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Marchant, S. & Higgins, P.J. (co-ordinating editors) 1990. Handbook of Australian, New Zealand & Antarctic Birds. Volume 1, Ratites to ducks; Part B, Australian pelican to ducks. Melbourne, Oxford University Press. Pages 1112-1113, 1124-1127, 1223-1228, 1351-1357; plate 96. Reproduced with the permission of BirdLife Australia and Jeff Davies.

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# 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 featherproteins 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 feature 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].

### REFERENCES

- Bauer, K.M., & U.N. Glutz von Blotzheim. 1968–69. Handbuch der Vögel Mitteleuropas. 2,3.
- Berkhoudt, H. 1980. Neth. J. Zool. 30: 1-34.
- Bock, W.J. 1969. Ann. NY Acad. Sci. 167: 147-55.
- Brush, A. 1976. J. Zool., Lond. 179: 467-98.
- Campbell, A.J. 1899. Ibis (7) 5: 362-4.
- Delacour, J. 1954-64. Waterfowl of the World.
- Delacour, J., & E. Mayr. 1945. Wilson Bull. 57: 3-55.
- Delacour, J., & E. Mayr. 1946. Wilson Bull. 58: 104-10.
- Driver, P.M. 1974. In Search of the Eider.
- Edkins, E., & I.A. Hansen. 1972. Comp. Biochem. Physiol. 41B: 105-12.
- Faith, D. 1989. Cladistics 5: 235-58.
- Frith, H.J. 1964a. Nature 202 (4939): 1352-3.
- Frith, H.J. 1964b. Emu 64: 42-7.
- Frith, H.J. 1965. CSIRO Wildl. Res. 10: 125-39.
- Frith, H.J. 1967. 1982. Waterfowl in Australia.
- Fullagar, P.J., et al. In press. Wildfowl 41.
- Hecht, M.K., & F.S. Szalay (Eds) 1977. Contributions to Vertebrate Evolution. 3.
- Hochbaum, H.A. 1944. The Canvasback on a Prairie Marsh.
- Hochbaum, H.A. 1955. Travels and Traditions of Waterfowl.
- Hochbaum, H.A. 1973. To Ride the Wind.
- Jacob, J., & A. Glaser. 1975. Biochem. Syst. Ecol. 1975 (2): 215-20.
- Johnsgard, P.A. 1965a. Handbook of Waterfowl Behavior.
- Johnsgard, P.A. 1965b. Wildfowl Trust Ann. Rep. 16: 73-83.
- Johnsgard, P.A. 1968. Waterfowl. Their Biology and Natural History.
- Kear, J., & A.J. Berger. 1980. The Hawaiian Goose. An Experiment in Conservation.

- Kooloos, J.G.M. 1986. Neth. J. Zool. 36: 47-87.
- Kooloos, J.G.M., & G.A. Zweers. 1989. J. Morph. 199: 327-47.
- Kooloos, J.G.M., et al. 1989. Zoomorphol. 108: 269-90.
- Livezey, B.C. 1986. Auk 103: 737-54.
- Madge, S., & H. Burn. 1988. Wildfowl.
- Madsen, C.S., et al. 1988. Auk 105: 452-9.
- Olson, S.L., & A. Feduccia. 1980. Smithson. Contr. Zool. 323.
- Owen, M. 1980. Wild Geese of the World. Their Life History and Ecology.
- Palmer, R.S. (Ed.) 1976. Handbook of North American Birds. 2,3.
- Phillips, J.C. 1922-26. A Natural History of the Ducks.
- Ramsey, E.P. 1878. Proc. Linn. Soc. NSW 1878: 154.
- Scott, P. 1972. The Swans.
- Scott, P. 1988. A Coloured Key to the Wildfowl of the World.
- Sibley, C.G., & J.E. Ahlquist. 1972. Bull. Peabody Mus. nat. Hist 39.
- Sibley, C.G., et al. 1988. Auk 105: 409-23.
- Simonetta, A.M. 1963. Arch. Zool. Ital. 48: 53-135.
- Sowls, L.K. 1955. Prairie Ducks. A Study of Their Behaviour, Ecology and Management.
- Todd, F.S. 1979. Waterfowl. Ducks, Geese and Swans of the World.
- Verheyen, R. 1953. Gerfaut 43 (Suppl.): 373-497.
- Woolfenden, G.E. 1961. Bull. Fla St. Mus., biol. Sci. 6: 1-129.
- Zweers, G.A. 1974. Neth. J. Zool. 24: 323-467.
- Zweers, G.A., et al. 1977. In: Hecht & Szalay 1977.

# Family ANATIDAE wildfowl

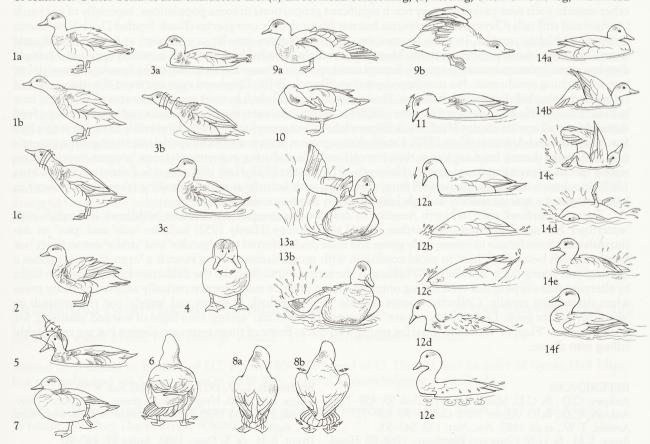
Waterbirds (some more or less terrestrial) with rather short legs and front toes connected by webs; hallux elevated and reduced. Though considerable adaptive diversity in outward appearance, size, colours of plumage, behaviour, and ecology, homogeneous in many characters, as attested by numerous, often fertile, interspecific hybrids reported, chiefly in captivity (see Gray 1958). About 160 species in six sub-families: (1) Dendrocygninae (whis-tling-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 bonesoccur in several species as projections near carpal joint; attached either to radial carpal or the metacarpal. Wingspurs 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; 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 syringo-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-moults 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 Sziji (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 nestsite 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, guacks, 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.

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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 'paddling' for duck on water. 'Flapper' is used to describe young wild duck. Some of these terms are elegant but are regrettably falling into disuse.

#### REFERENCES

- Ankney, C.D., & C.D. MacInnes. 1978. Auk 95: 459-71.
- Ankney, C.D., & D. Afton. 1988. Condor 90: 459-72.
- Arnold, T.W., et al. 1987. Am. Nat. 130: 643-53.
- Bauer, K.M., & U.N. Glutz von Blotzheim. 1968–69. Handbuch der Vögel Mitteleuropas. 2,3.
- Bengston, S.A. 1971. Ibis 113: 523-6.
- Boyd, H., & E. Fabricius. 1965. Behaviour 25: 1-15.
- Braithwaite, L.W. 1977. Aust. Wildl. Res. 4: 59-79.
- Briggs, S.V. 1990. Unpubl. Ph.D. thesis, Aust. Natn. Univ.
- Crook, J.H. (Ed.) 1970. Social Behaviour in Birds and Mammals.
- Drent, R.H., & S. Daan. 1980. Ardea 97: 480-90.
- Duncan, D.C. 1987. Can. J. Zool. 65: 234-46.
- Eyton, T.C. 1838. A Monograph on the Anatidae, or Duck Tribe.

- Fullagar, P.J., et al. 1988. Proc. Int. Symp. Wetlands, 1986. Shortlands Centre, Newcastle: 81-98.
- Goodwin, D. 1965. Domestic Birds.
- Gray, A.P. 1958. Bird Hybrids. A Checklist with Bibliography. Tech. Comm. No. 13, Cwealth Bur. Animal Breed.Genet, Edinburgh, Cwealth Agric. Bur.
- Hardy, E. 1952. The Bird Lovers Week-end Book.
- Harrison, C.J.O. 1967. Ibis 109: 539-51.
- Heinroth, O. 1911. Proc. Int. orn. Congr. V: 589-702.
- Heinroth, O., & K. Heinroth. 1954. Aus dem Leben der Vögel.
- Hess, E.H. 1957. Ann. NY Acad. Sci. 67: 724-32.
- Hochbaum, H.A. 1942. Trans. 7th N. Am. Wildl. Conf.: 299-307.
- Johnsgard, P.A. 1961. Wildfowl Trust Ann. Rep. 12: 58-69. Johnsgard, P.A. 1971. Wildfowl 22: 46-59.
- Johnsgard, P.A. 1973. Wildfowl 24: 144-9.
- Johnsgard, P.A., & J. Kear. 1968. Living Bird 7: 89-102.
- Kear, J. 1968. Beihefte der Vogelwelt 1: 93-133.
- Kear, J. 1970. Pp. 357-92. In: Crook 1970.
- Kingsford, R.T. 1989. Aust. Wildl. Res. 61: 405-12.
- Lack, D. 1967. Wildfowl Trust Ann. Rep. 18: 125-8.

- Lack, D. 1974. Evolution Illustrated by Waterfowl.
- Lessells, C.M. 1986. J. Anim. Ecol. 55: 669-89.
- Lorenz, K. 1935. J. Orn., Lpz., 83: 137-213, 289-413.
- Lorenz, K. 1951–53. Comparative Ecology of the Behaviour of the Anatinae.
- McKinney, F. 1965. Behaviour 25: 120-220.
- Olney, P.J.S. 1963. Proc. zool. Soc. Lond. 140: 169-210.
- Pellis, S.M., & V.C. Pellis. 1982. Aust. Wildl. Res. 9: 145-50.
- Rohwer, F.C. 1984. Auk 101: 603-605.
- Rohwer, F.C. 1988. Auk 105: 161-76.
- Ryder, J.P. 1970. Wilson Bull. 81: 5-13.
- Schutz, F. 1965. Z. Tierpsychol. 22: 50-103.
- Skutch, A. 1976. Parent Birds and Their Young.
- Sowls, L.K. 1955. Prairie Ducks. A Study of their Behaviour, Ecology and Management.
- Szijj, K.M. 1965. Vogelwarte 23: 24-71.
- Thompson, S.C., & D.G. Raveling. 1988. Wildfowl 39: 124-32.
- Toft, C.A., et al. 1984. J. Anim. Ecol. 53: 75-92.
- Williams, G.C. 1966. Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thopught.

# Sub-family ANATINAE ducks

Small to fairly large wildfowl. Tarsi scutellate in front. Marked sexual dimorphism in plumage and structure of syrinx in most species; correlated with sexual differences in visual displays and voice. About 70 species, composing four main groups: (1) so called 'perching ducks' and allies; (2) Torrent Duck (polytypic species in genus *Merganetta*, South America); (3) typical dabbling ducks (very large genus *Anas* and monotypic *Marmaronetta*) and (4) pochards (*Netta*, *Aythya* and extinct *Rhodonessa*).

Trachea of male usually with bony, asymmetrical bulla on left side of syrinx. Double annual moult in both sexes, resulting in two recognizable plumages. These usually closely similar and cryptic in females, though nonbreeding plumage usually duller. Breeding plumage of male of many species in temperate regions elaborate and colourful ('bright'), contrasting with sombre and cryptic non-breeding plumage (eclipse) usually worn for short period in boreal species, during and following flightless period and post-breeding moult and resembling plumages of females and juveniles. Loss of bright plumage in some austral species much more complex. Wing typically brightly coloured in both sexes, often with metallic speculum on greater coverts and secondaries, which contrasts with colourful median and lesser wing-coverts or tertials; this pattern maintained all year, wing being moulted only once. As a rule, juvenile plumage resembles female plumage, but juveniles separable by tail-feathers (notched tip with bare shaft protruding) and by narrower, shorter, and more pointed body-feathers and wing coverts. Juvenile body-plumage moulted within a few months of hatching (3-4 months). In some species breeding in first year, this plumage involves growth of only a few new feathers and is quickly replaced by breeding plumage; in others that defer breeding until second year, immature plumage more complete and retained longer, being only gradually replaced by breeding plumage during whole first year of life. In all, juvenile wing retained until first complete moult in summer of second calendar year, although tertials often and some wing-coverts sometimes replaced earlier.

TERMINOLOGY OF PLUMAGES. Bright (breeding) male plumage of most duck species (often termed 'nuptial' in ornithological literature and more accurately 'alternate'; see Humphrey & Parkes 1959; Humphrey & Clark 1964) usually worn for much of year when birds not actually breeding, including autumn and winter when pair-bonds initiated and maintained until nesting in spring (see below). Thus, males often attain non-breeding plumage (basic) soon after start of nesting when their reproductive activities (but not those of females) are over. In females, though timing of both moults tends to correspond roughly with those of males, also subject to adaptive variation. In many species, post-breeding moult of females more protracted, with greater individual variation in timing, particularly in successfully breeding females; moult usually inhibited during nesting, starting 1–2 months later than in males. Females of some species (e.g. some dabbling ducks) start moult shortly before nesting and therefore incubate and rear young in basic plumage. Although such females in fact nest in 'non-breeding' plumage, terminology sometimes maintained for reasons of homology.

### Perching ducks and aberrant species

Small to fairly large wildfowl, usually living in well-wooded areas, most freely perch in trees, and often nest in holes high above ground. Some semi-terrestrial. Highly diversified group of 19 species in 15 mainly monotypic genera, often showing striking convergences with other Anatidae and some regarded now as more properly assigned to other sub-families, specially Tadorninae. Most are here retained in Anatinae following Johnsgard (1965) and Peters. Two groups: (1) more generalized genera *Plectropterus* (Spur-winged Goose in Ethiopian Africa), *Cairina* (Muscovy Duck of neotropical America; White-winged Wood Duck of se. Asia), *Pteronetta* (Hartlaub's Duck of Africa), and *Sarkidiornis* (Comb Duck of South America, Ethiopian Africa, s. Asia); (2) more specialized genera *Nettapus* (three pygmy-geese of central Africa, India to Aust.), *Callonetta* (Ringed Teal of South America), *Aix* (Carolina Duck A. *sponsa* of North America and Mandarin A. *galericulata* of e. Asia), *Chenonetta* (Maned Duck of Aust.), and *Amazonetta* (Brazilian Teal of South America). Also considered here are two very specialized A'asian genera *Malacorhynchus* (Pink-eared Duck of Aust.) and *Hymenolaimus* (Blue Duck of NZ) and *Merganetta* (Torrent Duck of South America) and *Salvadorina* (Salvadori's Duck of New Guinea). Five species in our region.

Wings, often wide and rounded; bony, spur-like knob on metacarpal joint in some. Tails, fairly broad and elongated; slightly graduated but not pointed. Bill, rather thick and goose-like, not depressed, often heavy; large nail; highly specialized structures in *Malacorhynchus* and *Hymenolaimus*. Hind toe well developed, not lobed, and claws strong and sharp at all ages; legs set far forward, tarsus usually short (especially in *Nettapus*), but longer in some (especially semi-terrestrial *Plectropterus*). Usually do not dive, but *Hymenolaimus* specialized river duck. Male noticeably larger than female in some species. Sexes differ in tracheal structure to varying degrees; except in *Nettapus*, *Malacorhynchus* and *Hymenolaimus*, males with bony enlarged bullae; in *Aix*, rather large and rounded, somewhat resembling a dabbling duck. Plumage bright in many; often iridescent, especially in more

generalized genera. Patterns more complex in other genera, particularly *Aix*. No real speculum in most species but tertials and wing-coverts often bright and metallic. Sexual dimorphism slight in some, considerable in others, especially *Aix*. Eclipse plumage in *Aix*, *Nettapus* and *Chenonetta*. Juveniles, like adult females. Downy young, patterned dark brown and white or yellow, most like those of dabbling ducks; in some species remarkable for long stiff tails and capacity for climbing.

Cosmopolitan but most species tropical or subtropical. Most species surface-feeders, some very specialized, though others (notably *Plectropterus* and *Chenonetta*) terrestrial grazers. Often in flocks. **Pre-flight** signals diverse; include **Neck-craning**, **Chin-lifting**, and **Head-thrusting** movements, also lateral **Head-shaking**. Social patterns and behaviour of *Chenonetta* most like those of typical dabbling ducks. **Inciting** display of female also much as in *Anas*. In more generalized genera, however, pair-bonds weak or absent (Johnsgard 1965). Pre-copulatory behaviour varies; includes **Head-pumping** (as in *Anas*), **Head-dipping**, and **Bill-dipping**. Post-copulatory behaviour also varies, but little studied. Voice characteristics vary; sexually differentiated to greater or lesser extent. Male calls mostly whistles; female calls honking, quacking, or squeaking (characteristic **Decrescendo** calls of *Anas* lacking). Some species more or less silent. Torrent Ducks are specialized river-ducks inhabiting rapids and fast-flowing rivers of the Andes of South America; very noisy. *Salvadorina* is similarly specialized but is not necessarily closely allied to the Torrent Ducks. Little is known of its social behaviour and ecology.

Dabbling ducks (known also as surface-feeding, puddle, or river ducks)

Fairly small to medium-sized wildfowl. About 40 species in two genera, Anas and Marmaronetta (Marbled Teal of Mediterranean and w. Asia; has also been placed with pochards but not considered further here). More than 40 species in Anas, including following main species-groups, mostly in Holarctic, some or all formerly treated as separate genera: (1) wigeons, three species including A. sibilatrix vagrant to S. Georgia; (2) gadwalls, all Holarctic; (3) true teals, including several s. hemisphere species (about ten) typified by Grey Teal A. gracilis of Aust.; (4) pintails, including A. eatoni and A. georgica in our region; (5) mallards, including A. superciliosa of Aust. and NZ; and (6) blue-winged ducks, including Australasian Shoveler A. rhynchotis. Term 'teal' used loosely in ornithological literature to indicate small ducks generally, not only in different species-groups of Anas. Bodies fairly slender. No marked difference in size between sexes (males somewhat larger). Wings, long and pointed; in flight, wing-beats less rapid than in pochards and other diving ducks. Tails, usually fairly short, pointed; central feathers elongated in some species. Bills, fairly long in most species; flattened, with distinct lamellae. Legs, quite short and inserted centrally giving horizontal stance; hind toe much reduced, not lobed. Take-off from water and land with facility. Walk easily but with waddling gait; able to perch well, though only a few species regularly perch in trees. Dive rather poorly, submerging briefly with use of wings. Sexes differ in tracheal anatomy, males having enlarged rounded bony bullae on left side of syrinx. Plumage of both sexes usually with bright speculum. In many species, sexes alike also in other plumage characters; most of these rather sombre or wholly cryptic but some quite bright; in both types, non-breeding plumage differs little from breeding. In many species of Anas, particularly migrants within temperate parts of n. hemisphere, males only with bright plumage worn for much of year; alternates with eclipse plumage during flightless period at post-breeding moult. Females of these species highly cryptic at all times. Colour of bill or foot, or both, sometimes bright. Juveniles resemble adults in non-breeding plumage. Downy young, typically brown and buff or yellow, often with dark and light streaks on sides of head and light spot on each wing and on each side of back or rump.

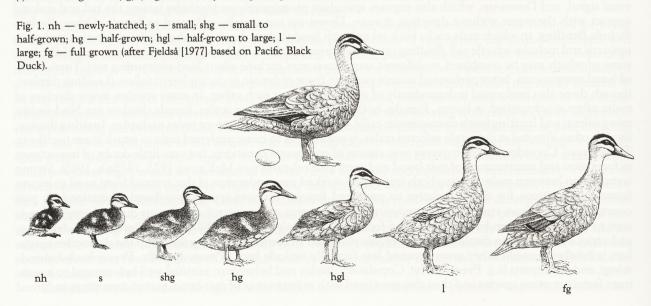
Cosmopolitan and predominantly continental in distribution, though some island forms. Adapted for living in shallow, biologically productive waters. Many species prefer plenty of vegetation, marginal, submerged, and often emergent and floating. Range widely through mid-latitudes, penetrating into Arctic tundra or even taiga zones only slightly. Widespread and often the dominant genus in s. hemisphere. Faster streams and unsheltered or offshore marine waters normally avoided. Though some species enter wooded habitats (especially flooded or swamp forests) and others tolerate and even prefer wide-open spaces, most occupy sites with more or less dense fringing vegetation at chosen waters, latter being either standing or slow-flowing with ready access to secure and sheltered resting and breeding places. Need for concealment when breeding or in flightless stage of post-breeding moult may force them, more or less deeply, into dense marginal or emergent vegetation and swamps with little open water; some species nest, at least at times, far from water. As main habitats unstable in many areas, exceptional powers of flight enable reconnaissance of wide range of waters and rapid shift when necessary. Vulnerable to reclamation of wetlands, especially when these few and scattered, but readily accept artificially created waters if they provide suitable feeding areas. Little information on breeding numbers because accurate counts of nests impossible but large-scale ground and aerial counts now sufficiently comprehensive to provide reasonable estimates of wintering numbers and main locations, and, sometimes, tentative indication of trends. Some species migrate over considerable distances, especially in n. hemisphere. Males moult during late summer and early autumn on or near breeding grounds. All large-scale movements mainly nocturnal, sometimes at high altitudes, often in irregular wavy lines.

Essentially surface feeders, though dive for food in some conditions. Some primarily vegetarian, on land and

in shallow water. Many omnivorous, taking chiefly seeds and invertebrates mainly from shallow water by dabbling at surface at the same time pumping water and mud through bill, using lamellae to sieve out food (Suzzling). Also filter-feed by dipping head and neck below water, and up-ending; some highly specialized filter-feeders (shovelers), others also forage on land. Feed singly, but most often in pairs and flocks; otherwise usually gregarious when not nesting. Main pre-flight signals: lateral Head-shaking and repeated vertical Head-thrusting. Before and during initial stages of nesting, each pair typically occupies home-range which overlaps with those of other pairs. Within home-range, one or more small areas frequented for feeding, loafing, and preening; variously named 'core area', 'activity centre', 'waiting area' (where male stays while female at nest and where pair meet at times during laving and at times during incubation); defended as territories, to greater or lesser extent, in some species (mainly by male). Monogamous pair-bonds, long-term in monomorphic resident or nomadic, often tropical, species (see Siegfried 1974; Fullagar et al. 1988) but more usually of seasonal duration, especially in boreal migratory species. In latter, pair-formation typically starts in flock during autumn and winter after assumption of breeding ('nuptial') plumage, though initial pairings often temporary; final pair-bond ended at some stage during incubation when males again flock. In addition to maintaining firm bond with eventual mate, males of many species also show promiscuous tendencies, displaying to other females and also copulating with them, mainly by forced copulation. Extent of such promiscuity subject to ecological factors that affect intensity of defence of own mate and territory (McKinney et al. 1983; Birkhead 1988). Same factors also influence types and frequency of pursuit-flights of a female, which are of three main types: (1) courtship-flights: chase by several males originating from displaying party on water and initiated by female; (2) three-bird flights: chase of intruding pair by single male based on own activity centre; (3) forced copulation intent-flights: chase by several males often ending in attempts at forced copulation. Second and third types connected by intermediates; much controversy over details and interpretation, especially role of such pursuits in dispersing pairs. Courtship, typically on water but sometimes on land or even in flight (during pursuits), of two main types: (1) communal courtship (also termed 'social display') and (2) pair-courtship ('directed courtship' of von der Wall 1965). In communal courtship, often starting in autumn or winter, group of several males typically display to one or more females, both unpaired and (increasingly as season advances) paired birds of both sexes taking part. Courting party develops progressively in many species. as more and more males join in; in some, notably A. superciliosa in our region, group typically assembles before display starts. Male displays often elaborate, consisting of secondary and major forms, males tending first to assume special Courtship-intent posture, indicative of impending display. Marked tendency for each male to align body parallel to courted female before displaying; components of some displays also show marked directional bias towards female (McKinney 1975a,b). Secondary displays, mainly derived from comfort-behaviour and closely similar to latter in form, usually silent; often precede one or other of major displays. These are: Upwardshake and Wing-flap (both involving brief rise as bird treads water), lateral Head-shake (with bill inclined down), and Head-flick or Head-roll (with vertical component most marked). Major displays often more elaborate; usually with vocal components produced by contortion of tracheal tubes, which determines posture of neck. These are: Grunt-whistle (or Water-flick) and Head-up Tail-up; in both of which tail elevated and speculum momentarily exposed, specially in latter. Grunt-whistle has loud vocal component and deliberate action of spraying stream of water towards female using rapid flick of bill across the surface. Burp display, which is mainly a vocal signal, and Down-up, which also exposes speculum prominently and includes raising the tail and making contact with the water without directing it away. Down-up not usually addressed to female. Other displays include Bridling, in which male rocks back on tail with head tucked down into shoulders; action thrusts breast upwards and includes whistle call. Bridling can be performed on land. Each species has own repertoire of displays, some of which may be combined in different sequences; may include silent Nod-swimming and Turn-backof-head components, latter performed as male swims in front of female, inducing her to follow (Leading display), though these also performed independently of other displays or each other. In many species, major displays of males often synchronized in bursts. Females noticeably less active than males. Female displays are Nod-swimming (silent) and Inciting (with characteristic calls), either of which may induce males to display. Inciting display, though often directed at definitely rejected males, is not such as to cause preferred male to attack them (unlike in Tadorninae). Considerable controversy over nature of communal courtship, but now little doubt of importance in formation and maintenance of pair-bond and extra-pair relations (see McKinney 1973, 1975a,b, 1985). Strong competition between males, arising both from often marked preponderance of that sex and from need to secure favourable positions for display relative to preferred female. In most species, pair-bond maintained by pair courtship distinct from communal courtship, though elements of communal often occur during latter as bonds start to form. Male Turn-back-of-head and female Inciting; also includes Bill-dip, full Ceremonial-drinking, and various Mock-preen displays, notably highly ritualized Preen-behind-wing (in which the distinctive speculum is briefly exposed); other areas preened less formally include back (Preen-dorsally, Preen-back-behindwing), and underparts (e.g. Preen-belly). Copulatory display and behaviour, initiated well before need to inseminate female in many species and thus also associated with maintenance of pair-bond, except sometimes in forced

copulations. On water, pre-copulatory displays consist typically of mutual Head-pumping; post-copulatory displays of males vary more but include Burp display, Bridling, and Nod-swimming. Marked sexual differences in voice. Calls of males vary; often weak nasal, rasping, wheezing, clucking, or rattling sounds but also include penetrating whistles (sometimes followed by grunts) in many species; uttered chiefly during display, when disturbed, aggressive, or separated from mate or companions in flock. Calls of females typically louder and coarser, often quacking; most characteristic vocalizations: Decrescendo call (pattern of which tends to be constant individually, facilitating identification) and Inciting call. In some species, pair call simultaneously while posturing during and after antagonistic encounters (Pair-palaver); when mates separated, often call: Decrescendo calls from females; Burp calls from males. Non-vocal sound-signals produced in some species. Behaviour includes mass dashing-and-diving during bathing. Most complex repertoire of displays found in almost all teals, pintails and mallards but some of these do not have certain displays; e.g. most pintails and some teals do not have the Down-up; most mallards do not have the Bridle, except post-copulatory bridling. Gadwalls resemble mallards but never bridle and some also do not Grunt-whistle, Head-up Tail-up, and Down-up. All wigeons, the silver teals (A. versicolor; A. punctata) and the blue-winged ducks (typified by the shovelers) do not have any of these displays but all the last group have the added display of Lateral Dabbling, often use the Jump-Flight (less common in most other Anas); courtship pursuit-flights are particularly significant for shovelers. For details see McKinney (1978).

Breeding strictly seasonal in most species; short breeding periods in those forms nesting in Arctic, but more prolonged in others. Sites often on ground, concealed in thick cover, sometimes well away from water; less often in open but in our region commonly either above ground in cavities in trees (will use artificial nest-boxes) and old nests of other species or in vegetation, surrounded by water in most, and again often using old nest-sites of other species. Nests usually well dispersed but sometimes grouped even quite densely, at protected places. Shallow depressions with rim of vegetation, lined copiously with down plucked by female. Building by female only. Eggs oval, yellowish or pinkish-white, grey-green, buff, rarely bluish; smooth. Clutches usually 6-12, averaging smaller in forms on remote islands (see Lack 1968); multiple layings sometimes occur. Replacements laid after loss of eggs and several species normally double-brooded. Eggs laid at 24-h intervals. Incubation by female only, leaving nest two or more times per day when usually joins male (if still present). Incubation periods usually 21-28 days (Johnsgard 1968; Todd 1979). Young cared for only by female in some species in our region, and is typical pattern in boreal ducks but male parental activity common for many austral or tropical species with long-term pair-bonds; in them, male and female accompany young though only female broods them (see Kear 1970; Siegfried 1974; Fullagar et al. 1988). Young and parents, particularly the female, communicate and recognize each other by characteristic calls. Young aggressively defended by both sexes in species with dual parental care, but main antipredator reaction otherwise distraction display of female in form of 'injury-feigning', parent flapping awkwardly over water or land with wings open, exposing speculum, and giving Distraction calls. In some species male also defensive but never as demonstrative as female. Young become independent just before or at fledging. Mature at 1 year old. Growth of ducklings can be described by reference to appearance that is usefully categorized in the sequence: newly-hatched (nh); small (s); small to half-grown (shg); half-grown (hg); half-grown to large (hgl); large (1) and full grown (fg) (Fig. 1 after Fjeldså [1977] based on Pacific Black Duck).



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## Pochards

Medium-sized, mainly freshwater diving ducks. Designation 'diving duck' used not as taxonomic term but as ecological characterization for these and other ducks that plunge from the surface and swim underwater. Sixteen species in three genera: *Netta* (three species) and *Aythya* (12 species); monotypic *Rhodonessa* (Pink-headed Duck of India and Nepal) recently extinct. *Netta* intermediate in some characters between *Anas* and *Aythya*. Latter composed of three species-groups: (1) typical pochards, none in our region; (2) white-eyed pochards, including Hardhead A. *australis*; (3) scaups, including New Zealand Scaup A. *novaeseelandiae*.

In Aythya, body, short and heavy; head, big; wings, broader and less pointed than in typical Anatinae, necessitating faster wing-beats, often producing whistling sound; tail, short; bill, rather heavy (less so in whiteeyed pochards), about as long as head, flattened and, in some, wider at tip; legs, short, with large toes and broadly lobed hind toe, and set well apart far back on body. *Netta* similar but body longer and narrower, bill narrower, legs longer and more slender. All take-off from water with some difficulty. *Aythya* clumsy on land; *Netta* much less awkward, with even more upright stance. Though *Netta* somewhat less well adapted for diving than *Aythya* (Delacour & Mayr 1945), all dive with considerable facility, typically without using wings. Sexes differ in tracheal anatomy; as well as showing 1–2 enlargements of tracheal tubes, males have large, rather angular bullae, with several fenestrae, not rounded and evenly ossified as in *Anas* males. Males, mainly patterned simply: black, brown, or chestnut and white; unstreaked females, varying shades of brown. Broad pale (often white) panel on rear half of upper wing; no metallic speculum. In most species, male eclipse. Females often nest in plumage homologous to non-breeding plumage. Bill, usually slate or bluish but red in two *Netta*; eyes, red (most pochards of both genera), white (males of white-eyed pochards), brown or yellow (females of scaup), or yellow (male scaup). Juveniles resemble females. Downy young mostly like other Anatinae but head-stripes faint or absent; young of scaups, dark.

Cosmopolitan, but most species Holarctic. Concentrated both as breeders and in winter on standing fresh water of moderate depth, usually 1–15 m; one Holarctic species (Greater Scaup A. marila) marine in winter, partial exception. Tolerate fairly restricted open waters with dense marginal vegetation, even in forest setting. In most areas, suitable sites are not plentiful and vulnerable to desiccation, drainage, and other adverse factors, leading to some instability in distribution and population. Some colonize modern artefacts such as reservoirs, gravel pits, and ornamental waters. All Holarctic species migratory to greater or lesser extent. Species in s. hemisphere have no migration but in Aust. A. australis has irregular and sometimes long dispersal movements with large congregations following rainfall and drought.

Range from chiefly vegetarian (e.g. Netta) to omnivorous; in some species (e.g. A. australis) animal food predominates. Food obtained in water, mainly by diving from surface to bottom. Usually submerge for shorter periods than Merginae. Difference between sexes in preferred depths of diving, and hence in mean duration of dives. recorded in some n. hemisphere species and probably widespread; may be contributory factors in partial winter segregation of sexes in those areas. Most species (especially in Netta) also dabble on surface at times, head-dip, and up-end. Feed mainly in pairs and flocks. Largely gregarious at most times. Repeated Bill-lifting main Pre-flight signal, but Head-flicks also frequent in some Aythya. Monogamous pair-bonds of short seasonal duration typical in Holarctic species. Promiscuous tendencies of males much less marked than in other Anatinae; except in Netta, attempts at forced copulation rare in Holarctic species, and pursuit-flights largely of courtship type. Communal courtship on water much as in other Anatinae though most major displays different. Often nocturnal as well as diurnal. Secondary displays of males are: Head-flick and Upward-shake, though latter infrequent in some species. Typical major displays, usually accompanied by calls, are: Sneak display, Kinkedneck, and Head-throw. Sneak takes two main forms: full version with head along water; incomplete version (or Crouch display) with head inclined forward. Kinked-neck involves sudden horizontal distortion of neck: Headthrow, the vertical posturing of head above centre of back with bill pointed upwards. Other displays include Turn-back-of-head, Neck-stretch, and Coughing, though some confusion in literature whether Neck-stretch and **Coughing** displays differ or are partly the same. In some species, females perform male-like major displays at times; Inciting display of same functional type as in other Anatinae but differs largely in form. In most species, some displays used by male in communal courtship also used in pair-courtship; others distinct, including unique Courtship-feeding of N. rufina. Displays performed by both male and female, sometimes mutually, include Ceremonial-drinking and Mock-preening. Copulation also part of pair-courtship. Pre-copulatory displays include Bill-dipping and Preen-dorsally; in Netta, also Anas-like Head-pumping. Prone-posture of female differs from that of Anas in that neck stretched diagonally forward not flat on water. Post-copulatory displays include characteristic Bill-down posture by male or both sexes. Calls of males often whirring or cooing and not far-carrying, but some (notably scaups) also whistle. Used chiefly in courtship, of two main types given (1) during Head-throw and Kinked-neck displays and (2) during Coughing display. Females usually not highly vocal; calls mostly growling and harsh, louder than those of males, include Inciting calls but Decrescendo calls lacking in most species. Non-vocal rattling sound produced in Preen-behind-wing display in all or most species.

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Holarctic species strictly seasonal breeders; probably similar for species in our region. Nests sited over shallow water or on ground never far from water; usually in thick cover. Well dispersed or grouped, sometimes close together. Shallow depressions with rim of available material, lined with down plucked by female. Building by female only. Eggs oval, green-grey or pale buff; smooth. Clutches usually 5–12; multiple laying common in some species. Single-brooded; replacements laid after loss of eggs. Eggs laid at 24-h intervals. Incubation by female only. Incubation period 24–28 days (Kear 1970; Todd 1979). Young cared for by female only. **Distraction** display, in form of 'injury-feigning', occurs (at least in *Aythya*) but less common than in other Anatinae. No true crèching but broods sometimes amalgamated. Young independent at or before fledging in most species. Mature in first vear.

### REFERENCES

- Baerends, G., et al. 1975. Function and Evolution in Behaviour.
- Birkhead, T.R. 1988. Adv. Study Behav. 18: 35-72.
- Crook, J.H. (Ed.) 1970. Social Behaviour in Birds and Mammals.
- Delacour, J. 1954-64. Waterfowl of the World.
- Delacour, J., & E. Mayr. 1945. Wilson Bull. 57: 3-55.
- Farner, D.S. (Ed.) 1973. Breeding Biology of Birds.
- Fjeldså, J. 1977. Guide to the Young of European Precocial Birds.
- Fullagar, P.J., et al. 1988. Proc. Int. Symp. Wetlands, 1986. Shortlands Centre, Newcastle: 81-98.
- Hafez, E.S.E. (Ed.) 1975. The Behaviour of Domestic Animals.
- Humphrey, P.S., & G.A. Clark. 1964. Pp. 167–232. In: Vol. 4, Delacour 1954–64.
- Humphrey, P.S., & K.C. Parkes. 1959. Auk 76: 1-31.
- Johnsgard, P.A. 1965. Handbook of Waterfowl Behavior.
- Johnsgard, P.A. 1968. Waterfowl. Their Biology and Natural History.
- Kear, J. 1970. Pp. 357-92. In: Crook 1970.
- Lack, D. 1968. Ecological Adaptations for Breeding in Birds.
- McKinney, F. 1973. Pp. 6-21. In: Farner 1973.
- McKinney, F. 1975a. Pp. 490-519. In: Hafez 1975.
- McKinney, F. 1975b. Pp. 331-57. In: Baerends et al. 1975.
- McKinney, F. 1978. Adv. Study Behav. 8: 1-38.
- McKinney, F. 1985. AOU orn. Monogr. 37: 68-82.
- McKinney, F. et al. 1983. Behaviour 86: 250-94.
- Siegfried, W.R. 1974. Wildfowl 25: 33-40.
- Todd, F.S. 1979. Waterfowl. Ducks, Geese and Swans of the World.
- von der Wall, W. 1965. J. Orn. 106: 65-80.

## Aythya australis Hardhead

Nyroca australis Eyton, 1838, Monogr. Anatid.: 160 — Australia = New South Wales, fide Mathews, 1912, Novit. Zool. 18: 239.

The Greeks had a word ( $\alpha$ i' $\theta$ u $\alpha$ ) for a seagull, petrel or diver and the generic name is a corrupt transliteration (Coomans de Ruiter *et al.* 1947; Thompson 1936); here specifically 'southern'.

OTHER ENGLISH NAMES Barwing; Brownhead; Copperhead; Coppertop; White-eye; White-wing; White-eyed Duck; Widgeon.

Australian White-eyed Duck is really the best name because it reveals the allopatrism of this species and A. *nyroca*, the European or Ferruginous White-eyed Duck. The name is cumbersome, though, and risks being abbreviated to White-eye with the consequent possibility of confusion with species of Zosterops. Hardhead is at least simple and popular in Australia where the species is as widespread as anywhere else.

MONOTYPIC However, extima Mayr, 1940, has been proposed for birds from Banks I., New Hebrides and New Caledonia (see Geographical Variation).

FIELD IDENTIFICATION Length 45–60 cm of which body about two-thirds; wingspan 65–70 cm; weight 800–900 g. Medium-sized neat chocolate-brown duck with contrasting white under tail-coverts (usually visible on water), pale bluegrey subterminal band on bill and prominent white iris in males. In flight, wing-pattern distinctive, unique among Aust. ducks. Sit low in water. Sexes differ. No seasonal differences and eclipse plumage not described. Juveniles like adult female, slightly paler on chin, throat and lower breast.

DESCRIPTION ADULT MALE. Head, neck and entire upperparts, dark chocolate-brown, richer chestnut on head and sides of neck; darker black-brown on lower back, rump, upper tail-coverts and tail. Faint pale mottling on mantle, back and scapulars only visible in close view. Underparts mostly brown, reddish brown on upper breast; lower breast, abdomen and under tail-coverts, white (faintly mottled brown) usually prominent against dark brown body when on water. Upper wing-coverts, dark brown; remiges white with narrow dark tips; outer two primaries with dark outer webs. Thus, general appearance in flight of very dark upperparts with striking broad white panel extending along trailing-edge of wing from body to wing-tip, bordered by narrow dark tips to remiges. Underwing, white with complete narrow darkbrown border round leading- and trailing-edges slightly broader at tip. Pale belly and white underwings conspicuous overhead in flight. Bill, grey-black except for broad pale bluegrey saddle near bill-tip, contrasting with black nail. Iris, white, obvious even at distance. Legs and feet, grey-black. ADULT FEMALE. Like male but paler on head and neck, often with paler chin and throat and lower breast and abdomen more mottled. Bill, like male but blue-grey saddle narrower. Iris, dark brown. DOWNY YOUNG. Upperparts, including forehead, crown, nape, hindneck and upperwing, brown with yellow tinge; sides of head, chin and foreneck, yellow (fading to white) with small brown mark on lores; small yellow patches at base of wings and on rump. Tail, dark brown. Underparts, pale vellow with brown flanks and thighs. Underwing, yellow with narrow dark-brown border. Upper mandible, blue-grey; lower mandible, pinkish white with blue edges. Iris, pale brown. JUVENILE. Like adult female but slightly paler, especially on chin and throat and with more dark mottling on underparts. Can be difficult to separate in the field.

SIMILAR SPECIES White iris of adult male distinctive and, combined with rich dark-brown plumage and pale saddle on bill, unmistakeable. Pattern of upper- and underwings also distinctive and should not be mistaken for any other duck. On water, female Hardhead superficially similar to **Blue-billed Duck** Oxyura australis, which lacks white iris; clear white under tail-coverts of Hardhead (mottled white in Blue-billed) and grey-black bill with contrasting pale blue-grey saddle and black nail (bill uniform blue in breeding male Bluebilled, dark blue-grey in eclipse males and grey-black in females and juveniles) ought to distinguish it. Blue-billed instantly distinguished if tail held erect. For differences from Freckled Duck *Stictonetta naevosa* see that species.

Usually in pairs or small flocks though occasionally in flocks of thousands; on permanent freshwater lakes and swamps, mainly in deep open water. Do not perch in trees, except on low branches and stumps close to water, when upright stance apparent (cf. Freckled Duck). Rarely on land except when breeding. Flight swift and direct with rapid wingbeats producing characteristic whirring sound; take-off steeply. Wings narrow, pointed and set well back on body giving noticeable forward projection of body. Sit low on water with tail sloping down and not with distinct stern; prominent somewhat elongate high-crowned head. Dive for food, leaping forward and submerging smoothly; occasionally dabble in shallow water. Breed solitarily, low, in thick vegetation. Generally silent though males have soft wheezy whistle and females soft harsh croak.

HABITAT On terrestrial wetlands and occasionally sheltered estuarine and inshore waters. Almost entirely aquatic, preferring large deep fresh waters with abundant aquatic vegetation; particularly deep swamps and lakes, and billabongs, pools and creeks on alluvial plains; even on fastflowing floodwaters (Frith 1959a,b; Fjeldså 1985). In some areas, favoured wetlands have little emergent vegetation (Gowland 1988); in others, where deep waters have tall emergent vegetation or shrubs (e.g. Nymphaea, Eragrostis, Typha, Eleocharis, Muehlenbeckia) (Lavery 1966; Frith 1959a; Gosper 1981), birds avoid dense cover and frequent open water in channels, deep central parts, and occasionally shallows (Frith 1959b). Also occur on freshwater meadows; seasonal swamps with abundant aquatic flora; reed swamps (Phragmites, Scirpus); wooded lakes and swamps (Eucalyptus, Melaleuca); shallow floodwaters over alluvial plains; ricefields; and sewage

ponds (Gowland 1988; Frith 1959a; Vestjens 1977; Corrick 1982; Gosper 1981). Avoid main streams of rivers, except calm reaches where aquatic flora developed (Frith 1959b). Farm dams and small storages used if deep enough, even if too turbid, unstable, and sparsely vegetated to attract other species of waterbirds (Broome & Jarman 1983). Uncommon on saline wetlands; occasional records from coastal lagoons, salt lakes and pans, mangrove swamps, and sheltered inshore waters (Gosper 1981; Corrick 1982; RAOU WA Group 1985; Wood 1985; Jaensch *et al.* 1988).

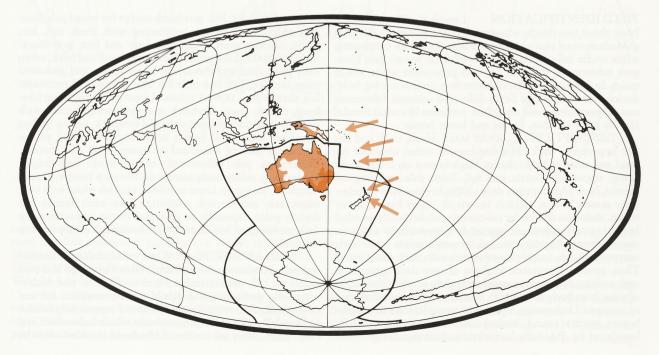
Breed in densely vegetated freshwater wetlands; either permanent waters or deep floodwaters (Frith 1982). At Booligal, NSW, breeding usually in swamps with high levels of organic matter, complex flora and diverse invertebrate population, in early stages of succession after drying and refilling (Crome 1988).

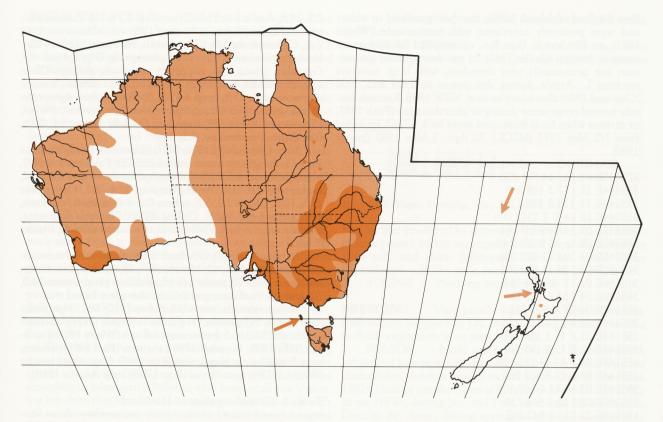
Fly freely to considerable heights, gaining height rapidly from steep take-off. Dive for food; thought to reach bottom in water 3 m deep (Frith *et al.* 1969).

Has declined in some areas (Dick 1973); breeding habitat much reduced by drainage of freshwater wetlands, diversion of water for irrigation, and flood-mitigation (Riggert 1966; Goodrick 1970; Corrick & Norman 1980; Corrick 1981, 1982; Frith 1982). Some irrigation storage swamps suitable for breeding, but most reservoirs and dams not stable enough to develop the dense vegetation needed (Frith 1982; Gowland 1988). Although birds occasionally enter ricefields, do little damage (Gowland 1988).

**DISTRIBUTION AND POPULATION** Endemic to Aust. and possibly formerly to NZ. Extralimitally, occasionally reported: Java (breeding, Hoogerwerf 1949); Sulawesi, one, 26 Mar. 1917 (Riley 1924) and recorded by WWF 1980; Vogelkop, Highlands and Merauke areas of New Guinea (Hoogerwerf 1964; Frith 1982), even regular Jan.–Apr. at Kiruk near Merauke; Banks I., New Hebrides (Mayr 1940); New Caledonia.

AUST. Widespread throughout mainland but rare or





absent in most arid areas of w. SA, inland WA and sw. NT, roughly S of 20°S and between 123 and 132°E (Aust. Atlas). Regular but scarce in Tas.; usually present at L. Dulverton (up to 324 birds) (Wilson 1980; Aust. Atlas); sporadic elsewhere on Tas. mainland and on Bass Str. islands (Green & McGarvie 1971; Sharland 1981; Tas. Bird Rep. 1971–89; Aust. Atlas). Breeds widely throughout e. districts E of line from Cairns, Qld, to Spencer Gulf, SA, and in sw. WA, S of line from Perth to Israelite Bay; stronghold in Murray-Darling drainage area of NSW, Vic. Occasional reports of nests outside these limits (Aust. Atlas) suggest that breeding may occur more widely but perhaps much influenced by wet or dry conditions. Report of breeding on King I. (Green & McGarvie 1971) but not on Tas. mainland (Aust. Atlas).

NZ Common to abundant when first recorded by Hutton in 1867 at Whangape and Waikare Ls, Lower Waikato. As the Maori had a name for the bird, it was probably established long before, perhaps by invaders from Aust. Declined and last recorded at Tutira, Hawke's Bay, in 1895 (Oliver). Since then, occasional vagrants: Hamurana, L. Rotorua, 1934 (NZCL); 1–8, Runanga L., Hawke's Bay (Anon. 1973; NZCL); one, Auckland, 30 Apr. 1980 (Jowett 1980).

NORFOLK I. Vagrant: one unconfirmed record, Nov. 1971; five in winter 1971 (Hermes et al. 1986).

POPULATION Annual indices of abundance from aerial survey of wetlands in about 12% of land-surface of e. Aust., 1983–88 were 8459; 480 267; 14 546; 6107; 14080; 2707 respectively; during these surveys, large proportion of total counted recorded at L. Galilee, central Qld (81–100% of total numbers, 1984), shallow wetlands of se. SA (21–40%, 1985), wetlands of floodplains at confluence of Lachlan and Murrumbidgee Rs (41–60%, 1986; 41–80%, 1988) and L. Moondarra, near Mt Isa, Qld (21–40%, 1987) (Braithwaite *et al.* 

1985a,b, 1986, 1987; Kingsford et al. 1988, 1989). Counts in Vic. in recent summer surveys, 1987-89, have been low: respectively 2584 on 332 wetlands; 2187 on 472 wetlands; 1980 on 626 wetlands (Martindale 1988; Hewish 1988; Peter 1989). Counts in sw. Aust., 1986-1988: 483 on 872 wetlands: 747 on 1201 wetlands; 1351 on 1398 wetlands (Jaensch & Vervest 1988a,b). During severe drought of 1957-58 in s. NSW, 80 000 gathered on L. Brewster and 50 000 on Barrenbox Swamp (Frith 1982). Count of 15 000, L. Learmonth, Vic., June 1957 (Thomas & Wheeler 1983). Flocks of 2000-10 000 on single lagoon in Myall Ls, e. NSW (Aust. Atlas); similar numbers, Moira Ls, NSW, Feb. 1978 (Chesterfield et al. 1984): near Mt Isa, w. Qld; and at Kerang, w. Vic. during RAOU Field Atlas (Aust. Atlas). In n. WA, 6000 at Anna Plains lagoon, Sept. 1981; 5000 on flooded coastal plains E of Wyndham, Mar. 1983 (Aust. Atlas).

Hunted widely but usually forms low proportion of total bag in se. Aust. (Norman *et al.* 1984; Briggs *et al.* 1985; Loyn 1987). Suggested that high proportion of Hardhead in Vic. shot in 1987 open season, but in that year probably large secure population in inland Aust. (Loyn 1987).

**MOVEMENTS** Dispersive and irruptive after good years. Main concentrations in Murray-Darling basin and sw. Aust. and widespread dispersal reported after dry years inland (Frith 1982). In se. Qld, numbers negatively correlated with rainfall inland (Woodall 1985) but no such relation found with numbers in coastal ne. NSW (Gosper *et al.* 1983). Reporting rate in Vic. highest spring and summer (Vic. Atlas) when varying numbers come to se. Aust. from inland (Norman 1970) though at least part of population appears to be resident (Vic. Atlas); dispersal of birds banded in s. Vic. generally N and NW as far as se. SA and Qld (Norman 1970). On

New England tableland, NSW, numbers increased in winter and were positively correlated with temperature (Whyte 1981); on Flinders I., Bass Str., congregated on permanent water in drought (Guiler 1961). In nw. Aust. usually uncommon but occasionally very abundant, with large numbers reaching L. Argyle during dry season in 1979 and 1980 (Gowland 1988) after heavy rains w. NSW 1978. Records outside normal range occur during or after droughts (Frith 1982) or at times when birds from coast move back inland: recorded from NZ May 1973 (NZCL), 30 Apr.–3 May 1980 (Jowett 1980).

BANDING (all returns ABBBS) 32S115E 01 J U 14 514 070 33S144E 12 J U 3 168 210 33S144E 12 J M 3 203 239 33S144E 12 1+ F 7 1512 005 34S142E 02 J U 36 490 164 34S142E 07 1+ U 9 301 240 34S145E 01 J M 73 428 206 34S146E 03 J M 11 510 001 34S146E 03 J F 46 404 147 34S146E 04 J M 4 135 139 34S146E 04 I F 4 497 216 35S144E 01 P U 1 120 226 35S144E 01 P U 1 136 127 35S144E 01 P U 1 195 261 35S144E 01 P U 14 217 190 35S144E 02 P U 8 802 067 35S144E 02 1+ U 1 267 104 35S149E 02 J M 1 564 230 35S149E 02 J U 2 542 262

FOOD Mixture of aquatic plants and animals, particularly mussels and freshwater shellfish. BEHAVIOUR. Most food obtained by diving, birds leaping forward and submerging with little disturbance to surface, swimming up to 40 m underwater using feet. Also sieve waterside mud, upend, and strip seeds from growing plants. Occasionally feed on grain in pasture (Frith 1982; Gowland 1988) and have been recorded catching shrimps in the air as they jumped to avoid Coots *Fulica atra* (Hall 1909). Also seen feeding in association with Australian Pelicans *Pelecanus conspicillatus* and Black Swan *Cygnus atratus* (Frith 1982). In some circumstances males will successfully steal food from Pacific Black Duck Anas superciliosa and conspecifics (Woodall 1984).

ADULT Summarized Table 1. In w. NSW (Frith 1959b) plants incl. Chenopodiaceae 0.8% vol., Polygonum aviculare 1.4, Rumex brownii 0.2, Fabaceae 1.4 (Medicago polymorpha, M. minima, Trifolium tomentosum) Cucumis myriocarpus 8.3, Myriophyllum 9.4, Cyperaceae 26.5 (Carex 18.3, Eleocharis plana 3.0, Scirpus 5.2), Poaceae 22.4 (Agrostis avenacea 9.3, Echinochloa crus-galli 2.9, Lolium perenne 7.3, Oryza sativa 2.5, Paspalum distichum 6.2, Phalaris paradoxa 1.6); animals molluscs bivalves Alathyria 1.4, gastropods Glyptophysa 4.9, Isidorella; crustaceans ostracods 0.2, freshwater crayfish Cherax albidus 0.8; insects odonatans Zygoptera larv. 0.8, bugs 3.6, Belastomatidae 1.2, Agraptocorixa eurynome 1.6, A. sp. 0.8, beetles 8.4, Dytiscidae 6.2, Dysticus 2.4, Berosus 3.1, caddisfly larv. 0.4.

In other samples Barrenbox Swamp, sw. NSW (Frith et al. 1969) plants incl. Ceratophyllum demersum 5.1% vol., Polygonaceae 2.5% vol., 11.6% freq., Vallisneria 1.2% vol., Potamogetonaceae 16.4 (Potamogeton ochreatus & P. pectinatus 14.5, 47.1), Ruppia 0.6% vol., Najas marina 13.1, 25.3, Typha 2.5, 24.5, Azolla 2.6, 23.5, Cyperaceae 3.2% vol. (Schoenoplectus validus 26.5% freq.), Poaceae 1.6% vol., Characeae 1.6% vol., Chlorophyta 2.9, 12.2; animals, molluscs, bivalves Corbiculina permena 14.1, 32.1, gastropods Glyptophysa 4.9, Gyraulus; crustaceans, copepods, ostracods, shrimps Caradina mccullochi, freshwater crayfish Cherax albidus; insects, odonatans 1.1, 17.1, bugs 5.4, 32.0, Diplonychus, Agraptocorixa eurynome 15.3% freq., Sigara, Naucoris, beetles 0.9% vol. Notomicrus, Ilybius, Hydrophilus, caddisfly larvae 5.1, 20.6, flies Chironomidae larv. 3.6, 35.9.

In n. Qld (Lavery 1970; 1971) plants incl. Nymphaeaceae 21.8, 21, Polygonum lapathifolium 25.5, 33, Fabaceae 2.1, 18.7, Menyanthaceae 4.5, 22.9, Ceratophyllum demersum 3.8, 19.2, Lemnaceae 2.9, 0.9, Najas graminea 11.8, 3.3, Cyperaceae 20.5, 70.6, Chara 2.3, 5.6, others 0.6, 9.8; animals, molluscs, gastropods 1.4, 3.3 incl. Gabbia affinis, Plotiopsis subornata, bivalves 2.4, 1.4 incl. Corbiculina, Velesunio wilsonii; insects 0.3, 5.6.

In nw. Aust. (10; Gowland 1988) plants incl. *Potamogeton tricarinatus* 21.5, 40, *Marsilea* 0.5, 10, aquatic plant stems, leaf tissue 10.0, 20, seeds 1.0, 10, unident. plant matter 24.0, 70; animals, molluscs, gastropods; also some baited rice.

Other records: seeds (Mathews 1910) incl. Nymphaea (Roy 1988), Polygonum, Trifolium (Vestjens 1977); shellfish (Mathews 1910) incl. freshwater molluscs (White 1913a), mussels (Hall 1909; Woodall 1984); shrimps (Hall 1909); insects, bugs Pristhesancus plagipennis (Roy 1988), large water beetles (White 1913b), gnat larvae (Roy 1988); carp (Morse 1919).

Table 1. Gizzard contents of Hardhead

Percentages	volume				frequency		
	1	2	3	4	2	3	4
PLANTS	74.3	56.8	95.8	57.0	91.1	98.6	100
ANIMALS	43.5	4.2	43.0	85.3	11.2	30	
Molluscs	9.6	24.0	3.8	43	52.3	30	
Crustaceans	1.0	tr.	< 0.1			1.4	
Insects	15.1	19.3	0.3	tr.		5.6	10
No. Gizzards	193	283	214	10		V WR	1/30

(1) Frith (1959b); (2) Frith et al. (1969); (3) Lavery (1970, 1971); (4) Gowland (1988).

DUCKLING In n. Qld, flightless young (4; Lavery 1971) contained clam shrimps 23.8% vol.

**SOCIAL ORGANIZATION** Little known. Commonly in small flocks but also in pairs; sometimes very large rafts of several thousand occur on large lakes (Wilson 1980; Frith 1982). During 1956 at Barrenbox Swamp and L. Brewster, near Griffith, NSW, *c*. 50 000 and 80 000 respectively; towards end of year, birds forced to move and flocks of 1000– 2000 appeared at coast and tablelands (Frith 1982).

BONDS No detailed study. Probably seasonal monogamy or sequential or successive polygamy (P.J. Fullagar).

PARENTAL CARE Little information. Female incubates and alone rears brood (P.J. Fullagar).

ROOSTING Often congregate in large flocks on water when loafing during day but will haul out and stand on sandbanks or other low perches and rest in characteristic, steeply inclined posture resembling that of Freckled Duck *Stictonetta naevosa* (*q.v.*).

SOCIAL BEHAVIOUR Little known in detail and no reported studies in wild. Most detail on displays from Johnsgard (1965) using captive birds and some information from P.J. Fullagar. Pre-flight signal silent; neck stretched upright and bill flicked upwards repeatedly.

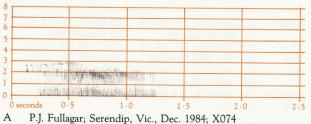
AGONISTIC BEHAVIOUR Kinked-neck used by males towards other males. Typical Aythya posture in which neck sharply and momentarily twisted at centre in flicking motion and call given (see Voice). Often given after Sneak, in which head lowered to water and pointed at opponent. Females use slightly ritualized (Johnsgard 1965) Inciting posture, in which head thrust towards adversary in overt threatening movements to side with distinctive rasping call (see Voice), followed by rapid retreat towards preferred male in Head-high posture.

SEXUAL BEHAVIOUR Male advertising. Main display Kinked-neck (see above). Males often repeat Kinkedneck many times as they manoeuvre about female. Used in same combination as described above with Sneak, or Sneak given alone. Conspicuous Head-throw: head thrown onto back towards tail with bill often pointing well past vertical and posture held for short time. Call same as that of Kinked-neck (Johnsgard 1965). Often Head-throw distinctly asymmetrical, with bill being sharply tilted towards female (Johnsgard 1965). Nod-swim reported as infrequent by Johnsgard (1965). Typical Turn-back-of-head used to lead female after her inciting towards others (Johnsgard 1965). Females use Inciting (see above) when with displaying males. Also give Head-throws according to Johnsgard (1965) but with hoarse call (see Voice). but his claim that females occasionally give Kinked-neck with call needs confirmation. COPULATION. Details from Johnsgard (1965). Male performs slight Head-pumping movement, alternating with Bill-dipping and Preen-dorsally, with no obvious response from female until she assumes receptive posture and male treads. Post-copulatory signal of male is Kinked-neck followed by swimming away in Bill-down posture. Female bathes.

**RELATIONS WITHIN FAMILY GROUP** Nothing known. Apparently male does not accompany female with brood (P.J. Fullagar).

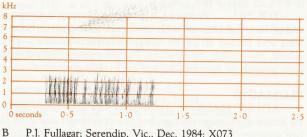
No detailed studies and poorly understood. VOICE Frith (1982) provides no useful information. Account largely based on Johnsgard (1965, 1978) with some details from P.J. Fullagar. Generally silent. Calls mostly given during courtship displays; sometimes by female of pairs in flight at time of breeding and by females when leaving nest or with brood. Tracheal tube of male enlarged towards middle and bulla lacks enlargement conspicuous in most Aythya; almost identical in shape to that of Ring-necked Duck A. collaris (Johnsgard 1965), having slightly inflated right chamber. Non-vocal sounds: wingbeats noisy in flight.

ADULT MALE (1) Call with Kinked-neck display, wheezy whistle (sonagram A). (2) Call with Head-throw, soft kHz



whirrrr. (3) Coughing call said to be given rarely by males; described as soft whistle.

ADULT FEMALE Loud, harsh, rattling noise (sonagram B) given when Inciting (Johnsgard 1965); likened by

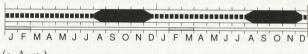




him 'to that produced by drawing a stick along a lathe fence'. Hoarse gaaack said to accompany female Head-throw may be same call, and claim (Johnsgard 1965) that female utters Kinked-neck call like male (see above) needs confirmation. YOUNG Nothing recorded.

BREEDING Very poorly known. No detailed studies. Information supplied by J.R. Starks. Breed solitarily, nesting in thick vegetation in or near wetlands.

SEASON Little exact knowledge. Probably much influenced by wet conditions and occurrence of flooding and claimed that clutches may be started at any time of year (Frith 1982). Main or regular times of breeding claimed (Frith 1982): in ne. NSW, during Jan. and Feb.; in inland NSW, Sept. to Dec.; in sw. Aust., during spring; in tropical monsoonal n. Aust., from Apr. and May. Start of clutches by months estimated from Aust. NRS: NSW, Mar. 1, Sept. 2, Oct. 1, Nov. 6, Dec. 2. Vic., Oct. 1, Nov. 4; in sw. Aust., Aug. 2, Sept. 3, Oct. 4, Nov. 3, Dec. 1; in NT, July 2.



(s. Aust.)

In dense vegetation (reeds, tea-tree, lignum, SITE cumbungi) above water along rivers and channels, round billabongs and dams; records (seven) as 10-90 cm above water and in vegetation reaching 60-150 cm above nest. Also on land up to 27 m from water in thick grass or bushes, on treestumps; often on islands (Frith 1982; Aust. NRS).

NEST. MATERIALS Trampled, slightly dishshaped platform of reeds, sedges, lignum, sticks, perhaps with canopy, sparsely-lined with down. Built by female, of material within reach from nest as in other Aythya spp. One nest measured externally 20 cm across, 17 cm thick; internally, 16 cm across, 8 cm deep (Braithwaite 1975; Frith 1982; Morse 1922).

EGGS Elliptical; fine-grained, glossy; creamy white (Campbell).

MEASUREMENTS: 57 (49-65; 105) x 42 (37-45) (Frith 1982): 57.9 (0.92; 57.2-59.5; 6) x 41.1 (0.67; 40.3-42.0) (Braithwaite 1975).

CLUTCH-SIZE No quantified, critically assesæd data. Range usually claimed as 6-18, mostly 9-13 (Frith 1982; Campbell) but dump-laying likely and eggs of Musk Duck Biziura lobata recorded in Hardheads' nests (Attiwill et 1l. 1981; Sandland & Orton 1922).

LAYING No information.

INCUBATION By female only. INCUBATION PER-IOD: 30–32 days (Braithwaite 1975) one determination and, if correct, 2–4 days longer than in other species of Aythya (BWP); 25 days (Frith 1982).

YOUNG Precocial, nidifugous. Downy; upperparts and pileum, light brown with small pale-yellow patch behind wing and similar strips on wing; underparts and face, pale yellow. No further information. No information on parental care, growth or maturation, nor on breeding success.

### PLUMAGES

ADULT MALE Attained in first year; no evidence for seasonal plumage change, but few specimens collected in late summer; no eclipse plumage known. HEAD AND NECK. Dark chestnut-brown with chestnut sides of neck and darkbrown (reddish 22) chin and throat. UPPERPARTS. Mantle, upper back and scapulars, dark brown with paler mottling; feathers dark brown (21) with brown (123) to yellow-brown (24) tips. Lower back, rump and upper tail-coverts, blackbrown (119) with concealed grey-brown (c119B) bases. TAIL. black-brown (19). UPPERWING. Marginal coverts, white. Other coverts and alula, dark brown (219). Most primaries, white with dark-brown (219) tips and outer edges; outer two primaries have dark brown (119A) outer webs. Secondaries, white with narrow dark-brown (219) outer edges, dark-brown (-) ends with faint green iridescence, and narrow white tips, lost with wear. UNDERPARTS. Upper and central breast, dark reddish brown (c32). Central breast sometimes scalloped white; feathers, dark greyish brown (119A) with red-brown (glossy 240) subterminal bands and white tips. Upper breastfeathers similar but lack white tips. Lower breast and upper belly, white with varying, usually slight, light brown mottling; feathers have greyish brown (119B) bases, more exposed when feathers ruffled or worn. Flanks, brown (121A). Lower belly and vent, brown with paler mottling; feathers, dark brown (119A) with light brown (223C) to white tips. Under tail-coverts and axillaries, white. TAIL, brown-grey (79). UNDERWING. Lesser coverts, dark brown (119A) to brown (119B) with white fringes; other coverts, white. Remiges patterned as above, but dark areas dark olive-brown (129); outer primaries have glossy brown-grey tegmen.

ADULT FEMALE Attained in first year. HEAD AND NECK, slightly paler in general than adult male, with darkbrown (21) hindneck. Varying, mottled white, patch on chin and throat formed by white tips to feathers, broadest on upper throat; tips can be entirely lost with wear. UPPERPARTS, as adult male. UNDERPARTS, white tips to lower breast and belly tend to be narrower than in adult males, causing more mottled appearance. TAIL, WING, as adult male.

DOWNY YOUNG HEAD AND NECK. Forehead, crown stripe, nape and hindneck, dark brown (c20) with yellow tinge caused by light brown (123B) tips to down filaments. Small dark-brown (119A) marking on lores, and sometimes narrow brown (119B) line from nape to hind edge of eye. Rest of head and neck, yellowish (c53) becoming white with fading and wear. UPPERPARTS, dark brown (c20) suffused yellow. Three pairs of small buff-yellow (54) spots: one at sides of lower rump, one at extreme sides of upper rump, and one at base of wing-pads, almost continuous with wing-stripe. TAIL, dark brown (c20). WING-PADS. Above, dark brown (c20) suffused yellow, with broad white trailing-edge from carpal joint to base. UNDERPARTS, mostly cream-white (c54); flanks and thighs, dark brown (c20) suffused yellow. WING-PADS. Under-

side, cream-white; narrow leading-edge and broad trailingedge, dark brown (c20) suffused yellow.

JUVENILE Generally slightly paler than adult female, with smaller body-feathers and more dark mottling on underparts. White tips to lower belly-feathers narrow, causing little contrast between dark vent and pale belly.

**BARE PARTS** Based on photographs in Pringle (1985), NZRD and Aust. RD; and notes from captive birds.

ADULT MALE Iris, white. Bill, mostly grey-black (82); pearl-grey (81) to pale grey (86) saddle in distal third of upper mandible contrasts sharply with circular grey-black (82) nail on upper mandible. Pale patch wider on sides of upper mandible (c. 20 mm) than on culmen, where narrowest point 5.8 (0.8; 4.7–7.1; 14); hind-border of saddle concave. Feet and legs, grey (84) or brownish grey (80) to grey-black (82), sometimes with pale-grey (86) patches on toes and front of tarsus.

ADULT FEMALE Iris, dark brown (c21). Saddle of bill, perhaps greyer than male; tends to be narrower, especially on culmen, and back edge more strongly concave. Minimum width of pale patch 4.8 (0.8; 3.0–5.9; 9), significantly smaller than in males but with some overlap. Feet and legs, as adult male.

DOWNY YOUNG Iris, pale brown (-). Upper mandible, blue-grey (-); lower, pinkish white (-) with blue (-) edge; feet and legs, blue-grey (Frith 1977).

JUVENILE Iris, hazel-brown (Frith 1977); otherwise similar to adult female. Unknown when white iris of males develops.

MOULTS Based on Braithwaite & Norman (1974, 1976), Norman et al. (1984) and skins (MV, HLW, ANWC).

ADULT POST-BREEDING Probably complete; primaries simultaneous. Wing moult occurs in mid- or late summer, timing perhaps varying from year to year. Proportion of adults in wing-moult shot on six opening days of duck season (late Feb. or early Mar.) has varied from 0 to 44%. Primary wear of most non-moulting birds in these samples suggests they have completed moult, but on most opening days some birds with worn to very worn primaries are shot, and have presumably yet to begin moult.

POST-JUVENILE Body- and tail-moult assumed to occur in first few months; lack of recognizable juveniles in museum collections made in late winter and early spring implies that partial post-juvenile moult occurred by this time. Primary wear of 'yearlings' (presumably previous year's juveniles) shot on open days suggests wing-moult occurs at end of first year, at about same time as adults.

**MEASUREMENTS** (1) Juveniles excluded, skins (MV, HLW, ANWC). (2) Adults, recently dead (Frith 1977).

		MALES	FEMALES	
WING	(1) (2)	218.9 (3.95; 211–227; 14) 215 (183–243; 99)	215.3 (4.47; 206–223; 12) 217 (186–234; 88)	*
8TH P	(1)	136.7 (2.28; 131-140; 14)	135.8 (3.47; 130–142; 12) 59.7 (3.39; 55–67; 11)	
TAIL BILL	(1) (1)	57.7 (2.61; 54–62; 13) 44.8 (1.08; 42.8–46.5; 14)	42.2 (1.48; 39.2-45.1; 12)	**
TARSUS	(2) (1)	44.8 (1.08; 42.8-46.5; 14) 39.9 (0.91; 37.8-41.5; 13)	42.2 (1.48; 39.2–45.1; 12) 38.5 (1.36; 34.9–39.8; 12)	**
TOE	(1)	64.9	addant of Freekled for	

WEIGHTS Adult males 902 (525–1100; 105); adult females 838 (530–1060; 88) (Frith 1977). No information on seasonal variation.

**STRUCTURE** Eleven primaries; p10 usually longest, p9  $-\frac{1}{2}$ -2, p8 4-8, p7 12-20, p6 25-29, p5 36-42, p4 50-56, p3 64-70, p2 76-82, p1 80-92. Slight emargination on outer web of p9, inner of p10. Seventeen secondaries, including five tertials. Tail, slightly rounded, 14 feathers, t1-t7 = 19-32. Bill, rather long (about same length as head), narrower at base than at tip, higher than broad at base; culmen slightly concave; saddle of bill has pitted texture; nail of bill, rather small (about half width of bill) and circular. Tarsus, slightly laterally compressed; scutellate in front, reticulate elsewhere. Middle toe longest, outer c. 99%, inner c. 80%, hind c. 29%.

**GEOGRAPHICAL VARIATION** Probably none. Birds collected breeding on Banks I., New Hebrides, sometimes recognized as separate subspecies *extima* Mayr, 1940, on basis of small size (wing 193–211 in males, 189–196 in females; bill 41–45) (Mayr 1940; Johnsgard 1978). However, only small samples measured (six males, five females) and it has been suggested that Banks I. population represents brief colonization by visiting Aust. birds (Madge & Burn 1988).

#### REFERENCES

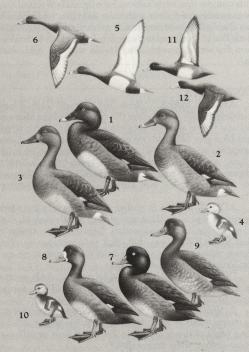
Anon. 1973. Notornis 20: 185.

- Attiwill, J.M., et al. 1981. Emu 81: 41-2.
- Braithwaite, L.W. 1975. Proc. Ecol. Soc. Aust. 8: 107-28.
- Braithwaite, L.W., & F.I. Norman. 1974. Tech. Pap. Div. Wildl. Res. CSIRO Aust. 29.
- Braithwaite, L.W., & F.I. Norman. 1976. Tech. Memo. Div. Wildl. Res. CSIRO Aust. 11.
- Braithwaite, L.W., et al. 1985a. Tech. Memo. Div. Wildl. Rglds Res. CSIRO Aust. 21.
- Braithwaite, L.W., et al. 1985b. Tech. Memo. Div. Wildl. Rglds Res. CSIRO Aust. 23.
- Braithwaite, L.W., et al. 1986. Tech. Memo. Div. Wildl. Rglds Res. CSIRO Aust. 24.
- Braithwaite, L.W., et al. 1987. Tech. Memo. Div. Wildl. Rglds Res. CSIRO Aust. 27.
- Briggs, S.V., et al. 1985. Aust. Wildl. Res. 12: 515-22.
- Broome, L.S., & P.J. Jarman. 1983. Emu 83: 99-104.
- Chesterfield, E.A., et al. 1984. Forests Comm. Vic. Res. Branch Rep. 240.
- Coomans de Ruiter, L. 1947. Beteckn etymol. Wetenschap. namen Nederle Vogels.
- Corrick, A.H. 1981. Proc. R. Soc. Vict. 92: 187-200.
- Corrick, A.H. 1982. Proc. R. Soc. Vict. 94: 69-87.
- Corrick, A.H., & F.I. Norman. 1980. Proc. R. Soc. Vict. 91: 1-15.
- Crome, F.H.J. 1988. Emu 88: 243-8.
- Dick, A. 1973. Birds 7: 60-61.
- Fjeldså, J. 1985. Emu 85: 141-9.
- Frith, H.J. 1959a. CSIRO Wildl. Res. 4: 97-107.
- Frith, H.J. 1959b. CSIRO Wildl. Res. 4: 131-55.

- Frith, H.J. 1977/1982. Waterfowl in Australia.
- Frith, H.J., et al. 1969. CSIRO Wildl. Res. 14: 17-64.
- Goodrick, G.N. 1970. Tech. Memo. Div. Wildl. Res. CSIRO Aust. 5.
- Gosper, D.G. 1981. Corella 5: 1-18.
- Gosper, D.G., et al. 1983. Aust. Wildl. Res. 10: 319-27.
- Gowland, P.N. 1988. RAOU Microfiche 35.
- Green, R.H., & A.M. McGarvie. 1971. Rec. Queen Vic. Mus. 40.
- Guiler, E.R. 1961. Emu 61: 61-4.
- Hall, R. 1909. Emu 9: 77-9.
- Hermes, N., et al. 1986. Notornis 33: 141-9.
- Hewish, M. RAOU Rep. 52.
- Hoogerwerf, A. 1949. Limosa 22: 1-279.
- Hoogerwerf, A. 1964. Bull. BOC 84: 70-84.
- Jaensch, R.P., & R.M. Vervest. 1988a. RAOU Rep. 31.
- Jaensch, R.P., & R.M. Vervest. 1988b. RAOU Rep. 46.
- Jaensch, R.P., et al. 1988. RAOU Rep. 30.
- Johnsgard, P.A. 1965. Handbook of Waterfowl Behaviour.
- Johnsgard, P.A. 1978. Ducks, Geese and Swans of the World.
- Jowett, C. 1980. Notornis 27: 392.
- Kingsford, R.T., et al. 1988. Tech. Memo. Div. Wildl. Ecol. CSIRO Aust. 30.
- Kingsford, R.T., et al. 1989. NSW NPWS Occ. Pap. 8.
- Lavery, H.J. 1966. Old J. agric. anim. Sci. 23: 573-90.
- Lavery, H.J. 1970. Wildfowl 21: 69-77.
- Lavery, H.J. 1971. Qld J. agric. Sci. 28: 255-73.
- Loyn, R.H. 1987. A Report on the 1987 Duck Hunting Season in Victoria. Nat. Parks Wildl. Div., Dept. Cons. Forests Lands, Vic.
- Madge, S., & H. Burn. 1988. Wildfowl.
- Martindale, J. 1988. RAOU Rep. 37.
- Mathews, G.M. 1910. Emu 10: 103-10.
- Mayr, E. 1940. Am. Mus. Novit. 1056.
- Morse, F.C. 1919. Emu 19: 141.
- Morse, F.C. 1922. Emu 22: 24-36.
- Norman, F.I. 1970. Emu 70: 126-30.
- Norman, F.I., et al. 1984. Tech. Memo. Div. Wildl. Rglds Res. CSIRO Aust. 20.
- Peter, J. 1989. RAOU Rep. 57.
- Pringle, J.D. 1985. The Waterbirds of Australia.
- RAOU WA Group. 1985. RAOU Rep. 9.
- Riggert, T.L. 1966. Study Wetlds Swan Coastal Plain. Dept Fish. Fauna, Perth.
- Riley, J.H. 1924. Proc. US natn. Mus. 64: 1-118.
- Roy, L.J. 1988. Sunbird 18: 95-8.
- Sandland, P.T., & O.L.E. Orton. 1922. Emu 22: 134-7.
- Sharland, M. 1981. A Guide to the Birds of Tasmania.
- Thomas, R., & J. Wheeler. 1983. Birds of the Ballarat Region.
- Thompson, D'Arcy W. 1936. A Glossary of Greek Birds.
- Vestjens, W.J.M. 1977. Tech. Memo. Div. Wildl. Res. CSIRO Aust. 12.
- White, S.A. 1913a. Emu 12: 179-85.
- White, S.A. 1913b. Emu 13: 16-32.
- Whyte, R.J. 1981. Emu 81: 243-7.
- Wilson, R. 1980. Tas. Bird Rep. 10: 11-18.
- Wood, K. 1985. Aust. Birds 19: 17-38.
- Woodall, P.F. 1984. Emu 84: 65-70.
- Woodall, P.F. 1985. Aust. Wildl. Res. 12: 495-506.

DIR





## Volume 1 (Part B), Plate 96

- Hardhead *Aythya australis*  **1.** Adult male **2.** Adult female **3.** Juvenile male **4.** Downy young **5.** Adult male **6.** Adult female
- New Zealand Scaup Aythya novaeseelandiae 7. Adult male 8. Adult female 9. Juvenile 10. Downy young 11. Adult male 12. Adult female

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