

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

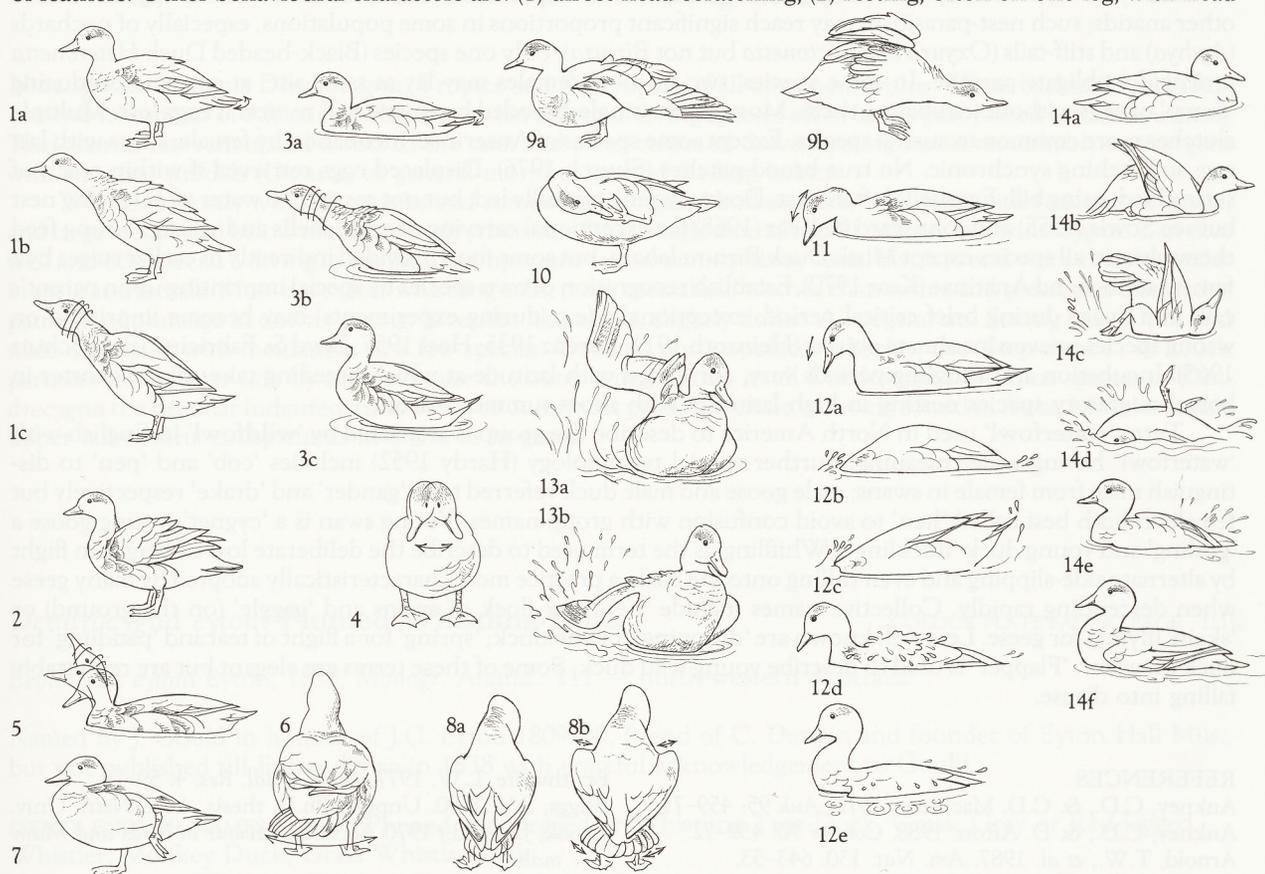
Waterbirds (some more or less terrestrial) with rather short legs and front toes connected by webs; hallux elevated and reduced. Though considerable adaptive diversity in outward appearance, size, colours of plumage, behaviour, and ecology, homogeneous in many characters, as attested by numerous, often 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 (tertiaries) often long and brightly coloured; diastataxic. 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 TADORNINAE sheldgeese, shelducks and steamer ducks

Fairly large, often semi-terrestrial, mostly goose-like wildfowl; most are moderately long-necked grazing birds with short toes and rather long tarsi inserted well forward. Tarsi scutellated in front. Intermediate in many characters between Anserinae and Anatinae. One aberrant group of solidly built, diving ducks, most flightless, considered allied to these birds rather than other ducks. Nineteen living species, predominantly in s. hemisphere, in six genera; two typical sheldgeese (*Cyanochen* from Abyssinia, *Chloephaga*; five species South America); two intermediate (*Neochen* from South America, *Alopochen* from Africa); shelducks (*Tadorna*) and Steamer ducks (*Tachyeres*; four species from South America). *Tadorna* consists of seven species in two groups (1) typical *Tadorna* (*T. tadorna* Palaearctic and *T. radjah* tropical se. Asia and Aust.); (2) *Casarca* (remaining five species from Africa, Palaearctic and A'asia).

Wings with bony, spur-like knob on metacarpal joint. Tails fairly long. Bills comparatively short and thick (sheldgeese), or depressed (*Alopochen*, shelducks) with distinct lamellae (shelducks generally) and turned slightly upwards (typical *Tadorna*). Steamer ducks have massive bills. Sexes differ in tracheal structure: that of females simple and goose-like, male with enlarged bullae; usually on left of trachea but in Shelduck *T. tadorna* enlarged on both sides; bullae much reduced in *Casarca* group. Calls differ between sexes. Sexes dimorphic in some *Chloephaga* and *Tadorna*; similar or nearly so in rest. Plumages of both male and female usually bright except *Tachyeres*; no discernible non-breeding plumage in most species. True eclipse plumages rare. Large metallic green speculum except in *Tachyeres* where secondaries white; lesser and median wing-coverts usually plain (often white). Juveniles like adults but colours duller. Downy young boldly patterned black-and-white but *Tachyeres* dull.

Largely cosmopolitan but most species subtropical and temperate s. hemisphere, and all absent from North America. Essentially birds of low or lower middle latitudes, or (as *Cyanochen* and some *Chloephaga*) of mountains in tropical zone. As a group, best characterized by continental warm or mild climatic requirements, acceptance of high altitudes; prefer inland waters or, at most, sheltered coastal waters, except for maritime Kelp Goose *Chloephaga hybrida* and Steamer ducks. *Cyanochen* and *Chloephaga* typically use grassland for terrestrial grazing; *Alopochen* and *Tadorna*, nest in holes and like unvegetated sand, silt, or mud margins, and are adaptable to semi-domestication. Orinoco Goose *Neochen jubatus*, atypically, a bird of dense tropical forests where (like *Alopochen*) it perches freely. In w. Palaearctic, *Alopochen* contrasts with *Tadorna* in being a partly tropical breeding species much more tolerant of forest country. When flightless during post-breeding moult, often frequent areas of open land or water where can observe and avoid terrestrial predators. Little detailed information of movements of sheldgeese and most other s. Tadorninae but many populations resident to greater or lesser extent. In *T. tadorna*, major moult-migration at end of breeding season to traditional moulting areas in w. Europe involves immatures and most adults, except those attending crèches of young, which moult *in situ*. Similar pattern known from *T. variegata*. Movements in most species mainly nocturnal and in flocks; do not hesitate to cross land-masses. Three species of *Tachyeres* flightless and fourth periodically so (Humphrey & Livezey 1982; Humphrey & Thompson 1981; Livezey & Humphrey 1986).

Some (e.g. *Chloephaga*, *Alopochen*) chiefly plant feeders, mainly by terrestrial grazing; some shelducks (e.g. *T. ferruginea*, *T. variegata* and *T. tadornoides*) omnivorous, feeding by grazing, dabbling and up-ending; others (e.g. *T. tadorna*) primarily animal feeders, mainly by dabbling in mud or shallow water, swimming with head submerged, and up-ending (cf. *Stictonetta* from our region). Steamer ducks dive using wings underwater and feed on marine animals. Often feed and otherwise associate in pairs and family parties or in flocks. **Pre-flight** signals consist mostly of lateral **Head-shaking** and repeated **Chin-lifting**. None in steamer ducks. Most species highly aggressive, specially steamer ducks. Maintain nesting territories at least while breeding, but territories of some *Tadorna* (e.g. *T. tadornoides*) mainly for feeding and meeting of pairs with nest-sites elsewhere, sometimes in groups. Long-term monogamous pair-bonds much as in Anserinae, though thought by Johnsgard (1965) to be less strong in shelducks than in sheldgeese. In some species, pair occupy territory together throughout year. Courtship often terrestrial; more elaborate than in Anserinae but less so than in Anatinae, with no true communal displays. Not fully studied in most species, especially in wild. Pair-formation in steamer ducks involves few rather hostile actions with loud vocalizations. In all other species, females play important or major role in pair-formation; mainly by use of characteristic aggressive **Inciting** display typical of most Anatidae but finding most complete expression in Tadorninae, where often directly functional in causing chosen male to attack others. Male pairing and other sexual displays include **Puffing**, **Bowing**, and **High-and-Erect**, often with wing-raising and strutting gait (Johnsgard 1965), but often difficult to distinguish from antagonistic behaviour; displays of different genera or even of different species-groups within *Tadorna* often divergent. In some sheldgeese (including intermediate *Alopochen*) and some *Tadorna*, mutual **Triumph Ceremony** much as in Anserinae. Displays more typical of Anatinae found in some species, mainly *Tadorna*; include unilateral and mutual **Bill-dip**, **Ceremonial-drinking**,

Mock-preening in form of **Preen-behind-Wing** display, and, in *T. tadorna*, vocal version of **Upward-shake** (male only). **Pursuit-flights** (see Anatinae) also reported from at least one species (*T. tadorna*). Copulation typically on water, sometimes in shallows or on land. Pre-copulatory behaviour resembles Anserinae with mutual **Head-dipping**. Post-copulatory behaviour distinctive; includes **High-and-erect** display by male, usually with wing lifted on side farthest from female. Voices often loud and sexually well differentiated. Females of all species with low-pitched rasping calls like those of some Anatinae (Johnsgard 1968). Males of most sheldgeese have whistling calls as also those of *T. tadorna* and *T. radjah*; in *Casarca* group of shelducks, however, voice of males loud and honking, while that of male *Alopochen* different again. Often call in flight and on water, land, or perch. In most species, male's vocal response to **Inciting** call of female of two types: aggressive (to other males), friendly (to female); see Johnsgard (1965).

Seasonal breeders. Nests on ground in open (*Chloephaga* and *Tachyeres*); in burrows and holes in ground, trees, or buildings (*Tadorna*); on ground in thick cover, cliff ledges, or in holes (*Alopochen*). Old nests of other species also sometimes used (*Alopochen*, *T. ferruginea*). Sites sometimes far from water. Usually solitary nesters but sometimes close in hole-nesting *T. tadorna*. Amount of nesting material varies, from mound of vegetation on ground to little or nothing in holes; lined with down. Building by female only. Eggs rounded, creamy-white and smooth. Clutches 3–12, averaging larger (8.4) in hole-nesting species than in open nesters (6.1) (Lack 1968). Multiple laying by females in one nest common in some species (e.g. *T. tadorna*). Replacement clutches produced after early loss of eggs. Eggs laid at intervals of 24 h. Incubated by female only, leaves nest once or more often each day when usually joins male; latter may stand guard in many species. Incubation periods 28–30 days (Kear 1970), with no significant difference between hole-nesters and others (Lack 1968). Young attended by both parents but brooded by female only. Both parents aggressively defend young at times in most or all species. **Distraction** display by female or both sexes, in form of 'injury-feigning', reported in *Chloephaga* and *Tadorna*, but evidently lacking in *Neochen* and *Alopochen* (Hebard 1960). Other anti-predator reactions by parents include 'tolling' (Sowls 1955 for dabbling ducks) i.e. moving or flying conspicuously, often while calling, away from or near predator. In most species, young not independent until fledging or after, remaining with parents for up to 6 months. In *T. tadorna*, broods may amalgamate into crèches, some parents then deserting own young. Mature usually at 2 years.

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Tadorna variegata Paradise Shelduck

COLOUR PLATE FACING PAGE 1229

Anas variegata Gmelin, 1789, *Syst. nat.* 1: 505; based on 'Variegated Goose' of Latham, *Gen. Syn. Birds*, 3: 441 — Dusky Bay, New Zealand.

OTHER ENGLISH NAMES Rangitata Goose, Painted Duck.

MONOTYPIC

FIELD IDENTIFICATION Length 65 cm; weight 1.5–2 kg. Large dark heavy-bodied duck. Sexes differ: males all dark, female with conspicuous white head and neck. Juveniles like adult male.

DESCRIPTION ADULT MALE. Head and neck, blue-black; back and flanks, black, lightly flecked with pale yellow; rump and tail, black. Upper wing-coverts, white contrasting with blackish remiges; speculum, metallic green; tertials, rusty brown on outer vane, flecked grey-brown on inner vane. Breast and abdomen, dark grey, flecked pale yellow; undertail, chestnut; underwing, like upperwing but secondar-

ies dark grey. Iris, bill, legs and feet, black. **FEMALE.** Head and neck, entirely white contrasting with dark-grey back, heavily flecked with pale yellow; rump and tail, black; upper and underwing, like male. Breast, abdomen, flanks and undertail, bright chestnut. Iris, bill, legs and feet, black. **FEMALE NON-BREEDING.** Feathers of underparts, tipped black and interspersed with dark, heavily flecked feathers giving dark-chestnut appearance. **DOWNY YOUNG.** White with brown crown; brown stripe from crown to tail; brown mark on wings and flanks. Iris, bill, legs and feet, black. **JUVENILE.** Like adult male but females smaller with white patch at base of bill. **IMMA-**

TURE. White head of female assumed during first moult, 1–2 months after fledging; breast and abdomen, dark chestnut.

SIMILAR SPECIES Generally unmistakable; white head and neck of adult female, distinctive at all times. Adult males and juveniles have dark heads and may possibly be confused with vagrant **Australian Shelduck** *T. tadornoides*, which has similar size, shape and posture when swimming, on land and in flight. Paradise Shelducks lack white collar, fairly uniform dark underparts, and contrasting broad chestnut band across breast and mantle of Australian Shelduck. Greatest risk of confusion between juvenile and female Australian Shelducks, and juvenile female Paradise Shelduck moulting body-feathers into adult plumage; in these moulting juvenile females, incoming white head feathers first appear at base of bill and round eye and chestnut-rufous feathers first develop on breast, thus resembling female and juvenile Australian Shelduck. Distinguished from female Australian Shelduck by lack of white collar and chestnut, not black, under tail-coverts. Best distinguished from juvenile Australian Shelduck by appearance of breast and mantle: breast of juvenile female Paradise Shelduck at best has ill-defined band on breast (sharply defined at all ages in Australian) with remnant dark feathers present that give mottled appearance (band evenly coloured in Australian) and also show some emergent rufous-chestnut feathers on belly and flanks (though fewer than on breast).

Usually seen in pairs or family groups grazing on low pasture, round dams or in flocks near larger water-bodies, on open grass flats or gravel river beds. On water, recognized by stout build and short neck. On land run strongly on quite long legs. Persistently vocal on land and in flight. Alarm note deep *zonk-zonk* in male; shrill penetrating *zeek-zeek* in female. Numerous territorial and courtship calls, territorial calls often as duet in air.

HABITAT Endemic to NZ; in NI, stronghold in deeply dissected hilly farmland, with soft underlying strata, large areas of improved pasture, numerous farm dams, natural pools formed by slumping, remnants of forest cover, and fertile riverside flats; SI stronghold in river valleys and high-country lakes in tussock grassland of e. foothills of S. Alps; throughout NZ, small numbers of birds on mountain and forest creeks and on coastal flats, inlets and lagoons.

Breeding territories established round water-body used as nursery area for young; panoramic view from on or near water. Tokomaru Bay, NI: of 103 territories, 87 round dams or pools, seven on sections of river, nine on freshwater seepage or marshy area. For open aspect, pools on hillsides or flats used most often; hilltops used occasionally, but deep gullies avoided. Size of water-body, depth, abundance of zooplankton or clarity does not influence selection. Marginal or emergent vegetation (e.g. *Juncus*) not major requirement; present on 54 of 87 dams and pools. In rivers, nursery area in wide slow-flowing parts with access from gently sloping banks or flats. In breeding territory, adults and young feed in moist areas with succulent grasses; marshy ground, wet gullies, riverside pools and margins, and freshwater seepages (Williams 1979a). In Canterbury, SI, breeding territories sited along rivers or round swampy areas bordered by grassed flats and terraces (Bisset 1976).

Non-breeding birds flock in sites of open aspect close to water and rich feeding areas. Tokomaru Bay, NI: most sites (9/10) on river flats, riverbeds, or terraces or hillsides near river; birds centre activities along river or round nearby dams

and feed in pasture or swampy areas, avoiding grass >8–10 cm tall (Williams 1979a). Canterbury, SI: non-breeding birds gather on small available areas of improved pasture or on green grazed areas of riverflats (Bisset 1976).

Moulting birds gather on open water: farm dams, lakes, reservoirs, rivers. In Gisborne, NI, largest (0.2–52 ha) available waters free from disturbance chosen. Most sites have high open hillside rising from water's edge as vantage point; wide valleys or basins acceptable, but narrow valleys avoided. Many sites have dense cover for refuges (e.g. reedbeds, forest), and grassland at water's edge so that birds can feed near security of water; lakes encircled by dense vegetation may be used, birds feeding at night (Williams 1979b).

Before European settlement, confined to scarce and localized tussock grassland. Range has extended, especially in NI, because forests cleared and converted to pasture, and farm dams constructed. Well-sited farm dams are occupied rapidly (Williams 1971). Forest-felling provides numerous nest-sites in decaying logs and stumps and holes left by roots (Williams 1974); abandoned buildings may be used for nesting (Child 1975). Grazing and cutting of grassland may encourage use by flocks, as tall grass avoided (Williams 1979a). Flocks may damage grain crops or pasture. Lakes used for public recreation avoided as moulting sites (Williams 1979b).

DISTRIBUTION AND POPULATION Endemic NZ, where widespread on NI and SI. Populations have fluctuated since European settlement; perhaps related directly to exploitation (Williams 1971). Vagrant to Chatham Is (Fennell 1984), where formerly occurred naturally, and Lord Howe I. (Hindwood & Cunningham 1950).

NZ **NI.** Widespread and most numerous in Northland, Gisborne, Hawkes Bay, ne. Taranaki and Tongariro NP districts. Scattered elsewhere, but uncommon in Waikato and s. Wellington (NZ Atlas; Williams 1981b; Falla *et al.* 1981). **SI.** Widespread; most common in E, from Marlborough to Southland; scattered elsewhere, but scarce in Canterbury Plains and sw. Otago to se. Southland; generally absent from high parts of S. Alps (NZ Atlas; Williams 1981b; Falla *et al.* 1981). Resident on Great and Little Barrier (Bell 1976; CSN 30, 34), Kapiti (CSN 32), D'Urville and Stewart Is (CSN 19).

CHATHAM IS Vagrant; single, South East I., 20 Jan. 1984 (Fennell & Merton 1984). Possible earlier sightings not authenticated. Perhaps small population in pre-European times (Williams 1971).

LORD HOWE I. Vagrant; five (possibly six) birds, first noted 5 Mar. 1950, present till Apr. (Hindwood & Cunningham 1950).

POPULATION NI: 1981, c. 70 000 (Williams 1981b). SI: 1981, c. 50 000 (Williams 1981b), including Southland, 1984, 20 000 (CSN 34).

Distribution before Polynesian colonization of NZ was mainly associated with lowland short-tussock grasslands and swamplands; probably never widespread or numerous because suitable habitat was scarce (Williams 1971). Distribution of semi-fossil bones is correlated to these habitats in Maori times (R. Scarlett). During early European colonization, common through e. SI but rare in NI N of 39°S (Buller 1868; Williams 1971). Replacement of native forests with pasture since c. 1840 allowed increase in numbers and extension of range (Williams 1972). However, populations declined in late nineteenth century, probably caused by over-exploitation, accidental poisoning and introduced predators (Williams 1971;



Buller 1893; Kirk 1895). Numbers increased in consequence of various protective measures between 1900 and 1920 and limit to shooting in SI from 1923 to 1939 (Williams 1972); by 1935 numbers in SI were greater than ever before in recent history, although range was contracting (Williams 1971). In NI, releases in Tongariro NP district between 1915 and 1920 (T. Shout) allowed expansion into Wanganui, Hawkes Bay (1936) and Gisborne (1943–44) (Anon. 1936; A. Blackburn). Since 1950s, rapid declines in numbers in Southland, Westland, N. Canterbury, Nelson and some parts of NI resulted from increased shooting. This decline halted in areas where Shelducks were later protected (Williams 1971). Between 1959 and 1969, range on NI extended N to Waikato and S. Auckland districts, coupled with releases into Northland (McAllum 1965; Williams 1971). Becoming increasingly common in King Country, Manawatu, Wairarapa and Waikato; attempts to establish populations in coastal Taranaki under way (Williams 1981b; CSN 36).

Hunted widely. Formed <5% of total waterfowl harvest in 1978; but more intensely exploited in Taihape–Wairarino (33%), Gisborne–East Coast (32%), Southern Lakes (48%), Wanganui, West Coast and Nelson (10–13%) regions (Caithness 1979). In Taihape–Gisborne, hunting accounts for 9–18% of breeding population each year, and young birds more liable to be shot than adults (Williams 1981b). Vulnerable to hunting; easily decoyed and circle repeatedly even when hunter in sight. From 1950 to 1971, population declined in Taihape–Wairarino, Gisborne–East Coast, Southern Ls, Wanganui, West Coast, Nelson, Hawke's Bay, Wairarapa and e. foothills of S. Alps, attributed to over-harvesting; some populations failed to recover and others needed long period of protection to recover (Williams 1971). Hunting now more controlled with restrictions on sizes of bag, hunting areas and length of open season. Population trends carefully watched

(Williams 1979a,b).

MOVEMENTS Largely sedentary, birds from different moulting flocks rarely mixing (Williams 1972). Movements affected by topography; those in hilly parts of NI ranging over smaller areas than those from flat tussock grasslands of SI (Williams 1981a,b). Moulting flocks gather at traditional sites late Dec. with arrival of one- and two-year-old birds, followed by failed breeders; successful breeders arriving late Jan.–early Feb. Most fledgelings accompany parents to moulting sites, others disperse independently from territory, gathering first with other fledgelings before eventually joining another moulting flock (Williams 1979a). First departures from moulting areas occur early Mar. as adults return to breeding territories. Immatures remain in flock, dispersing gradually to prime feeding habitat through year. At Waimea Inlet, n. SI, non-breeders gather Mar. or Apr., at about time of duck shooting season, having completed moult (Owen & Sell 1985). Will change moulting site if disturbed, usually to nearby site but up to at least 84 km (Williams 1979b).

BANDING From recoveries of banded birds of all ages caught at moulting sites, most birds in Gisborne and Taihape Districts, NI, and from Manapouri and L. Matiri, SI, probably did not travel more than 40 km to moulting site (Williams 1981a) but a site used when species first became established in Gisborne district attracted birds farther afield (Williams 1979b). Birds from Tardale, Benmore and Von Lake, SI, have been recovered at distances of 41–60 km, medially and modally (Williams 1981a,b), perhaps because topography featureless with few improved pastures. Males disperse more widely than females after moulting (Williams 1979a), 50% of females banded at sites in SI recovered less than 20 km from banding site, 51% of males recovered more than 60 km away (Williams 1981a). Relation between distance

of dispersal and topography holds less well for ducklings: in hilly Gisborne district, NI juveniles dispersed farther than adults but in similar habitat in SI they were as sedentary as adults (Williams 1981a). Vagrants recorded Lord Howe I. (Hindwood & Cunningham 1950) and Chatham Is (Fennell & Merton 1984) suggest infrequent long-distance movements.

FOOD Adults mostly herbivorous; young eat principally insects for first 5 weeks. **BEHAVIOUR.** Most food taken by grazing on pasture and crops, stubble and seedheads of grass and weeds; insects, earthworms and various crustaceans taken when available. Young take aquatic insects during first week after hatching. Newly hatched ducklings take from surface of water but after 1 week will dive and graze on land (Williams 1979a).

ADULT In Canterbury district, SI, NZ, (204 gizzards; Bisset 1976) plant material 98.5% freq., animals 35.3; 1.0% contained no identifiable material. Plant material consisted of vegetative parts of *Ranunculus fluitans* 3.4% freq., *Colobanthus* 0.5, *Rumex acetosella* 6.9, *Salix fragilis* 0.5, *Acaena* 1.5, *Haloragis* 0.5, *Anisotome aromatica* 0.5, *Orcomyrrhis* 2.5, *Plantago lanceolata* 0.5, *Nertera depressa* 0.5, *Achillea millefolium* 1.5, *Cotula* 0.5, *Hypochoeris* (fl. buds) 6.9, *Taraxacum* 6.9, *Elodea canadensis* 0.5, *Lemna* 1.5, Poaceae 56.4 (incl. *Anthoxanthum odoratum*, *Lolium perenne*, *Poa pratensis*), Chlorophyta 21.6 (incl. *Mougeotia*, *Oedogonium*, *Ulothrix*), moss *Drepanocladus aduncus* 4.9; fruits and seeds of *Gaultheria depressa* 0.5, *Corokia cotoneaster* 1.0, *Rubus cissoides* 0.5, *Gunnera dentata* 3.9, *Discaria toumatou* 0.5, *Lilaeopsis* 0.5, *Pratia angulata* 0.5, *Pseudopanax crassifolium* 0.5, *Coprosma* 2.0, *Potamogeton cheesemani* 4.4, *Carex* 4.4, *Scirpus*, unident. Cyperaceae 23.0, *Avena* 5.4, *Poa pratensis*, unident. Poaceae 5.9; and leaves, fruit, seeds of *Muehlenbeckia axillaris* lvs. 2.5, freq. 15.2, *Cyathodes fraseri* lvs. 1.0, freq. 4.4, Fabaceae lvs. 65.2, freq. 11.3 (incl. *Medicago sativa*, *Trifolium dubium*, *T. repens*, *T. subterraneum*), *Juncus* lvs. 20.1, freq. 5.9. Clover (*Trifolium*) sometimes >80% of the bulk and grass and clover predominated with a soft leaved *Juncus*, *Rumex acetosella* and *Taraxacum* of secondary importance. Of seeds, *Juncus* less important than apparent because hard and slowly digested but berries of *Muehlenbeckia axillaris*, *Gunnera dentata* and *Cyathodes fraseri* and flower-buds of *Hypochoeris* important during summer when many stomachs contained little else. Animals incl. nematodes *Dorylaimus* 7.8, molluscs bivalves *Sphaerium novaezealandiae* 2.5, gastropods *Potamopyrgus antipodarum* 3.9, *Lymnaea tomentosa* 1.0, *Gyraulus corinna* 1.5; crustaceans cladocerans 1.0, ostracods 4.9; arachnids Halacaridae 1.0; insects mayflies *Daleatidium* larva 0.5, ad. 0.5, odonates *Xanthocnemis zealandica* 0.5, stoneflies *Megaloptera* 0.5, *Zelandobius* 2.5, psocids 3.9, bugs Saldidae 0.5, beetles Elmidae larv. 0.5, ads. 0.5, caddisflies *Hydrobiosis* 0.5, *Oxyethira albiceps* 17.6, *Olinga feredayi* 8.3, *Pycnocentroides aureolus* 10.3, flies Tipulidae 0.5, Chironomidae 3.4, *Austrosimulium* 0.5, Ceratopogonidae 1.5, Blepharoceridae 0.5, Empididae larv. 1.5, ad. 0.5, other 1.0, hymenopterans Formicidae 0.5. Most animals probably consumed accidentally but 8–10 birds collected May 1972 contained caddisfly larvae almost entirely. Paired birds contained more aquatic food than did those collected from flocks. Three birds collected during moult contained virtually no food.

YOUNG In first week take insects and plant material from water surface (five stomachs; Williams 1979a): plants: *Callitriche stagnalis* apical rosettes 20% freq., max. no.

per bird 5, fruits 100, 100's; animals insects odonates Zygoptera nymph 40, 2, bugs *Sigara arguta* imago 60, 15, *Anisops assimilis* imago 40, 3, flies *Culex* larv. 20, 7, *Chironomus zelandicus* 20, 1, Tipulidae 20, 1; by second week feeding on land and thought to take mostly plant material but five ducklings, three or four weeks old, collected while diving contained mostly insects: plants: aquatic detritus 100% freq.; animals: earthworms 20, 1, insects odonates Zygoptera nymph 60, 2, bugs *Sigara arguta* imago 40, 2, flies *Culex* larv. 60, 8, *Chironomus zelandicus* 100, 1786, crustaceans ostracods 100, 100's; but three ducklings, eight or nine weeks old, shot while grazing contained only plants: *Trifolium* leaves 100% freq., *Taraxacum* leaves 100, *Festuca rubra* tillers 33, *Glyceria declinata* 67, *Poa pratensis* seed heads 100.

SOCIAL ORGANIZATION Based mainly on studies by Williams (1979a) on farmland west of Tokomaru Bay, NI, from 1973 to 1976 and information supplied by M.J. Williams. During breeding season two social classes: pairs holding territories and large flocks of non-breeding birds that typically remain at specific sites near water or good feeding area. Flocks mainly young of previous season although may include a few two-year-olds and unpaired adults. For about 2 months of year during summer, established adult pairs abandon territories and, together with newly fledged young and non-breeding birds, assemble at traditional communal moulting sites, usually on large ponds, reservoirs, lakes and rivers (Williams 1979b). Numbers at moulting sites start building up rapidly in late Dec. when non-breeding first- and second-year-old birds arrive, followed later by failed breeders and finally successful breeders, often accompanied by fledgelings. Birds flightless for about four weeks but stay with flock longer. Start to leave moulting site Mar.–Apr., often forming small flocks on breeding areas with birds of all ages. Experienced breeders invariably associate with small flock closest to territory of previous year and wait for return of previous year's mate. After Apr., no adults in flocks at moulting sites. Once reunited, pair leaves small flock to reoccupy territory and gradually the small flocks disintegrate. Male of breeding pair usually first to be recorded in these flocks, which suggests difference in departure times of males and females from moulting site, this may explain post-moulting flocks in Feb. and Mar. composed of significantly more females than males (Williams 1979a). In Apr. and May sex-ratio in post-moulting flocks equal but in June significantly more females again, perhaps because in May shooting season, males more likely to be shot (Williams 1972). Williams (1979a) considers that other factors must contribute to composition of flocks in June, such as second-year males may pair with older females, leaving surplus of second-year females in flocks. By June experienced breeders back on former territories, newly mature pairs on unclaimed areas, and first- and a few second-year birds rejoin large flocks at moulting site or specific site nearby. These large non-breeding flocks gradually disperse, as small flocks move away to prime feeding areas. In NI, small non-breeding flocks tend to remain for rest of year at single site, usually close to a concentration of territorial pairs; in SI, flocks of pre-breeding juveniles may roam widely in search of suitable pastures (Williams 1979b). Failed breeders will only associate with juvenile flocks at moulting site. Number of birds in flocks doubled each year between July and Oct. because arrivals (mostly males) from near coast. Some birds in juvenile flocks are paired but do not try to breed; these pairs may leave flock about Sept.–Nov. to search for territories. Temporary occu-

pation of territories and temporary formation of pairs by non-breeding birds suggest considerable competition for space and mates.

BONDS Lifelong monogamy among established pairs. Some first-year, and all identified second-year, birds associated in pairs, many of which were temporary (Williams 1979a). Sex-ratio within flocks varies throughout year. Age of first breeding associated with territory establishment; few 1-year-olds and most 2-year-olds occupy territories but first attempt breeding when 2 or 3 years old. Physiologically capable of breeding at 2-years-old but, though most males bred at this age, only half of the females did so. Proportion of two-year-olds that breed may vary annually, birds need to acquire a preliminary territory in first year in order that they may try to breed in second year; in some years territories may be scarce and some first-year birds cannot find a site until second year so that they postpone breeding until their third year. Established pairs reunite in Mar. to June after leaving moulting site; if partner dies other re-mates quickly about this time. Pairing of non-established birds without territories takes place in juvenile flocks during breeding season; courtship, formation and break-up of temporary associations are major non-feeding activities in non-breeding flocks. New pairs from non-breeding flocks start to prospect for territories towards end of breeding season, Sept.–Nov., though some may start as early as July, but do not attempt nesting until following year; pairing among these prospectors may still be temporary. Female incubates; both parents care for young throughout fledging period of about 8 weeks. Brood amalgamation may occur. Break-up of brood usually occurs when adults abandon territory to flock at moulting site; sometimes young accompany parents and parents often continue association at moulting site.

BREEDING DISPERSION Nests singly in territorial pairs spaced out over available habitat; most activities confined to territory (Williams 1979a); most adult territorial pairs attempt to breed (87%). Suitable nest-sites may be scarce in places and multiple nesting possibly common; records of groups of 15–20 ducklings suggest this unless they represent extensive brood amalgamation (Williams 1979c). In 125 km², Williams (1979a,b) found 25, 22, 27 and 25 occupied territories in 4 successive years; changes in density did not positively reflect breeding success of previous years. Pair defends breeding territory against all other Shelducks; will even drive away small post-moult flock if it invades pair's territory. Few birds return to breeding territories in Mar., most from Apr. to June. Breeding areas reoccupied gradually, first by experienced breeding pairs, then those attempting to breed for first time and lastly by juvenile pairs setting up territories after breeding has begun. Female usually attempts to establish territory at or near her natal area. Changes in site of territory rarely occur even if mate lost but on two occasions it did: once, juvenile male defended its natal area one year with sibling but bred with established female on nearby territory next year; on another, male lost mate, re-mated on original territory, later moved to new territory near female's natal pond (Williams 1979a). Nursery site, where young reared, usually centred on pond, lake, river or swampy soak on hillside; usually within breeding territory (98%), though occasionally site where one brood has been successfully reared may be used a second time by late breeding pair; sometimes over 1 km from nest-site. In NI, each brood reared separately and different families will not use same nursery area simultaneously, although once, 19 ducklings derived from at least three broods, reared on same pond by one set of adults. Many first-year and most second-

year pairs leave non-breeding flock for varying periods and try to settle at site near female's natal area. If unoccupied and close by, pair often spend most of day there before returning to flock in evening. Eventually occupy site continuously and pair begins to defend it as territory. Later may abandon site and establish territory elsewhere but eventually pair makes some preliminary attachments to potential territory but do not try to breed, and rejoin flocks before annual moult (Williams 1979a).

ROOSTING Moulting site characterized by resting and grazing area, usually on hillside, near edge of water because moulting birds feed much during daylight and dark, seldom moving from safety of water; from hillside birds have view of surrounding terrain; some sites have dense cover along edge of water where they can hide. In breeding season, pairs roost in their territories; if two or more ponds in territory, all can often be seen from pair's main roosting site. All flock-sites have wide-open aspect, giving feeding birds uninterrupted view of large area; usually associated with river and close to territorial pairs; may roost on tops of hillocks that have wide view.

SOCIAL BEHAVIOUR Based mainly on study by Williams (1979a) at Tokomaru Bay, NI. Information supplied by M.J. Williams. Both male and female have piercing call given by birds in flock to others flying overhead, or by birds flying in to join flock. Pre-flight signals consist of **Chin-lifting** with some lateral **Head-shaking** (Johnsgard 1965).

AGONISTIC BEHAVIOUR Sometimes small groups of females seen landing, often near to adult males waiting alone on territories; usually these females immediately attacked and forced away. If partner incubating, male may tolerate solitary intruding female until partner appears to feed. Defend territory mainly by boundary flights and physical attacks. On sighting intruder, male and female call in duet from air or high point on ground (Falla *et al.* 1981). In **Boundary-flights**, defending pair flies alongside intruding bird or pair in steadily widening circuits over territory until intruders are outside defended area, when defenders wheel away and return to territory. Defending pair occasionally tries to strike or peck at intruders in flight. If two pairs involved, both pairs call, females uttering Inciting call and males with a disyllabic call. Appears to be principal defence during re-establishment of territory and before laying. **THREAT**. Sometimes male adopts **Threat Posture** with head close to ground and bill horizontal (Fitzgerald 1969) or female adopts Inciting posture or Inciting call in defence of territory. **Inciting**: display by female of varying intensity, on water or land. On water, at low intensity, forward-stretched neck and head both inclined at angle of 20°–30° and head often turned down so that bill near water; at high intensity, outstretched body lying almost flat on surface, head and neck stretched as far forward as possible. Often points to and swims towards opponent(s), swinging body from side to side, the swinging movement and calling increasing before she charges. Calls continuously in loud, rapidly repeated high-pitched note. On land, at low intensity, body held at about 25° to ground, head and neck held low and stretched well forward; with increasing intensity lowers head farther and usually charges. Male responds initially by moving alongside his female, uttering monosyllabic note; if Inciting persists, male's call changes to more highly-pitched, disyllabic note, and adopts **High-and-Erect** posture in which head and neck stretched forward and upward, and feathers of lower neck raised; utters call in rapid succession while pivoting, first

toward threatened bird, then back to female; usually follows with Threat posture and charge. **FIGHTING.** If male beaten in fights, female often changes mate. Female and successful male indicate bond by **Mutual Trumpeting Ceremonies**, male adopting High-and-Erect posture and giving disyllabic call, female adopting **Erect** posture with neck stretched up vertically, head horizontal and calling continuously. When female stops calling, male Triumph calls and takes up associated posture. **Triumph posture:** during short first syllable of call, jerks head up rapidly; in longer second syllable, moves head forward with neck fully stretched. Non-breeding pairs of first- and second-year birds occupying potential territories often meet other pairs and individuals; then, Inciting and fighting common with usually one pair constantly attacking others, both on ground and in air which often leads to changes in pairings. **DOMINANCE HIERARCHY.** May develop among young birds with some pairs establishing territories on very suitable areas and maintaining their pair-bond; less successful pairs occupy less suitable areas from which they try to occupy better sites and among which pair-bonds may not be permanent; some pairs may fail to establish themselves at all; remain in flock for another year. **DISTRACTION DISPLAY.** In response to predators, adults with young invariably perform **Broken-wing** display and run away from brood in very crouched posture, raising and lowering half-opened wings; sometimes half-flutter and then run again; if they are followed, one parent eventually returns to brood.

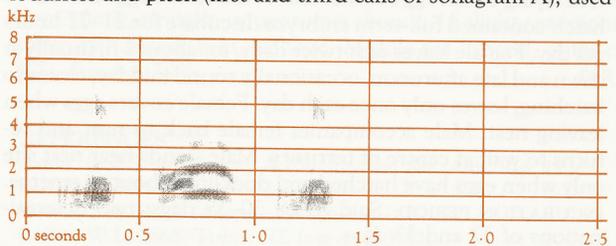
SEXUAL BEHAVIOUR Sexual displays not elaborate. Female, approaching maturity, selects male by **Inciting** males to attack other potential mates or females; winner of fight chosen as partner. Success of male in repulsing challenges appears to be basis for maintaining pair-bonds; if male beaten in fights, female often changes mate. Female and successful male indicate bond by **Mutual Trumpeting Ceremonies** and male **Triumph** calls. Triumph calls and postures also used for maintaining pair-bonds (see above). **GREETING.** When female joins male to feed during incubation, gives brief greeting display; female holds head low and points towards male uttering growling note similar to that in Inciting; male adopts **High-and-Erect** posture and repeats rapid disyllabic honk.

RELATIONS WITHIN FAMILY GROUP Nest prospecting can begin up to 2 months before laying but usually takes 2-3 weeks. By Aug., pair spends much of day, particularly morning, away from principal resting and feeding areas while female looks for suitable nest-site: looking in hollow logs, sometimes entering, moving on to other sites, then returning. When investigating trees she lands on branches and moves to lip of hollow to look inside. Male remains alert nearby, may sometimes join her. Laying daily, usually early in morning. Incubation by female only; leaves nest to feed for about 1 h every 5-6 h during daylight, usually starting at dawn and finishing late afternoon; as hatching approaches leaves only once a day. From laying onward male particularly aggressive in defence. To feed, female flies directly to water where male usually waits; as she nears area, female gives contact call and male responds by flying to join her, then landing together on pond, they perform Greeting display. Female then drinks, bathes and feeds avidly, spending on average 93% of her time during these excursions feeding. Male remains alert and very occasionally joins her to feed, usually after female has been there 90 min or more. Male accompanies her back to nest and returns to wait at centre of territory. Male seldom lands at nest-site; only stands near nest when eggs have

hatched and ducklings about to emerge. When waiting alone male spends 65% resting, 25% feeding, 5% bathing and preening, 3% walking or flying and 2% in defence of territory. Male particularly aggressive and immediately pursues or attacks intruder. Chicks brooded in nest for about 24 h; Ollerenshaw (in Oliver) observed that when nest-site in tree, parents call from ground and young one by one launch themselves from nesting hole, landing on ground unhurt. Brood then accompanies both parents to suitable nursery area; male seldom walks with young but remains alert nearby. Reared at nursery site, usually centred on pond within territory (98%). Guarded by both parents throughout fledging period c. 8 weeks on average. Female constantly stays close to ducklings throughout development. Ducklings brooded several times a day until 8 days old, then young rest by huddling together on water's edge. **COMMUNICATIONS.** Almost constant communication between female and young, which keeps young in tight group and close to female; at about 25 days continuous calling ceases and young tend to range widely. Male's role more of guardian; stands alert on lookout points, often 100-200 m away. **Alarm Calls.** Adults give alarm call when Swamp Harriers *Circus approximans* attack, to which young respond by assembling in tight group in centre of pond. Male's alarm call a goose-like honk. Young escape by diving. Older ducklings on water may hide among marginal vegetation or underneath overhangs of bank but, if disturbed from hiding place, dive. Those reared away from open water hide in tall vegetation or under logs, but if caught in open without cover, simply freeze. After fledging, young and parents remain as family group on territory for up to 2 months while adults undergo most of their body-moult (Williams 1979a). Brood may break up when adults leave nursery to undergo wing-moult, though young often accompany parents to moulting site where, sometimes, parents and young continue to associate. Those that do not accompany parents make daily flights near of natal area, eventually joining nearby juveniles and making their way to a moulting site where they join large flocks. After losing contact with parents, siblings tend to stay together within these large flocks. Traditional use of moulting sites probably established among newly fledged young when accompanying their parents to moulting site and may be further reinforced when they remain there as flock throughout most of subsequent year; after fledging, males disperse more widely than females.

VOICE No detailed studies. Can only be described as persistently noisy. Several different calls recognized. Form of calls resemble those of Australian Shelduck but easily distinguished.

ADULTS Male and female have piercing monosyllabic **Flock Call**, given by birds to others flying overhead, or by birds flying in to join flock. Several calls associated with courtship and territorial defense, most obvious being female **Inciting Call**: a very loud, high pitched note, increasing in loudness and pitch (first and third calls of sonagram A); used

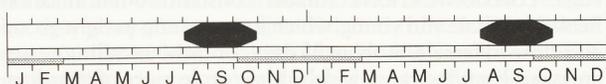


A K. & J. Bigwood; P102

in advertising and threat behaviour; similar note also used when greeting mate (see Social Behaviour). Male call, a goose-like honk (second call of sonagram A). During territorial defence, male utters his disyllabic call; also uses same call in Trumpeting Ceremonies. Male's **Triumph Call** follows mutual Trumpeting Ceremonies; during short first syllable of call, jerks head rapidly upwards; in longer second syllable moves head forward with neck fully stretched. When greeting mate, repeats rapid disyllabic honk.

BREEDING Based on Williams (1979a). Information supplied by M.J. Williams and J.R. Starks. Breed in simple pairs, solitarily.

SEASON Laying begins early Aug.; occasionally Oct., rarely Nov. Peak of laying, Aug.



SITE Inside hollow logs, under fallen logs, in holes in ground or trees (to 20 m high), rabbit burrows (Drummond 1912), under haystacks, piles of fence posts, tussocks, in crevices in rocks, under buildings, among tree roots, in culverts. Of 47 nests, 29 (62%) were inside or under fallen logs, 11 (23%) in tree hollows, four (9%) in holes or burrows in ground and 3 (6%) in holes at base of cabbage trees. Of nests in tree hollows, ten were less than 3 m above ground and one at 20 m. Female spends 2–3 weeks prospecting sites before laying. Territories used by same pair each year and will reuse same site if previous clutch successful.

NEST, MATERIALS A mere depression in ground, hole, thickly lined with down and perhaps some adventitious debris.

EGGS Ovoid, nearly elliptical; smooth, close grained, glossy; white when fresh, discolours to dirty yellow-brown.

MEASUREMENTS: from Gisborne: 67.2 mm (61.7–72.3; 223) x 48.6 (44.5–52.1)

WEIGHTS: 84.5 (5.2; 72.0–90.7; 10).

CLUTCH-SIZE Five to 15 eggs recorded; usually 8–10. Mean 9.4 (2.0; 5–15; 36). Clutches of more than 12 eggs probably result from dump nesting, laying by unmated females or by two females, as happens fairly often where natural sites few. C/5x1; C/6x2; C/7x1; C/8x8; C/9x7; C/10x10; C/11x1; C/12x5; C/15x1.

LAYING Daily, usually early in morning. Replacements laid after loss of eggs perhaps in only 20% of examples. Interval between loss and replacement 14 to 16 days (n=2). Late breeders may succeed successful early breeders on same pond, which has led to erroneous belief that species double brooded.

INCUBATION By female only, perhaps starting before laying of last egg because half of the fertile eggs that fail to hatch contained full-term embryos. Incubate for 21–22 hours per day. Female leaves nest twice daily, for about 1 h; usually at dawn and late afternoon, occasionally round midday; closer to hatching, leaves only once each day. Female covers eggs when leaving nest. Male accompanies female back to nest and returns to wait at centre of territory. Male stands near nest site only when eggs have hatched and ducklings about to emerge. **INCUBATION PERIOD:** Said to be 30–35 days; two determinations of 32 and 33 days.

YOUNG Precocial, nidifugous. At hatching,

covered in down; white with head and back, brown and brown on flanks and wings. Black feathers appear on flanks and shoulders when about half-grown. **FLEDGING PERIOD:** Said to be 8 weeks on average.

GROWTH Weight at hatching 49 g (3.1; 43.0–53.1; 10), about 58% (50–62%) of weight of fresh eggs.

PARENTAL CARE Brooded in nest till dry, then led by female to nearby nursery area (pond, lake or creek), usually within breeding territory and less than 500 m from nest. After leaving nest, young up to 8 days old brooded several times a day. Female stays close to young throughout development, male staying alert nearby. Female keeps young in tight group till about 25 days old; young range more widely after this. Young feed independently from hatching. Adults perform broken-wing display to distract predators. Young assemble in tight group in centre of pond or creek if threatened; dive to avoid danger or may hide among emergent vegetation or freeze if in open without cover.

SUCCESS From 282 eggs laid, 233 (83%) hatched. From 163 hatchlings (7.8 young/nest; 21 nests), 145 (89%) reached nursery area. From 365 ducklings (6.8 ducklings/brood; 54 broods) at nursery areas, 222 fledged. Survival of age-classes of ducklings at nursery area: at 7 days old, 85%; at 26 days old, 72%; at 47 days, 64%; at 63 days, 61%. Thus for all eggs laid, hatching success, 83%; reaching nursery area 74%; fledging success 45%; average 4.2 fledged young/clutch. Estimated 50% of fledged young survive to 1 year old; 27.5% to 2 years old; 17.6–19.3%, to 3 years old. Main causes of mortality of ducklings are bad weather and predation by feral cats; some young fail to climb from nest-chamber.

PLUMAGES

ADULT MALE BREEDING Definitive alternate and basic. Assumed in first year; age of first breeding 2 years (M.J. Williams). **HEAD AND NECK**, black (c89); crown and neck have faint blue-black (173) iridescence. **UPPERPARTS.** Mantle, blackish with copper-brown dusting; feathers, brown-black (c119) with fine light-brown (123A) speckling near tip. Scapulars and back, blackish (c82) vermiculated white. Rump and upper-tail coverts, black (89) with faint blue-black (173) iridescence. **TAIL**, black (89); upperside has faint blue-black iridescence. **UPPERWING.** Primaries, alula and greater primary coverts, brown-black (119); shafts, blackish (82). Outer webs of secondaries, iridescent dark green (c162A), forming speculum; inner webs concealed, black-brown (119); rachis, whitish. Median primary coverts, grey (84), usually concealed by alula. All other coverts, white. Humeral, white with grey (84) inner webs. Outer webs of tertiaries, deep rufous-brown (c38), merging to buff (124) at tip. **UNDERPARTS.** Upper breast, as mantle; flanks, axillaries and breast, as back. Belly looks rufous-brown mottled black; feathers deep rufous-brown (c38) with irregular fine grey-black (82) bars. Vent and under tail-coverts, rufous-brown (c340); feathers occasionally have a little black (82) speckling near tip. **UNDERWING.** Outer two primary coverts, and tips of other primary coverts, grey-black (82); tips narrower on inner feathers. Rest of under wing-coverts, white. Primaries, grey-black (82). Secondaries, dark grey (79) with white bases to inner webs; these white areas exposed in outer secondaries.

ADULT MALE NON-BREEDING At time of complete moult, males sometimes develop a few white feathers in head and neck, especially behind eye, on throat and at base of bill.

ADULT FEMALE BREEDING Definitive alter-

nate. Attained in first year; age of first breeding 2-3 years (M.J. Williams). Differences from adult male: Head and neck, white. Mantle, breast and anterior flanks, rufous-brown (136-340); edges and bases of feathers, sometimes dark brown (c20) with trace of white vermiculation. Back, similar to male, but brownish (c121C) bases of feathers sometimes exposed.

ADULT FEMALE NON-BREEDING Definitive basic. Difference from adult female breeding: Mantle, breast and upper flank-feathers, dark brown (20) with off-white to light rufous-brown vermiculations. Most females in this condition retain a few breeding feathers, especially on upper breast.

DOWNY YOUNG **HEAD AND NECK.** Forehead, white, bisected by narrow grey-brown (c119B) line down centre. Centre of crown, light brown (119C). Lores and sides of crown, dark brown (219), junction with white face runs just below eye; feathering of lower eyelid, dark brown. Narrow white line above eye. Nape and hindneck, dark brown (119A) with light-brown (c119C) centre; rest, white. **UPPERPARTS,** dark brown (light 119A) with curved white band running from base of wing to under tail-coverts (this band bisected by narrow dark line in Australian Shelduck). **TAIL,** dark brown (c119A), semi-plumulaceous. **WING-PAD,** light grey-brown tip; posterior half, white, front half, dark brown (119A). **UNDERPARTS,** white, with narrow dark-brown (c119A) line from sides of rump to base of hind thigh. **WING-PAD,** white; light grey-brown tip.

JUVENILE MALE Similar to adult male. Neck lacks blue-black gloss. Breast feathers, smaller and narrower than in adult, with narrow white tips (perhaps lost with wear); rest, brown-black (119) with rufous-brown band near tip, and rufous-brown (c240) central spot, wider and paler (c119C) near base. Breast looks blackish with dark rufous and white mottling. Belly feathers, similar to breast, but broader white tips and rufous-brown band near end cause slightly barred appearance. Innermost secondary coverts, and sometimes indistinct shaft-streaks of other secondary coverts, light grey (85) to grey (84). Upper wing-coverts do not have pale rufous fringes (*contra* Madge & Burn 1988).

JUVENILE FEMALE At fledging, similar to juvenile male. White head feathering spreads backwards from base of bill. According to McAllum (1965) there is a grey area at base of bill, broader than that in male; absent in specimens examined. Breast and mantle, similar to juvenile male; claims that female has redder tinge perhaps based on birds that had started post-juvenile moult.

IMMATURE FEMALE Lost c. 6 months after fledging (Williams 1981b). Similar to non-breeding female, but one or two feathers of ear-coverts grey-black (82), forming dark spot near ear. Immatures of both sexes retain grey innermost secondary coverts until first wing-moult at 13-15 months.

BARE PARTS

ADULTS, JUVENILES, DOWNY YOUNG Iris, black-brown (119). Bill, grey-black (82) to black (89). Legs and feet, grey (84) to grey-black (82), usually dark grey (83); webs generally the darkest area.

MOULTS Based on Williams (1979b, 1981a) and information supplied by M.J. Williams.

ADULT POST-BREEDING (Pre-basic). Complete. Replacement of body feathers begins when ducklings about 40 days old in females, usually after ducklings fledged in

males. Failed breeders begin in early Nov. Body-moult first recorded in non-breeders in early Oct.; heavy by mid-Nov. Body-moult almost complete when adults arrive at communal moulting site. Pre-breeders arrive Dec. and Jan., successful breeders in Feb.; failed breeders at any time between the two. Simultaneous wing- and tail-moults occur at these sites; individuals flightless for c. 3-4 weeks. Sexes moult at same time, but duration of flightlessness may be shorter in female. Non-breeders usually arrive at moulting grounds first, followed by failed breeders and later, successful breeders.

ADULT PRE-BREEDING (Alternate). Both sexes replace body-feathers in Apr., May or June; captive females moult body-feathers between early Mar. and July-Aug. (Stead 1938).

POST-JUVENILE Moult of body- and tail-feathers occurs c. 2-3 months after fledging. First wing-moult (including secondary coverts) occurs Jan.-Mar. at c. 13-15 months of age; most complete moult in Jan.

SUBSEQUENT MOULTS Immatures probably undergo some body-moult about June, when females lose blackish ear-spot and become generally lighter.

MEASUREMENTS All wild NZ birds. (1) Adults, fresh measurements; flattened chord, other methods as HANZAB (data from several consistent observers, compiled by M.J. Williams). (2) Adults, skins (NMNZ). (3) Juveniles, fresh birds; methods as (1) (M.J. Williams).

	MALES	FEMALES
WING	(1) 374.5 (10.99; 356-393; 14) (3) 369.2 (8.49; 355-384; 16)	347.3 (11.91; 320-368; 10) ** 336.9 (6.08; 325-350; 21) **
8TH P	(2) 237.1 (11.20; 225-255; 9)	217.7 (6.86; 208-234; 10) **
TAIL	(1) 128.2 (8.76; 110-145; 21) (3) 120.5 (6.43; 111-134; 16)	116.3 (9.51; 102-128; 10) ** 117.9 (6.13; 105-132; 21)
BILL	(1) 43.7 (1.63; 41.1-46.6; 25) (3) 43.5 (1.14; 41.8-46.0; 16)	40.0 (0.93; 38.2-41.3; 10) ** 39.2 (1.84; 36.3-42.5; 21) **
TARSUS	(1) 67.1 (1.86; 63.8-70.7; 25) (3) 66.4 (1.74; 63.9-70.5; 16)	61.0 (1.34; 59.4-64.1; 8) ** 60.4 (1.72; 56.7-63.2; 21) **
TOE	(1) 67.0 (2.00; 63-70; 24) (3) 65.5 (2.23; 60.7-68.8; 16)	61.5 (1.35; 59.4-64.1; 8) ** 60.2 (1.55; 57.4-63.2; 21) **

WEIGHTS Sources as above. Adult males: 1712 (144.6; 1422-200; 23); adult females: 1387 (178.2; 1059-1799; 10); juvenile males: 1533 (85.1; 1450-1700; 16); juvenile females: 1241 (70.8; 1100-1400; 19).

STRUCTURE Wing, long, rather narrow. Eleven primaries, p9 longest, p10 7-12 shorter, p8 11-16, p7 28-36, p6 47-59, p5 70-85, p4 90-11, p3 108-125, p2 128-153, p1 143-169, p11 minute. Inner web of p10 and outer p9 emarginated. Seventeen secondaries, including five tertials. Tail, rounded, rather short, 12 feathers. Bill, slightly shorter than head, higher than broad at base, sides parallel; culmen, slightly concave; tomia, straight; upper tomia show c. 16 slight serrations when bill closed. Feet, webbed. Middle toe longest, outer c. 97%, hind c. 29%.

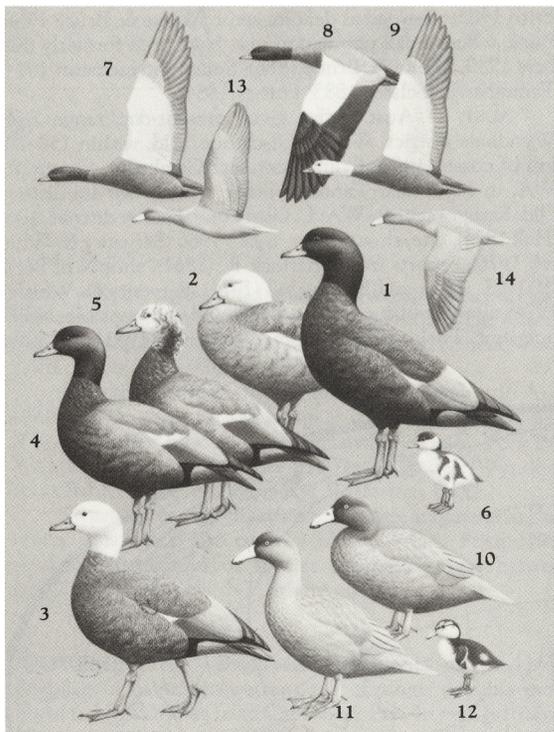
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Paradise Shelduck *Tadorna variegata*

1. Adult male
2. Adult female breeding
3. Adult female non-breeding
4. Juvenile male
5. Juvenile female
6. Downy young
7. Adult male, ventral
8. Adult male, dorsal
9. Adult female, ventral

Blue Duck *Hymenolaimus malacorhynchos*

10. Adult
11. Juvenile
12. Downy young, male
13. Adult, ventral
14. Adult, dorsal

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