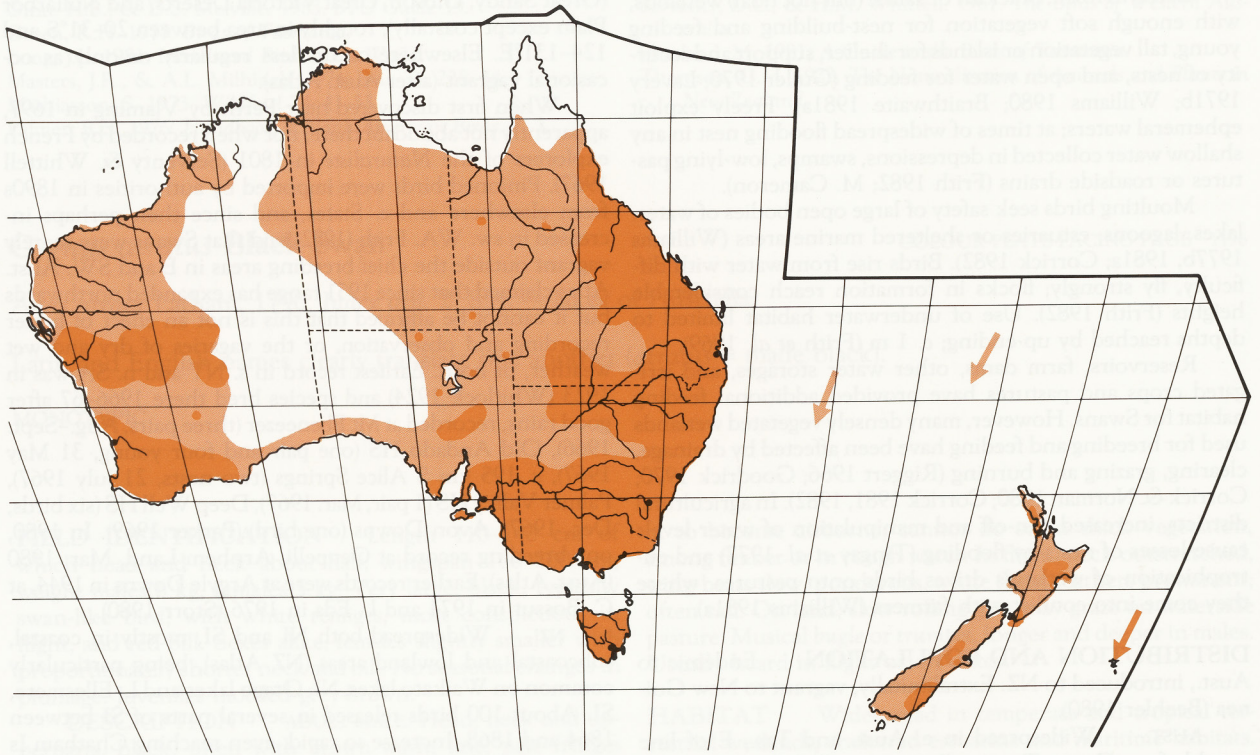
AUST. Widespread in e. Aust. and Tas., E of line roughly from Cairns-Townsville area, ne. Qld, down drainage lines of Diamantina R. and Cooper Ck to L. Eyre and thence S to Eyre Pen.; also in sw. WA within line from drainage area of Gascoyne and Murchison Rs inland to L. Carnegie, Laverton, Kalgoorlie and so to Esperance. Breeds widely throughout these areas wherever and whenever conditions suitable but specially common in s. and e. NSW, Vic., Tas. and se. SA and most s. parts of WA. Absent or merely vagrant on C. York Pen., N of about 15°S, and also absent from driest parts of WA

(Great Sandy, Gibson, Great Victoria Deserts, and Nullarbor Plain except coastally), roughly in area between 20–31°S and 124–131°E. Elsewhere occurs less regularly or only as occasional vagrant (after Aust. Atlas).

When first discovered near Perth by Vlaming in 1697, apparently not abundant there, nor when recorded by French explorers of the *Naturaliste* in 1801 (Serventy & Whittell 1967). Pinioned birds were imported by authorities in 1890s from elsewhere and e. States, and since then perhaps increased in sw. WA. Frith (1982) said that Swans were merely vagrant outside the chief breeding areas in E and SW. Aust. Atlas claimed that since 1951 range has expanded northwards but it cannot be affirmed that this is not an effect of better recording and observation, or the vagaries of dry and wet weather, or both. Earliest record in s. NT and n. SA was in 1923 (Whitlock 1924) and species bred there 1966–67 after good rains; recorded at Mt Ebenezer (three pairs, Aug.–Sept. 1966), Old Andado HS (one pair and four young, 31 May 1967), c. 195 km S Alice Springs (two nests, 21 July 1967), Palmer Valley HS (1 pair, Mar. 1967), Deep Well HS (six birds, Dec. 1967), Avon Downs (one bird) (Parker 1969). In 1980, one breeding record at Oenpelli, Arnhem Land, Mar. 1980 (Aust. Atlas). Earlier records were at Argyle Downs in 1944, at C. Bossut in 1974 and L. Eda in 1976 (Storr 1980).

NZ Widespread both NI and SI, mostly in coastal, subcoastal and lowland areas (NZ Atlas), being particularly common on Waikato lakes, NI; Otago lakes and L. Ellesmere, SI. About 100 birds released in several parts of SI between 1864 and 1868. Increase so rapid, even reaching Chatham Is before 1922 (Thomson 1922 in Long 1981), that probably at about same time birds also arrived naturally from Aust. (Williams 1981a). Widespread and common in both NI and SI by 1900. Until 1968, main concentration (c. 70 000 birds) on L. Ellesmere but storm in that year killed many birds and badly damaged vegetation of Lake so that decline to 23 000 next year and further decline to c. 7000 birds in 1980 with few breeding. No breeding occurred between 1968 and 1971, when 3000 pairs bred. In subsequent 5 years, <1000 pairs attempted to





nest. Numbers on L. Ellesmere so large before 1968 that organized shooting was undertaken and eggs collected in large numbers as control measures (Williams 1979; M.J. Williams).

LORD HOWE I. Vagrant: two birds recorded about 1916; single, about 1933 (Hindwood 1940).

NORFOLK I. Vagrant: recorded early this century; two, 26–27 Aug. 1974, of which one stayed till 8 Oct. (Hermes *et al.* 1986).

POPULATION **AUST.** Annual indices of abundance from aerial survey (transect count) e. Aust. wetlands 1983–88 were 49 977; 156 843; 31 229; 22 715; 16 057; 13 827 respectively (Braithwaite *et al.* 1985a,b, 1986, 1987; Kingsford *et al.* 1988, 1989). Large concentrations (10^3 – 10^4) at times on favoured waters such as Ls Cowal, Brewster and George, NSW; Moulting Lagoon, Tas.; and The Coorong, SA (Frith 1982). **NZ.** Estimated for both Islands in 1980 as 60 000 plus 3000 on Chatham I. (M.J. Williams).

MOVEMENTS Adults sedentary in permanently suitable habitat but young and adults from ephemeral habitat move far and often. In Aust. may be mostly sedentary in suitable habitat but some birds highly dispersive and young birds gather regularly in flocks after breeding season. Although reporting rate in Vic. shows no seasonal variation (Vic. Atlas) and regular Oct. counts in se. Qld show no correlations with environmental variables (Woodall 1985), regular late summer and autumn flocking reported on large water bodies throughout se. Aust. (Hobbs 1961; Missen & Timms 1974; Davis & Reid 1975; Frith 1982). In Vic., flocks seen flying N across Bass Str., Apr. (Morton & Braithwaite 1976) and at other times (Ashby 1928). Parties (<40) often seen flying N and S off se. coast NSW (S. Marchant). Congregates on permanent water during drought (Sefton 1958; Guiler 1961; White 1987).

In NZ, young swans tend to remain at or near natal lake in first year but more likely to be recovered > 10 km from natal lake between 2 and 4 years, at least during shooting season, returning to natal lakes as adults. Adults largely sedentary. After storm disrupted ecology at L. Ellesmere in 1968, fewer immatures returned there to breed and some recruited to other breeding populations (Williams 1975).

BANDING Populations marked at L. George, se. NSW (Frith 1982) and in Tas. (Hemsley 1973) dispersed widely through se. Aust., those from L. George recovered from as far away as The Coorong, SA, s. Tas. and coastal NSW, those from Tas. as far N as Muswellbrook, NSW. Observations of colour-marked birds suggest small populations in a state of constant flux with most movement occurring late evening to dawn (Braithwaite & Wilson 1969). In NZ, birds from L. Ellesmere, SI, tend to be recovered to SW or from s. NI, those from L. Whangape, NI, close to natal lake though may move to Northland where few shot so few bands recovered (Williams 1975).

FOOD Almost entirely herbivorous, usually taking leaves and shoots of aquatic plants, in some places subsisting on pasture. **BEHAVIOUR.** Food taken mainly while swimming, either at surface or from bottom, up-ending in deep water to reach depths down to 1 m. Occasionally stand in shallow water while feeding from bottom or water surface or graze on land. Require freshwater; when moulting at The Coorong, SA (hypersaline), congregate round freshwater soaks (Frith 1982).

ADULT Summarized Table 1. At **Barrenbox Swamp**, w. NSW (81 oesophagi; Frith *et al.* 1969) plants including *Vallisneria americana*, *Potamogeton*, *Typha*, *Azolla* 5.8, 31.1, *Chara* 5.7, 11.1, Chlorophyta 23.6, 33.3. *Azolla* particularly important autumn and winter, the proportions of

Table 1. Gizzard contents of the Black Swan in Aust.

	% volume			% frequency		
	1	2	3	1	2	3
PLANTS	100	99.9	99.9	100	100	100
<i>Vallisneria</i>	9.7	3.8	1.3	16	15	
<i>Potamogeton</i>	14.4	15.9	56.6	19	16	21
Cyperaceae		1.5	24.1			56
<i>Typha</i>	17.6	19.7		28	34	
Algae	29.3	22.6	1.6			
ANIMALS	0	0.1	0.1	0	10	6

(1) oesophagi, (2) gizzards; Frith *et al.* (1969); (3) Lavery (1967, 1971a).

deep-water and pasture plants varying with swamp levels. In gizzards collected at the same site (906) plants incl. *Ranunculus* 1.6% vol., *Atriplex semibaccata*, *Chenopodium pumilio* and *C. nitriaceum*, *Rumex* 0.9, *Lepidium hyssopifolium*, Fabaceae 2.5, 10.4 incl. *Melilotus indica*, *Medicago polymorpha*, *Trifolium repens*, *T. subterraneum*, *Myriophyllum* 3.8, *Convolvulus erubescens* 0.8, *Cirsium vulgare*, *Vallisneria americana* 3.8, 15.1, other Hydrocharitaceae 7.5, Potamogetonaceae 15.9, 16.4 incl. *Potamogeton crispus*, *P. ochreatus*, *P. pectinatus*, *Ruppia* 3.2, 53.0, *Najas marina* 3.7, 7.0, Lemnaceae 0.8% vol., Juncaceae 0.8, *Schoenoplectus validus* 1.5, Poaceae 7.1 (*Criteasion marinum* 7.9% freq., *Paspalum distichum* 5.7), Typhaceae *Typha* 19.7, 34.1, Azollaceae *Azolla* 4.9, 30.3, Chlorophyta 22.6, 34.9 incl. *Spirogyra*, *Chara* 2.1% freq.; animals were insects and molluscs, probably ingested by accident.

In n. Qld. (58 gizzards; Lavery 1967, 1971a) plants incl. Nymphaeaceae 2.0, 3, *Myriophyllum verrucosum* 1.5, 2, Hydrocharitaceae 1.3, 3 incl. *Hydrilla verticillata*, *Vallisneria*, *Potamogeton pectinatus* 55.6% vol., *P. javanicus* 1.0, *Eleocharis dulcis*, *Scirpus litoralis*, Poaceae 1.1, 7, Characeae 1.6, 7 incl. *Chara*, *Nitella* 1.5% vol., *Oscillatoria*, *Spirogyra*, others 1.7, 21 (incl. *Ceratophyllum demersum*, *Najas graminea*); animal incl. aquatic insects <0.1, 6 and crustaceans <0.1, 2.

At L. Ellesmere, NZ, took mostly *Ruppia megacarpa* with *Myriophyllum* and *Potamogeton* also being eaten (Adams 1971; Bucknell 1969) but now grazes on pasture grasses (Williams 1979); at L. Whangape *Egeria densa* dominated diet but *Glyceria*, *Ranunculus*, *Potamogeton* and *Juncus*, as well as pasture plants, also taken; in estuarine or marine habitat takes *Zostera* (M.J. Williams).

Other records: *Myriophyllum*, *Vallisneria* (Vestjens 1977), *Ruppia* leaves (Delroy *et al.* 1965), *Halophila* leaves (Campbell & Mattingley 1907); small flounder (Wilson 1957).

CYGNETS Thought to resemble adults in w. NSW (Frith *et al.* 1969) and in NZ (M.J. Williams) although inability to reach deep food means diet dominated by floating seeds (Lavery 1967). Young given young shoots of willow leaves (Blomfield & Black 1963).

SOCIAL ORGANIZATION In Aust., based on study of captive birds and occasional observations of wild birds by Braithwaite (1981b). No detailed studies in NZ; information mainly supplied by M.J. Williams.

Found in pairs, family parties or very large flocks sometimes numbering thousands (Guiler 1966; Frith 1982) throughout range and at different times of year. Breed solitarily or colonially; opportunistically or seasonally (Frith 1982; White 1986). In Aust., large concentrations (tens of thou-

sands) found on brackish lakes; smaller numbers on lagoons and floodwaters of inland and coastal estuaries in SE such as Moulting Lagoon, Tas., and The Coorong, SA (Braithwaite 1970). In NZ, mostly associated with still water but uses estuaries for feeding and moulting, though on most large estuaries some resident. Generally, flocks form at moult-sites on safe large waterbodies, keeping far out from shore; also form where food abundant (Braithwaite 1981a; Williams 1981a). In saline environments, birds leave water to drink at freshwater soaks where may gather in large numbers e.g. The Coorong, SA. **ASSOCIATION DURING MOULT.** (also see Moulting). Aust. Up to 3000 birds recorded moulting at Corner Inlet, Vic. (R.S. Brown & D.M. Deerson in Aust. Atlas). Banding studies in NSW have shown that composition of congregations not static (Frith 1982; Braithwaite & Wilson 1969). Numbers greatest at moult-sites after main breeding season. NZ. Non-breeders begin moult in Oct., gathering in large flocks at marine, estuarine or main breeding areas; pre-breeders tend to join flocks away from natal area; breeders moult after young have fledged. Once birds reach breeding age, most probably return to natal area and remain more or less permanently. Successful breeders moult, Nov.-Apr., after fledging of young but while family still together. During Nov.-Mar. each year, up to 13 000 birds congregate to feed on *Zostera* at Farewell Spit, NZ, many in full wing-moult (Williams 1977a). **ASSOCIATION AFTER MOULT.** Towards winter, concentrations of moulting birds disperse as available waterbodies increase inland and breeding begins. Concentrations again form in main breeding season containing breeders and large numbers of non-breeders, significance of latter not fully understood. In 1963, 2000-3000 swans in L. George, NSW, but only 400 clutches begun; non-breeders probably included immatures and adults unable to procure nest-sites (Frith 1982). In NZ, only about one in five swans nest in any year and no more than a third at a breeding locality try to nest (M.J. Williams), implying that either onset of breeding long delayed, or not all mature adults breed every year, or both. After breeding, families may move as a unit (Cooper 1967).

BONDS In captivity, generally monogamous with some promiscuity but high degree of flexibility in pairing arrangements; older birds tend to maintain relationship permanently; others may display for as little as two or three days before pair-formation. Five forms of breeding associations identified by Braithwaite (1981b) among captive birds: (1) single male who completes incubation when female deserts after laying clutch; (2) single female deserted by male; (3) pair with fixed roles in incubation and rearing of young, female's role being mainly incubation and close attendance of young and male's territorial defence; (4) homosexual pair where two

males maintain stable association, often indulging in heterosexual displays and procuring nest and eggs by brief association with female or driving other swans from nest; (5) trio with one stable, successful breeding association of two males and one female. In trio, cygnets left in care of males after 2–3 months while female re-laid; all joined in precopulatory displays but only one male mated and maintained close attendance to nest, the second assuming territorial role. Nevertheless, performance in captivity probably of little significance as regards wild birds, which are probably influenced by differing circumstances of solitary and densely colonial nesting. In wild, constant association in pairs or family parties suggests sustained monogamy (Frith 1982). However, while banding, Braithwaite (1981b) captured heterosexual pairs on five nests, two males on one nest, single males on three nests and single females on seven nests and suggested pairing associations may vary as in captivity. Flexible social relations would allow use of broad range of environmental situations such as breeding in temporary wetlands and unsynchronized individual flightlessness in moult. In Aust., first-time breeders may pair only temporarily; either sex may desert partner at some stage after laying and usually mates again to rear another brood; in this way female may lay up to four clutches a year. Swans in NZ usually mate with partner of previous year and bonds seem to be maintained throughout year; divorce occasionally takes place, but changes of mate mainly result from death of partner (Williams 1981b). In captivity, sexual behaviour (precopulatory displays) occasionally appear in young birds accompanying parents and in juveniles (nest-building). Swans usually attain sexual maturity and breed at 18–24 or 33–36 months and within 1–2 years of attaining adult plumage, although captive females may lay at 1–1.5 years-old (Braithwaite 1981a). In NZ, age at first breeding not determined in field but thought to be in fourth year for L. Ellesmere population; also probable that age of sexual maturity varies between populations within NZ (M.J. Williams). Courtship behaviour and pairing intensifies just before breeding (Guiler 1970; Tingay *et al.* 1977); in captivity, occurs Mar.–May; in Busselton, WA, in May (Tingay *et al.* 1977); in Tas., near breeding sites by Mar. or early Apr. (Guiler 1966); in Griffith, NSW, probably mainly autumn (Braithwaite & Frith 1969). In established pairs in captivity female mostly incubates (Braithwaite 1981a), though S. Gurney (in Delacour 1954–64) claimed that both sexes incubate; at isolated nest near Moruya, se. NSW, both birds incubated (S. Marchant). In wild colonies, single birds attend most nests rather than pairs (Frith 1982; Braithwaite 1970) and both sexes reported to incubate (Frith 1982; Tingay *et al.* 1977; Williams 1981a; but see Breeding). In captivity, adults of stable relationships defend 4–5 m round brood. At territorial sites in NZ, parents guard and attend cygnets in family broods; in colonies, up to four or more broods amalgamate and appear to be reared by one pair of adults (M.J. Williams); nothing known about post-fledging family relations (see Social Behaviour).

BREEDING DISPERSION Nest in territorial pairs and colonies depending on habitat (Cooper 1967; Williams 1981a); adoption of colonial or territorial dispersion attributed to distribution of nest material (Tingay *et al.* 1977) but social factors also involved (Braithwaite 1982). In colonies each bird maintains pecking distance and only defends area round nest. Size of colonies varies: at L. George in 1962, 120 nests (Braithwaite 1982); in Tas., four to 454 nests, average 1.625 m apart at Cockatoo I. (Guiler 1966); at L. Ellesmere, colonies of 97 to 5160 nests recorded from 1961–71 (Miers & Williams 1969; Adams 1971); in same area, mean distance

between nests, 3.05 m in 1960, 2.4 m in 1961; in 1960 and 1961, 93% and 94% of nests were within 6.1 m of another; 7% and 38.3% were ≤ 1.5 m apart; proportion of unsuccessful nests greater for closely spaced nests (≤ 1.5 m) (Miers & Williams 1969). Colonially nesting swans show little evidence of aggression (Frith 1982; Braithwaite 1970) though later in season when fewer remaining nests, territorial behaviour apparent (Tingay *et al.* 1977). Captive birds in unstable associations temporarily establish small territories during pair-formation and courtship, then usually only maintain pecking distance round nest resulting in loose colonies. In territorial pairs, size of territory, from which all other swans chased, varies depending on temporal factors associated with breeding, form of social organization maintained and densities of breeding birds. In captive colonies established pairs or groups defend favoured roost or traditional nesting site. Area defended smallest (c. 5–20 m²) for more subordinate associations (heterosexual pairs) at all times and for trios or homosexual male pairs during times of low sexual activity; when breeding, male pairs defend 500–1000 m². Heterosexual pairs, when first established in absence of competition, patrol entire ponds (1400 m²); after hatching often leave territories to graze; and, with less defence, territories shrink; then defend 4–5 m round brood, always avoiding other nesting Swans. At Barrenbox Swamp, NSW, increased aggression from Mar.–Aug. probably related to establishment and defence of territories (Braithwaite & Frith 1969). Single pair will defend small wetland (less than 1–2 ha) and territorial defence also apparent in larger swamps where pools and islets in reed beds apparently facilitate demarcation of territories (Braithwaite & Frith 1969). Braithwaite observed two families where other Swans remained outside radius of 30–50 m from each family; once, families moved within 60 m of each other and males gave brief aggressive display towards each other; then broods and males moved apart. In NZ, territorial pairs defend several hectares of open water (where all feeding occurred) and swamp edge (where nest constructed) for several months before nesting and maintain them through breeding season until cygnets have flown. Too few data to determine what factors cause solitary or colonial nesting and differences at the same nesting area between years.

ROOSTING Pairs sometimes rest together on nest (Guiler 1966). After captive cygnets hatch, generally return to old nest-site to rest. In colonies, once wild young leave nest it is not used again but single territorial pair and brood use nest as resting position for rest of season (Tingay *et al.* 1977).

SOCIAL BEHAVIOUR In Aust., based mainly on captive birds (Braithwaite 1981b); agonistic behaviour includes additional material on wild birds from Tingay (1974). Disturbance, particularly handling of nesting birds, may cause disruption of breeding patterns (Braithwaite 1977, 1981a,b, 1982), though no effect noticed when handling chicks by Guiler (1966). Birds trumpet to one another in contact and use black-and-white plumage to signal intentions. When flock alarmed, first beat of wings, exposing flash of white, is signal to take flight, pattering across water into air with necks outstretched and rising in long skeins or Vs; mottled wings of juveniles appear to be less effective in causing flock to take flight. Braithwaite (1981a) also attributes colour of iris as having a role of signalling in social behaviour. In colonies, pilfer nest material, often destroying nests; as eggs deserted and scattered, neighbouring Swans often scrape them together into

their nests and incubate them (Guiler 1966; Miers & Williams 1969).

AGONISTIC BEHAVIOUR Aggression common among feeding Swans and increases as size of flock increases (Tingay 1974). White plumage of wings appears important in displays, which include Wing-lifting, Pecking, Parading and Trumpeting (Tingay 1974). **THREAT.** Among non-breeding flocks, aggression greatest when feeding and at certain times of day, most often with Wing-lifting and Pecking, choice of display apparently determined by distance between individuals: if density low, Wing-lifting common; among loose flocks on lakes, Pecking uncommon, occurring most often in preening birds, but commonly used when density high e.g. among flocks at small body of fresh water. **Wing-lifting:** bird lifts wings vertically from body, sometimes exposing primaries; neck curved or erect with feathers of neck raised and bill pointed down at c. 45°. Usually aggressive bird moves towards rival, which moves away. **Pecking:** varies in intensity from slight head movements in direction of rival to actual grasping with bill, sometimes for several seconds; may lift wings at same time. Usually causes rival to move away but appears to be used more often in defence than attack because pecking birds seldom move from original position. **Parade:** males of adjacent territories approach to within 1 m of each other on boundary of territory, with wings lifted and, with bills pointed down; sometimes touch breast-to-breast and head-to-head forming V with bodies; then swim along boundary for several metres and turn, either keeping breasts together or turning backs and swimming back along border. May involve up to 30 turns and last up to 10 min; occasionally interrupted by Fighting (see below), beating wings, Pecking and various comfort movements and ends simply with birds returning to own territories. Braithwaite (1981b) suggests bar on bill of males possibly involved in intimidation, when heads of males very close and bills pointed vertically down. Display not seen in females. **Trumpeting:** most evident in well-established pairs; given by male as territorial threat, or by female, usually while sitting on nest, to incite male to attack; strong trumpeting call given as head and neck thrown forward in wave-like motion resulting in bird stretching out horizontally. Incubating females may stretch neck and lunge at nearby birds (Guiler 1966). In addition, Johnsgard (1965) notes Wing-flapping as threat display. **Wing-flapping:** two or three strong wing strokes with wings fully opened accompanied by call. This may be same as Tingay's (1974) Wing-lifting or Fighting. **FIGHTING.** Rare; occurs in confrontation, if rival fails to move away; beats with fully open wings at rival, which retaliates similarly; interactions usually very short and not associated with submissive postures (Tingay 1974). **TRIUMPH CEREMONY.** Display performed vigorously by male when rejoining female after repelling opponent; lifts wings and calls repeatedly while extending neck and chin-lifting (Johnsgard 1965; Kear 1972); to conclude display, male usually gives two or three rapid wing beats that expose white in wings to maximum advantage and possibly helps to intimidate other birds (Braithwaite 1981b). **SOCIAL DOMINANCE.** By combination of above activities, dominant pairs obtain territories round favoured roost- or nest-site, which less dominant birds tend to avoid. Least aggressive birds without stable associations compromise, selecting nest-site between least-favoured situations, where harassed least, and most-favoured, where harassed most. Such dominated pairs often form loose colony where combined threat probably gives measure of protection. **APPEASEMENT.** Less dominant birds, when with cygnets, show combination of submiss-

ive and aggressive behaviour in presence of dominant birds; swim rapidly away from direction of threat holding neck out at 45° from horizontal and pointing head down 10° from horizontal; neck and wing feathers slightly raised. **ALARM.** In pre-flight alarm, bird swims rapidly downwind or to position giving maximum manoeuvrability for flight; neck held vertically and head and bill slightly below horizontal; then raises head through arc of c. 40° to give Trumpet-alarm; often makes several half-turns towards direction of take off. Nesting wild birds, when disturbed, slip off nest and swim quietly away with head held low (Frith 1982).

SEXUAL BEHAVIOUR Significant differences between sexes in amount of white plumage in wings may be factor in recognition and displays (Braithwaite 1981b). **PAIR-FORMATION.** In captive birds, frequency and intensity of displays vary. Pairing arises out of aggressive behaviour, usually kindled by female **Inciting** male to **Parade** towards or chase male rival. Female follows him. **GREETING.** When rival repelled, male turns, faces female and they perform **Greeting Ceremony** (Fig. 1), similar to **Triumph Ceremony** but calls and movements less vigorous. With repetition, pair-bond reinforced and tempo increases in vigour, evolving into true **Triumph Ceremony**; used for pair-maintenance by well-established pairs often when not feeding or otherwise engaged in agonistic display. In contrast, young birds breeding for first time perform Greeting Ceremony spasmodically at low intensity and not often. Individual recognition appears to be by vocalization, mainly Greeting Ceremony. **COPULATION.** In captive birds, frequency and intensity of displays vary. Pair displays for up to 20–25 min in 'wave-like' ducking activity, usually in water 30 cm or more deep. Neck and body held parallel to surface with brief (1–2 s) immersions of head, neck and body; repeated rapidly from two to five times with breaks



Fig. 1

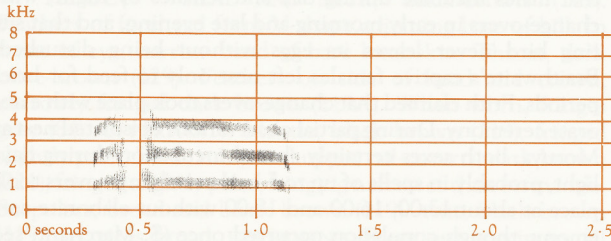
lasting from 10–20 s to several minutes; wings held close to body concealing white feathers in wings. Johnsgard (1965) notes mutual **Head-dipping** as pre-copulatory display. Treading effected when female ceases display and becomes outstretched and immobile, often after manoeuvring herself beneath male. Post-copulatory displays differ according to nearness of other swans who, if nearby, are attracted by copulatory displays. Thus on completion of copulation, may Parade or chase other swans, **Bill-dip** or participate in Greeting or Triumph Ceremonies; in post-copulatory display described by K.M. Davy (in Johnsgard 1965) both birds call with necks stretched and bills pointed upward, then holding their necks stretched at c. 45° and bill pointed downward at right angle to neck, swim in a circle. Copulation once observed in wild at Moruya: female came off nest and was joined by male; when alongside, male began to twine neck with that of female, both plunging necks repeatedly into water with much splashing and male apparently trying to mount on neck and shoulders of female; after about 3 min, female stretched head and neck out along water, male mounted and copulation occurred quickly; male slid off into water and both birds, sitting alongside, simultaneously shot head and neck vertically up to full stretch; one or both gave soft explosive *pink* call and relaxed. Female immediately swam to bank (10–15 m), stood out of water, flapped wings once and swam away; male walked up on nest, flapped wings 2–3 times, preened and settled on eggs (S. Marchant). In established pairs, if either bird undergoes moult, Greeting Ceremony becomes markedly less intense; rarely performed by moulting birds. Homosexual pairs frequently indulge in Greeting Ceremony, extended precopulatory display and mounting; may form brief association with female, then drive her away from nest and clutch.

RELATIONS WITHIN FAMILY GROUP Courtship displays and copulation in both captive and wild Swans generally occur near possible nest-site or at base of nesting mound, usually in water >0.3 m deep (Braithwaite & Frith 1969; Tingay *et al.* 1977). Incubating bird sits tightly, tolerating close approach of other Swans. With female's return, captive birds perform Greeting Ceremony, which results in exposure of eggs, allowing her to push male aside; Kear (1972) ascribes special two syllable note to this display. Newcomer climbs on nest from behind, still calling and dipping head over mate's body (Kear 1972). Female may perform aggressive Incitatory display at male who then responds with aggressive Parading or chasing. Departing bird may pass 2–3 beakfuls of nest material to sitting bird. Not entirely clear in Aust. literature that both sexes incubate in wild (see above); BWP states correctly that they do so and that 'elaborate nest-relief ceremonies recorded'. At Moruya, three change-overs witnessed (all without greeting ceremony): once, copulation occurred after sitting bird joined relieving bird alongside nest; once, relieving bird walked onto nest, preened plumage, shook itself and settled on eggs after sitting bird had eased itself onto water while pulling in nest-material; once, sitting bird left nest, swam away 50 m to join mate and started to feed, then mate came to nest 4 min later and settled on eggs (S. Marchant). In Braithwaite's study, separation of well-established pair during incubation resulted in desertion. Wild cygnets in WA remain on nest for one or two days (Tingay *et al.* 1977); in Tas. and NZ, <24 h (Guiler 1966; M.J. Williams). Often, first young leave nest with one parent while other incubates remaining eggs (Frith 1982), otherwise young remain on nest until hatching complete (Guiler 1966); cygnets then led to water. In colonies, once young leave nest, it is not used again and fam-

ilies leave nesting site; single territorial nests used by family as resting position for remainder of season (Guiler 1966; Tingay *et al.* 1977). **COMMUNICATIONS.** Within 48 h of hatching, captive cygnets become imprinted on immediate surroundings, after which close contact with surroundings, parents and other Swans (usually young of previous brood if not yet fledged) important; growth and age at fledging appear influenced by nutrition and these social factors; separation within first 30–40 days usually results in cygnets' death; thus imprinting probably related to cygnets ability to find food and to feed efficiently. Captive cygnets begin feeding within 24 h of hatching and parents defend area round brood; maintain family cohesion by Greeting Ceremony. Calls of cygnets described by Kear (1972; see Voice). When feeding, captive cygnets of about same age mingle, then separate to respective parents, evidently recognizing latter by soft **Pleasure Call**; also heard when feeding, preening or exploring with each other or parents; when greeting another family member, extends neck and utters similar but louder call. **Sleepy Call** given when cygnets tire or nestle together; probably encourages synchronized sleeping and female brooding. **Distress Call** attracts parent when cygnet isolated, cold or hungry; holds body erect, neck stretched upwards, down on head erect, mouth open and calls. **Alarm Call**, a loud and high pitched shriek. Captive cygnets of markedly different age often attacked by adults other than their parents. Within brood, social hierarchy often first evident at 70–80 days. If birds too closely confined feather picking will occur. Williams' work on cygnets at L. Ellesmere indicates broods reared as family by solitary nesters, which raise brood within strongly defended territory and guard closely; also colonial nesters occasionally rear as family unit (Williams 1981b). Tagging at L. Ellesmere in 1976, has shown 32% cygnets reared in family broods, mostly of which hatched early, and taken by parents to more remote parts of lake. Remainder reared in amalgamations of varying sizes guarded by one adult pair; c. 70% of amalgamations contained cygnets derived from two, three, or four broods; cygnets constantly change from one amalgamation to another and adults may end up guarding amalgamation containing none of their young; in one amalgamation of 40 cygnets, 19 tagged young were from 15 different broods and in all there may have been cygnets from 30 broods. Amalgamations occur when food patchily distributed and many broods have to feed within small area; lack of aggression between guardian adults allows much interchange; also occurs at L. Wairarapa, Okarito Lagoon and Vernon Lagoon, locations where food is patchily distributed. Whereas at L. Whangape and L. Omapere, food evenly distributed and colonial nesters seem to rear family broods. **DEPENDENCE OF YOUNG ON ADULTS.** In WA, if ephemeral water bodies start to dry out, families move to permanent water; cygnets, incapable of flight, eventually deserted by parents (Tingay *et al.* 1977). In captivity, family cohesion maintained usually for 70–120 days; brood sometimes breaks up about time of fledging (108–140 days); in wild, fledging estimated to extend to 170 days in NSW (Braithwaite 1981a) and in NZ records range from 95 to >140 days. In captivity, separation of broods apparently coincides with increased courtship behaviour between parents; usually female Incites male to Parade or chase real or imaginary opponents, then follows him and, at first, juveniles follow as well; juveniles and parents will also perform repetitive Greeting and Triumph ceremonies together; but eventually young ignored or occasionally chased by adults and stop taking part in these displays. Cygnets may maintain subordinate associ-

ation with parents and not breed while in this role e.g. one female maintained this for 8 years; one male for 34 months until his father died, then established bond with mother and successfully bred. In captivity, birds of stable associations most successful at rearing cygnets. Other forms of associations regularly hatch eggs but cygnets rarely survive, presumably because opportunities of feeding reduced and much harassing by other birds.

VOICE Little known and no detailed studies. Details of various calls have not been studied; information from Kear (1972). Most commonly heard call, musical bugle (sonagram A). Probably functions as contact call, being heard when birds



A R. Buckingham; Melbourne, Vic., Dec. 1979; P35

in flight and also among flocks on water. When defending nest or young, like other swans, give loud hisses. High-pitched whistles also frequently heard. Vocabulary probably large. In flight, wings produce whistling sound.

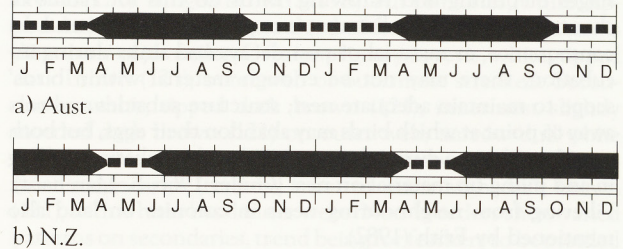
ADULT As above; no further details.

YOUNG Similar to other cygnets, but few details known (for circumstances of use see Relations within family group). **Pleasure Call:** series of *cleeps*, repeated two to five times; louder version used in family Greeting, usually on rising and falling cadence. **Sleepy Call:** low soft trill, rather like quiet sighs; consisting of number of slurred notes rapidly delivered. **Distress Calls** more highly pitched, louder and regular and given more slowly than Pleasure calls and for longer. Also given by hungry or cold cygnets but a little harsher. High-pitched shriek used by cygnet if hurt (stepped on, pecked or grasped by predator). As cygnet grows, develops hiss as expression of defence or aggression.

BREEDING Not at all well known in wild. Some studies by Frith (1982) and Braithwaite (1977, 1981a) in NSW, Guiler (1966, 1970) in Tas., and Tingay *et al.* (1977) in WA. In NZ studied by Miers & Williams (1969) and by M.J. Williams. Studied in captivity in Aust. by Braithwaite (1981a,b). Breed in simple pairs: solitarily on small (<2 ha) waters and on larger waters with fringe of aquatic plants or with constant level of water in winter-spring; or in large colonies (10³) on larger lakes and swamps with fluctuating levels of water and abundant food.

SEASON **AUST.** Nests may be started throughout year if local conditions favourable. At Booligal, NSW, Frith (1982) recorded nests in Jan., Feb., June, July, Aug., Sept. and Dec. in different years after heavy rains. At L. George, NSW, between Dec. 1962 and Feb. 1964 nests started in every month, particularly from Dec. 1962 to Feb. 1963 when many more were started than in expected season from Apr. to Aug. In ne. Qld, nests usually started in Mar.-May (Lavery *et al.* 1968). In coastal se. NSW, on small waters solitary pairs or small groups start nests from mid-May with replacements, perhaps second clutches or late breeding until Oct. or later

(Aust. NRS). Though probably a regular time for starting to lay, perhaps Apr. to Sept., controlled by fixed annual factors, breeding occurs whenever conditions suitable (Frith 1982). **NZ.** Solitary nesting regularly starts in July and lasts to Oct. Colonial nesting highly irregular, depending on water-levels; never starts before Sept. as water-level falls, and in some years not till Nov. or even Jan. At L. Omapere, Northland, occurs in two bursts: c. 20% of population starts in Sept.; rest in Mar.



SITE **AUST.** Very catholic in choice of wetlands from small ponds, dams and ornamental waters to large vegetated swamps, wooded or otherwise, lakes and broad still estuarine waters. Use permanent as well as impermanent waters such as flooded wheatfields, small depressions in arid plains (Frith 1982). Also nest on land but apparently only on islands in lakes (Frith 1982), where first pairs build on shallow banks near shore and late-comers expand colony to cover island. In water, nests usually in depths of 30–60 cm and as far from shore as that allows; attached to, and supported by, emergent vegetation such as cumbungi *Typha* and cane-grass *Eragrostis*. Nest sometimes on top of flooded stumps, in bases of trees in wooded swamps, and in floating masses of debris (Frith 1982). Choice of site probably much influenced by availability of nearby material but also by visibility from nest, ease of access and protection from predators (Frith 1982; Tingay *et al.* 1977). Spacing of nests: closest 1 m with average 1.625 m (Guiler 1966) and c. 1.5 m (Frith 1982) on island sites; c. 14 nests/ha on lakesides (Braithwaite 1982). Where clumping or colonial nesting not developed, 0.14–1.1 pr/ha in *Eleocharis* and *Glyceria* swamps (White 1986). **NZ.** Similar situations as above. On water, in stands of *Typha*, *Eleocharis*. At L. Whangape below dense scrub canopy of ponga *Cyathea dealbata*, manuka *Leptospermum scoparium*, willow *Salix*; also on open ground on islands. In large colonies (e.g. 5000 nests, L. Ellesmere) nests spaced 2–3 m apart in places, average 2.4–3.0 m in different years; has nested up to 150 m from water; rushes or tussocks form effective barrier between nests in centre of colony, where nests densest (Miers & Williams 1969).

NEST, MATERIALS In water, large buoyant heap of vegetation (e.g. water-ribbons *Triglochin*) up to 150 cm across and 90–120 cm thick with 30 cm above water and bowl at top for eggs; cup lined with some down but down not used to cover eggs. Usually anchored to rooted plants but may break loose and float about as bird incubates. On land, usually less substantial, 60–90 cm across and 30 cm high, made of whatever material is available nearby and sometimes little more than scrape lined with down (Frith 1982; Miers & Williams 1969). New nests usually built each year by isolated pairs, old nest having disappeared during non-breeding period, but in colonies old mounds, some many years old, refurbished in successive years (Tingay *et al.* 1977) and same nest often used several times in same season (Frith 1982). Material is dragged into site or nest from within reach (Williams 1981a). In anser-

iforms generally material is not carried in bill and males do not bring material to nest. Both male and female collect material but do not pass material between themselves and do not build nest in the sense that, say, passerines do. For nests on water, stretch out with head and neck, grab and drag in water-ribbons or submerged vegetation, and drop them on either side of their tails. If near enough to nest, material thus piled up into adequate mound. As adjacent material depleted, birds collect farther away and transfer material to nest in several stages of pulling and throwing. Birds do this for radius of about 10 m from nest but may not persist much beyond. In consequence, as material of nest decays and sinks during incubation, there may not be enough material within birds' scope to maintain adequate nest; structure subsides and rots away to point at which birds may abandon their eggs, but both spend much time during laying period and incubation pulling in and piling up material on nest (Guiler 1966; S. Marchant). Pilfering from neighbouring nests in colonies on land also mentioned by Frith (1982).

EGGS Elliptical; coarse grained, slightly glossy; pale green to dull greenish white, becoming stained and scratched.

MEASUREMENTS: 105 (0.1; 95–117; 1555) × 67.3 (0.1; 60–72) (Braithwaite 1977).

WEIGHTS: Fresh: 264 (1.32; 200–320; 123) (Braithwaite 1977).

Eggs from different localities taken in different years measured and weighed significantly differently. Second-laid egg of clutch tended to be largest on average (Braithwaite 1977).

CLUTCH-SIZE Large samples from colonies have given the following averages:

ne. Qld: 4.5 (1–8; 187) (Lavery in Frith 1982)

NSW: 5.5 (4–10; 407) (Frith 1982)

Ls George, Bathurst: 5.32 (0.05; 3–9; 403) and 5.20 (0.07; 1–14; 446) (Braithwaite 1977 by two different assessments)

Tas.: 4.46 (n=10 365) (Guiler 1970, who found significant differences in means for different sub-colonies; Guiler 1966);

various NZ colonies in different years: 4.9–5.7 (3–14; 70–1000) (Miers & Williams 1969).

None of these samples was critically assessed for completeness of clutches, except perhaps those of Frith and Braithwaite. Most clutches over 8–9 were certainly laid by two females (Frith 1982; Braithwaite 1977; M.J. Williams) and Frith also emphasized that floating eggs from one nest are often retrieved by owner of another. Thus, the average clutch-size for an individual is not established but is probably c. 5.0. In spite of smaller average in Qld, there is no evidence for smaller clutches in lower latitudes (Frith 1982). As L. Ellesmere, NZ, deteriorated and colony decreased from 1975 to 1979, average clutch-size decreased from 5.0 (n=1034) to 4.0 (n=500). Average clutch-size increased during season at L. George from 4.86 on 1–5 Dec. 1962 to 6.15, 220 days later (Braithwaite 1977). Clutch-size of solitary nesters not assessed. Replacement laying after loss of eggs. Second or more broods probable by solitary nesters on small waters, at least in coastal se. NSW (Aust. NRS).

LAYING Eggs added to clutches at average rate between 1/2 days and 2/3 days (Braithwaite 1977; Tingay *et al.* 1977) or daily at c. 24-h interval (M.J. Williams). In NZ colonies, laying highly synchronized: rarely more than 3 weeks between first and last eggs.

INCUBATION Starts after laying of penultimate

egg in clutches of four or after the pre-penultimate egg in larger clutches (Frith 1982). Gurney (in Gould 1865), wrote saying that in his captive birds in Britain 'both sexes assist in the duty of incubation' (Delacour 1954–64). Recent authors (e.g. Frith 1982; Tingay *et al.* 1977) assert that this is so, without making it plain that they confirmed it and that they were not merely copying previous statements. M.J. Williams says that both birds incubate during daylight in 3–4 h spells but female mainly at night. Braithwaite (1977), with captive birds, says that both sexes 'may participate in incubation' but his brief description of the behaviour suggests that the male's share may be very little. One of Campbell's correspondents wrote that 'the female only sits (?)'. Tingay *et al.* (1977) state that males incubate during day and females by night, with change-overs in early morning and late evening, and that sitting bird never leaves its eggs without being disturbed. Braithwaite's captive females left nest only to feed for brief periods. Frith claimed that change-overs took place with elaborate ceremony. During partial observations of isolated nest at Moruya, both sexes certainly shared incubation during daylight, probably in spells of up to 5 h; three change-overs took place at about 13:00, 16:00 and 18:00 without elaborate ceremony, though copulation occurred once (S. Marchant; see Social Behaviour, Relations within family group, above). Matter needs further study in wild, especially because this is the only species of *Cygnus* in which males take a share of incubation. **INCUBATION PERIOD:** Aust.: average 40.5 days (0.26; 35–48; 89); slightly longer by 2 days on average for C/7 than for C/4 and C/5 and significantly different seasonally (summer 38.3 days, autumn 40.1, winter 41.5, spring 38.8) (Braithwaite 1977); in Tas.: 39 ± 2 days (Guiler 1966). NZ: average 36 days (32–43) (M.J. Williams). Hatching somewhat asynchronous, in 24–48 hours (Frith 1982).

YOUNG Precocial, nidifugous. At hatching, eyes open, grey-brown; covered in light-grey down; bill, legs, dark grey; weight c. 170 g. Egg-tooth lost by about 10 days old; head, neck and body begin to feather at 25–35 days; colour (red?) appears on bill at about 60 days old; wing-quills appear about 50 days old; fully feathered, 95–140 days old; some down remains on neck till at least 80 days old and on back till more than 100 days old (Braithwaite 1981a; other details in Plumage). Cygnets brooded in nest for <24 h and then led to water. Begin to feed within 24 h of hatching; become imprinted on parents and surroundings within 48 h and for successful rearing cannot be separated from familiar environment for 30–40 days. In solitary pairs, both parents attend and guard young assiduously. At L. Ellesmere, c. 32% of cygnets reared as family broods; the rest joined into groups; at maximum 30 different broods amalgamated with a group but 70% of such groups formed from 2–4 broods. Amalgamations probably induced by patchy distribution of food, forcing broods into close contact; each attended apparently by only one pair of adults; also recorded at L. Wairarapa, Okaraito, Vernon Lagoon, where food also patchy; not at Ls Whangape, Omapere, where food well distributed. **FLEDGING PERIOD.** Primaries fully grown by about 150–170 days old, when cygnets may begin to fly (Frith 1982; Braithwaite 1981a) but probably varies much according to availability of food, e.g. 95+ to 140 days at various localities in NZ (M.J. Williams).

GROWTH At hatching weigh c. 170 g, at 30 days old 380–590, at 90 days 1600–3200 and at 180 days 4000–5000. Details of other aspects of growth in captive birds, see Braithwaite (1981a).

FLEDGING TO MATURITY Broods remain clo-

sely associated with parents and amalgamations do not disband until near end of fledging period. In captivity some evidence of sexual inclinations when birds still in juvenile plumage but birds do not breed while still in juvenile wing-plumage; perhaps achieve sexual maturity shortly after moult into adult wing-plumage. Most birds bred for first time when 18–36 months old.

SUCCESS No data but Frith (1982) said that with mean clutch-size of 5.5 eggs, 4.1 cygnets hatched and 2.7 survived to fledging. No information on predation but many eggs lost by being rolled out of nests.

PLUMAGES

ADULT HEAD AND NECK, black-brown (119). Feathers of forehead form V-shape adjoining base of bill. In front of eye, narrow band of bare loreal skin. Throat, dark olive-brown (129). Feathers on side of head and crown, narrowly fringed dark brown (119A). When worn, fringes grey (84). **UPPERPARTS**. Mantle, black brown (119), fringed slightly paler. Back, rump and upper tail-coverts, dark brown (221), fringed slightly paler; fringing narrower than on mantle. Scapulars, broad and black brown (119). **TAIL**, black brown (119); rectrices broad. **UPPERWING**. From one specimen: all coverts, dark brown (221). Primaries and some secondaries, white; p2 has black-brown (119) wedge on outer web. Secondaries, white; basal third of outer and inner webs of s7, dark brown (121); s8–10 and s12–14 (tertials), white; s11 white but inner web streaked at tip. Rachis of tertials, white for half length of feather; rest tipped dark brown (221). Outer webs of tertials, upturned; innermost greater coverts also have outer webs slightly upturned. Outer alula feather, white; innermost, tipped dark brown (221). Much variation in colour of remiges and coverts (white, black, black with white tips and white with black tips); details for sample of 451 adults in Braithwaite (1981a). Typically (proportion >20%), adults show: p1–9, white; p10, black; primary-coverts, white; first feather of alula, black; second, black with white base; third, white or tipped black; fourth, white; s1–8, white; s9–11, mostly white but varying; s12, mostly black or white; s13–s17, black. Details of differences between sexes (in adults) based on feather characteristics given in Braithwaite (1981a). **UNDERPARTS**, dark olive-brown (129), fringed slightly paler. Flank-feathers, elongate and broad. Axillaries, dark brown (221); rachis, white basally, merging to grey-black (82). **UNDERWING**. Glossy tegmen on primaries. Greater primary coverts and greater coverts, glossy brown-grey (79). Rest of coverts, dark brown (121).

DOWNY YOUNG HEAD AND NECK. Down on crown and lower hindneck, light grey-brown (119C); at lower foreneck, brown grey (79). Rest, dull white. When older, down on upper neck, dull light grey-brown (27). **UPPERPARTS**, combination of grey (-) and light grey-brown (27); down longest on back. **TAIL**, similar to upperparts. **UPPERWING**, combination of grey (-) and light grey-brown (27). **UNDERPARTS**. Breast to vent, dull white; down shorter on upper breast than on rest of breast; longer on flanks and combination of grey (-) and light grey-brown (27). Vent to tail, similar to flanks. When older, underparts, dull brownish-white (-). **UNDERWING**, dull white. Rectrices appear at 20–30 days; some feathering round eyes at 30–35 days. First feathers appear on scapulars at c. 55 days and on lower neck and upper tail-coverts at c. 65 days. Between 75 and 95 days, cygnet fully feathered. Primaries and secondaries fully grown 140–180 days (Frith 1982). Fledging 108–141 days in captive birds, c. 170 days in wild birds

(Braithwaite 1981a). Full details of plumage changes to juvenile also given in Braithwaite (1981a).

JUVENILE Plumage attained 3–4 months after fledging (Braithwaite 1981a). **HEAD AND NECK**. Crown, dark brown (121), narrowly fringed light grey-brown (27). Sides of head, throat and neck, pale dark-brown (121), fringed light grey-brown (119C). **UPPERPARTS**, dark brown (121), fringed brown (119B). **TAIL**, dark brown (121), fringed brown (119B); tips of rectrices notched. **UPPERWING**. Most coverts, dark brown (121), fringed brown (119B). All primaries, white, tipped dark brown (121) for a third of feather. This character is diagnostic of juveniles. Greater primary coverts, white, tipped dark brown (121); outer web of outermost streaked. Secondaries, white, tipped dark brown (121); innermost slightly mottled dark brown (121) on outer web; narrow dull-white fringe; rachis white basally, at tip, pale brown (119B). Outermost secondaries (tertials), most of outer web dark brown (121), with whiter basal inner webs. Non-breeders show varied patterns on secondaries, trend being for feathers to be mottled in young birds; greater coverts, are white, mottled or black (see Braithwaite 1981a for details); Braithwaite (1981a) also gives proportions of pattern of remiges for sample of 20 juveniles. **UNDERPARTS**. Breast to vent, pale dark-brown (121) with open pennaceous dull-white fringes. Flanks and under tail-coverts, dark brown (121), fringed dull white. Axillaries, dark brown (121); rachis white basally, merging to brown (119B). **UNDERWING**. Greater primary-coverts and greater coverts, very dark brown-grey (79). Rest of coverts, pale dark-brown (121). Adult plumage attained after post-juvenile moult.

ABERRANT PLUMAGES Occasional pale or leucistic birds observed (M.J. Williams).

BARE PARTS Based on photos in Pringle (1985) and observations of dead and living birds (R. O'Brien), except where stated.

ADULT Iris, red (11) though Braithwaite (1981a) also reports white, pink and light red; colour apparently differs between sexes and is related to weight and, in males, sexual condition (see Braithwaite 1981a). Redness of eye may have signalling role in social behaviour (Braithwaite 1981a). Bill and loreal skin, red (12); behind nail, on upper mandible, saddle-shaped subterminal white band. Legs and feet, dark grey (83) with olive-brown (29) shade.

DOWNY YOUNG Iris, dark brown (221). At hatching, iris grey-brown, changing to brown at 60–80 days; red-brown at 135–170 days (Frith 1982). Iris, grey-brown until c. 90 days (Braithwaite 1981a). Bill, grey-black (82); tip, dull white. Dark grey bill, changing to red at 85–120 days (Frith 1982); bill colour (probably red but not stated) acquired c. 40 days (Braithwaite 1981a). Legs, toes and webs, grey and vary little in colour with age (Braithwaite 1981a).

JUVENILE Iris, as adult, with traces of brown; varies from red to white; colour related to sex (see Braithwaite 1981a). At fledging, bill of juveniles, dull red with traces of brown and grey. By first moult, bill and iris similar to adult (Braithwaite 1981a). Photo in Pringle (1985), shows bill, red (10) with dull white saddle-band; in front of this band, on upper mandible, narrow margin of brown-grey (79). Legs and feet, as adult.

MOULTS Based on Braithwaite (1981a), except where stated. Non-breeders moult towards end of main breeding season before breeders; in se. Aust., numbers greatest at

moult-sites following main breeding season in spring and early summer, and least in June–July; though moulting can occur at any time of year (Guiler 1966; Frith 1982; Braithwaite 1981a). During moult, captive Swans flightless for c. 6–7 weeks, probably as in wild, though, in NZ, Williams estimates flightlessness for c. 4–5 weeks.

ADULT POST-BREEDING **Captive birds.** Complete; body- and wing-moult in Oct.; remiges simultaneous; loss of feathers takes 1–2 days; moult occurs c. 6 months after laying; flightless. Replacement of remiges in captive birds takes 6–7 weeks; probably about same period of flightlessness in wild birds. Breeders moult later in year and more often than non-breeders. Non-breeders moulted before Nov.; breeders Oct.–Jan. In adults, replacement of p10, 44.3 days (38–51; 7). Period between moults 7–36 months; most moulted at intervals of 9–21 months; moulting more frequent as birds aged (see Braithwaite 1981a for details). Moult in all months of year, except Apr. and May; most Aug.–Jan. Moult has no fixed relations to breeding season. One in 4 birds bred in successive seasons without moulting; 50% of the time, moulting occurred within 6 months of laying final clutch in season. **Wild birds.** Moult occurs at refuges. Moult during all months of year; fewer moulting June–July (see Braithwaite 1981a for seasonal proportion data of birds showing new plumage). Most had new plumage in spring, indicating tentatively an annual cycle. Proportion of birds, based on state of plumage wear, indicated that retention of wing plumage for periods exceeding 18–24 months is possible. Most moult Aug.–Jan., though moult can occur at any time, with interval between moults 7–36 months. In n. Qld, moult in adults, Mar.–July (Lavery 1967).

POST-JUVENILE Complete; moult occurs at 8–17 months, representing maximum juvenile age. In 38 captive birds, 21 males and 17 females, age at moult varied from 8 to 26 months; most 8–17 months. Moult occurs in all months of the year except Apr. and Dec.; majority Aug.–Nov. Replacement of remiges takes c. 38–51 days; interval between moult of wing plumage, 7–36 months, period decreasing significantly with age.

MEASUREMENTS (1) NZ, live adults; methods unknown (M.J. Williams); (2) Bool Lagoon, SA, recently dead birds (via SAM) (R. O'Brien).

	MALES	FEMALES	
WING	(1) 511.7 (17.82; 425–550; 111) (2) 469.3 (42.59; 410–508; 3)	487.5 (15.52; 440–530; 76) 459.3 (10.14; 445–467; 3)	*
BILL	(1) 70.8 (3.01; 58.9–79.6; 111) (2) 74.4 (7.80; 67.7–90.8; 6)	65.3 (2.83; 59.4–70.5; 76) 64.3 (2.84; 59.2–67.9; 6)	*
THL	(1) 141.4 (3.02; 136.2–145.2; 6) (2) 141.4 (3.02; 136.2–145.2; 6)	129.6 (2.61; 127–133.2; 6) 129.6 (2.61; 127–133.2; 6)	*
TARSUS	(1) 100.3 (4.41; 82.3–113.6; 111) (2) 94.5 (5.52; 85–100.3; 5)	93.4 (3.83; 86.6–102.7; 76) 89.2 (3.85; 82.6–95.8; 6)	*
TAIL	(1) 105.5 (5.92; 92–120; 111) (2) 114.5 (8.36; 104–130; 6)	104.9 (6.14; 93–120; 76) 109.6 (1.88; 107–112; 6)	*
TOE	(1) 125.3 (5.16; 106.9–136.8; 111) (2) 127.1 (4.16; 121.3–133.2; 6)	117.0 (4.89; 104.2–127.6; 76) 118.7 (4.52; 111.2–125.8; 6)	*

More measurements in Frith (1982). Full details of growth rates of cygnets given in Braithwaite (1981a).

WEIGHTS In Aust., dates unknown, recently dead birds: males 6270 (4600–8750; 247); females 5100 (3700–7200; 219) (Frith 1982).

In NZ, locality and dates unknown, live birds: males 6093.6 (674.30; 3800–7700; 111); females 5090.7 (566.88; 3900–6900; 76); males significantly heavier than females ($P < 0.05$; M.J. Williams). No data on seasonal changes in weight. Details of changes of cygnets given in Frith (1982) and Braithwaite (1981a).

STRUCTURE Wing, long and broad. Neck long. Eleven primaries, p8 longest p10 11, p9 1, p7 7, p6 42, p5 80, p4 112, p3 139, p2 165, p1 186. P11 reduced, concealed by greater primary coverts. P10 strongly emarginated on inner web, p9–8 emarginated on outer and inner, slight on p7. Seventeen secondaries, seven of tertial form. Tail, rounded; 16 broad rectrices, t1 longest, t8 30–39 mm. Bill, long but narrow and deep at base; coarse lamellae along length of upper mandible; visible, but narrow in cygnet. Nail, very broad; pale saddle-shaped subterminal band adjoin nail. Legs, short. Feet, large and webbed. Outer toe c. 99% of middle, inner c. 79%, hind c. 17%.

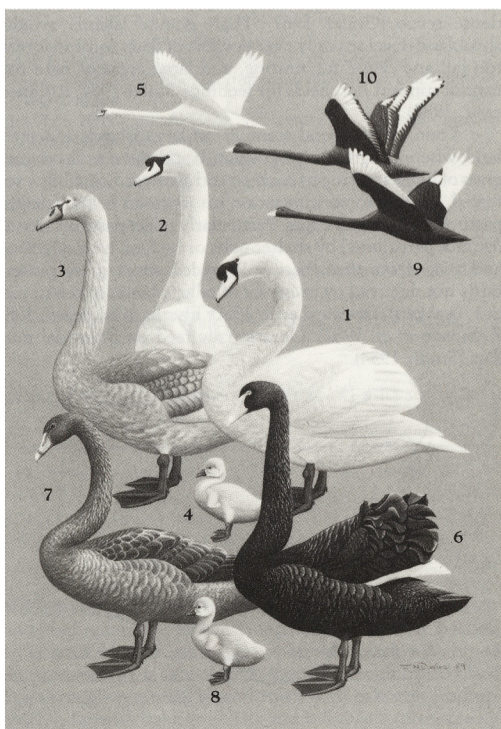
SEXING, AGEING Penis evident in juvenile birds <10 months old. By time of post-juvenile moult, penis varied in size from stage of marginal development, 4–5 mm, to that of breeding adult, 50–60 mm. Females retain juvenile cloacal characteristics to post-juvenile moult (see Braithwaite & Norman 1974). Ageing criteria have limitations. In cygnets growth and age at fledging influenced by nutritional and social factors. In single cygnet of poor health, fledging 108–170 days; in healthy birds estimate c. 108–160 days (Braithwaite 1981a). Width of exposed loreal skin, narrower in juveniles than in adults.

RMO

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Volume 1 (Part B), Plate 85

Mute Swan *Cygnus olor*

1. Adult male
2. Adult female
3. Juvenile
4. Downy young
5. Adult male

Black Swan *Cygnus atratus*

6. Adult
7. Juvenile
8. Downy young
9. Adult
10. Juvenile

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