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Australian waterbirds – products of the continent's ecology

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Abstract. Some aspects of the ecology of 93 waterbird species, found predominantly on freshwater ecosystems, are reviewed. These species**,** belonging to six major orders — Anseriformes (ducks, geese and Black Swan), Podicipediformes (grebes), Pelecaniformes (Australian Pelican and cormorants), Ciconiiformes (herons, ibis, spoonbills and bitterns), Gruiformes (cranes, rails, crakes and gallinules), and Charadriiformes (waders and terns) — use a wide range of habitats and about half occur throughout the continent. Knowledge of their ecology remains poor for many waterbirds, particularly cryptic and rare species, and is moderate to good for hunted species. Life histories of Australian waterbirds differ from their counterparts elsewhere. Australia's highly variable climate and river-flooding patterns create wetland habitats, the spatial and temporal variability of which strongly influence the ecology of local waterbirds. Many waterbirds respond to newly generated habitats to feed and/or breed and then disperse or die as wetlands dry. Regular movements are not common in most Australian species although some, particularly waders, migrate between Northern Hemisphere breeding grounds and non-breeding habitat in Australia. Breeding of Australian waterbirds coincides with food abundance in the southern spring, the wet season in the tropics and following floods inland. Habitat loss through draining of wetlands, regulation of rivers, diversion of water for irrigation and floodplain development are currently the major threats to waterbirds. Other potentially threatening processes include exotic plants and animals, pollution, climate change and over-harvesting but evidence for the impact of these factors remains poor. Understanding of waterbird, particularly waterfowl, ecology has contributed significantly to the conservation management of wetlands in Australia. Research on single species, studies of movements using satellite technology, further investigation of the effects of hunting, long-term monitoring and large-scale analyses of the availability of wetland habitat should be future research priorities.

Introduction

To early European visitors, the waterbirds of Australia were probably not particularly different to those of the Northern Hemisphere, unlike Australia's other fauna (see Neville 1997; Moyal 2001). There were some surprises. Swans were black and the Musk Duck was 'a very peculiar' bird with 'a bag like that of a lizard hanging under its throat', smelling 'intolerably of musk' (G. Vancouver, in Frith 1982, p. 308). Most early explorers remarked on waterbirds only when they shot them for food although directions of waterbird movements in the inland were considered clues to distant water. Even Wheelwright (1861), interested in the local 'game', commented little on novel species. Despite this, many of Australia's waterfowl (duck and geese species) are unique and only South America exceeds Australia in the number of genera (e.g. Magpie Goose, Cape Barren Goose, Musk Duck and Pink-eared Ducks) found nowhere else (Weller 1964; Cowan 1973; Fullagar *et al.* 1988). But many other waterbirds are found elsewhere (e.g. Intermediate Egret, Black-necked Stork, Glossy Ibis, Eurasian Coot, Black-winged Stilt) or exhibit minor morphological and behavioural differences from their counterparts on other continents (e.g. Australasian Shoveler, Red-necked Avocet). It is instructive to identify what makes the ecology of Australian waterbirds different and how this contributes to a greater understanding of the continent and its biotic and abiotic interactions. Ultimately, this information should assist effective conservation of waterbirds and their habitats.

Research in the Northern Hemisphere, with its diverse waterbirds (e.g. loons, flamingos, sea ducks, screamers, geese and swans, phalaropes), has provided a platform on which to base an understanding of local waterbird ecology. For northern waterbirds, a clear ecological model has emerged, one where movements, reproductive ecology and moulting are centred on marked seasonal factors (photoperiod, temperature and food availability). In contrast, what is currently known of the ecology of many Australian waterbirds reflects the unpredictable climate (Stafford Smith and Morton 1990) with movements, feeding ecology, reproductive ecology, moult and use of habitat all exhibiting a plasticity driven by climatic patterns. This variability poses major hurdles to research but it has also meant that waterbird

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studies have contributed substantial insight into the nature of ecological processes on the continent.

We review knowledge of some of the ecology of 93 of Australia's waterbird species, about 13% of Australia's birds (Christidis and Boles 1994), from six orders (Table 1; see Appendix 1 for scientific names), within the context of the continent's highly variable climate, hydrology and patterns of wetland availability. We exclude species that spend most of their lives in terrestrial habitats, vagrant species or those not generally regarded as waterbirds (e.g. Banded Lapwing, Clamorous Reed-warbler, and birds of prey). We also ignore most international migratory species and most seabirds, since the focus here is predominantly on freshwater systems. The review follows a framework based on some steps advocated by Caughley and Gunn (1996, pp. 223–224). Broadly, this covers waterbird ecology (distribution, abundance, status, movements, mortality and survival, habitats, moulting, feeding ecology, reproductive ecology and behaviour) and threatening processes. We try to identify major gaps in ecological data and the future conservation of this major group of birds. Inevitably in such a review, we discuss some areas and ignore others and, as will be evident, the work of Frith (1982, and references therein) and his colleagues formed a substantial basis for this discussion.

Waterbird Ecology

Habitats

Waterbirds use an array of habitats, ranging from swimming pools and sewage ponds to swamps, lagoons, mudflats, estuaries, embayments and open shores, freshwater and salt lakes, rivers, floodplains and dams (Lavery 1970*a*, 1971; Braithwaite 1975; Maher 1981; Frith 1982; Lane 1987; Norman and Corrick 1988; Marchant and Higgins 1990; Maddock 2000). These habitats occur at all altitudes, from the tropics to the sub-antarctic, and all are affected by flooding regimes. Apart from Victoria (e.g. Corrick and Norman 1980; Norman and Corrick 1988), relatively little is known about the broad distribution and extent of wetland habitat in Australia at a State level (Finlayson *et al.* 1999), let alone its temporal variability. This remains an important objective for wetland and waterbird conservation.

Australia probably has the most variable wetland and floodplain systems in the world, reflecting the status of the continent's rivers (Puckridge *et al.* 1998; Roshier *et al.* 2001*a*). Large rainfall events produce considerable flooding and create widespread habitat on the floodplains. These contribute to a large population increase ('boom' period) or conversely a substantial decrease in population ('bust' period) when important habitat for large numbers and high diversities of waterbirds is created (Morton *et al.* 1990*a*, 1990*b*, 1993*a*,1993*b*, 1993*c*; Kingsford *et al.* 1999*a*). Most natural wetlands reflect the geomorphology, local and regional rainfall and the flow regime of the rivers that supply them. These factors vary across the continent at a wide range of temporal and spatial scales and, with abiotic, physical (size, shape and depth) and chemical variables, influence the abundance and diversity of waterbirds (e.g. Kingsford 1992; Halse *et al.* 1993*a*; Storey *et al.* 1993; Kingsford *et al.* 1997, 1999*a*). Biotic factors clearly also affect waterbird populations.

Farm dams (Lavery 1966*a*; Kingsford 1992), off-river storages and reservoirs (Table 2) also provide waterbird habitat but, in their creation, there is a trade-off with the loss of wetland habitat downstream (Kingsford 2000*a*) and changes to seasonal patterns and reduced temperature of flow that may affect waterbirds (Walker 1985). Further, waterbird numbers, densities and numbers of species are usually higher on natural wetlands than on large reservoirs (Table 2). Thus, most large storages in upper catchments

Table 1. Subjective assessment of level of current information about aspects of ecology in six major orders of waterbirds in Australia
The six orders considered are: Anseriformes (ducks, geese and Black Swan), Podicipediformes (grebes), Pelecaniformes (Australian Pelican and cormorants), Ciconiiformes (herons, ibis, spoonbills and bitterns), Gruiformes (cranes, rails, crakes and gallinules), and Charadriiformes (sandpipers, stilts and terns). Status is defined as the number of species in each order currently listed on at least one of the States, Territories or Commonwealth's lists of threatened species (Garnett and Crowley 2000)

Measure	Anseriformes	Podicipediformes	Pelecaniformes	Ciconiiformes	Gruiformes	Charadriiformes
Number of species	20	3	6	19	17	28
Habitats	Good	Moderate	Good	Good	Poor	Good
Distribution	Good	Good	Good	Good	Poor	Good
Abundance	Good	Poor	Good	Good[A]	Poor	Poor
Movements	Moderate	Poor	Poor	Moderate	Poor	Poor[B]
Mortality and survival	Moderate	Poor	Poor	Poor	Poor	Poor
Status	8	1	0	8	5	6
Moulting	Moderate	Poor	Poor	Poor	Poor	Poor
Feeding ecology	Good	Good	Good	Good	Moderate	Moderate
Reproductive ecology	Good	Moderate	Moderate	Good	Poor	Poor
Behaviour	Good	Moderate	Moderate	Moderate	Poor	Poor

[A]Poor for bitterns
[B]Moderate for migratory wading birds

(e.g. Dartmouth Dam in Victoria, Cordeaux Reservoir in New South Wales) support few waterbirds because they are deep and are not suitable for feeding or breeding (Frith 1959*a*) (Table 2). Nevertheless, large numbers of waterbirds may occur on some storages (e.g. Lake Moondara in north-western Queensland: Table 2) while other artificial impoundments can provide temporary nest sites.

Habitat requirements are known broadly for many waterbird species (Braithwaite 1975; Frith 1982; Marchant and Higgins 1990; Maddock 2000). In four of the six orders of waterbirds**,** detailed information for habitat requirements is categorised as 'good' but 'poor' in cryptic species (e.g. rails and crakes) (Table 1) but there is considerable variation even within orders. Thus, data for some anatids are good for some species (e.g. Australian Wood Duck or Magpie Geese) but for not for others (e.g. Radjah Shelduck, pygmy-geese, Wandering Whistling-Duck, Australasian Shoveler).

Distribution

Australia is predominantly arid (about 70% receives <500 mm rainfall per year) and, although there are strong temperature differences between seasons, rainfall is unpredictable across much of the continent (Stafford Smith and Morton 1990). Climate is more regular in the temperate 'regions' of the south-east and south-west, where seasonal temperature and rainfall strongly influence biota. Similarly, predictable rainfall in tropical Australia determines wet and dry seasons. These regions provide a useful framework for considering the distribution of Australian waterbirds, contrasting with the four habitat regions (central, southern, Murray–Darling and northern) previously proposed for waterfowl (Braithwaite 1975, 1976*a*; Frith 1982). Certainly, delineation of the Murray– Darling Basin as a separate region now seems arbitrary, given the distribution of waterbirds across the inland (e.g. Kingsford and Halse 1999; Roshier *et al.* 2001*a*, in press).

Using the maps provided by Blakers *et al.* (1984), distributions for the 93 species considered can be coarsely categorised into northern, southern or continental (Frith 1982) and subsets of these. This crude analysis showed that about 47% of the 93 species have a continental distribution, 15% are essentially northern, 15% southern and the remainder a combination of either south-eastern, south-western or north-eastern (Appendix 1). Some species, including various waterfowl, crakes, snipe and Red-necked Avocet, are confined to temperate latitudes while others are restricted to the south (e.g. Cape Barren Goose and Tasmanian Native-hen; see Appendix 1) or inland (e.g. Pink-eared or Freckled Duck: Frith 1982; Norman *et al.* 1994; Kingsford 1996). In addition, some tropical species are more common in coastal regions than inland (e.g. Magpie Goose, Plumed and Wandering Whistling-Duck, Green and Cotton Pygmy-goose, Radjah Shelduck: Lavery 1966*b*). A more quantitative assessment of hypotheses about distribution of waterbirds, in relation to biogeographic variables (e.g. temperature, climate, wetland type and availability), awaits testing.

The ranges of some waterbirds (e.g. Grey Teal, Pacific Black Duck, Black Swan, Intermediate Egret, Cattle Egret, Black-necked Stork) extend to sub-antarctic islands, New Zealand and Papua New Guinea (Maddock 1990; Marchant and Higgins 1990; Maddock and Geering 1993) while some Northern Hemisphere species may occur as vagrants in Australia (Marchant and Higgins 1990; Christidis and Boles 1994). Some tropical species occasionally extend their range into temperate areas. For example, Pied Herons bred in the inland Macquarie Marshes in 2000, well outside their normal range (Marchant and Higgins 1990).

Knowledge of waterbird distribution in Australia may be categorised as **'**good' (Lavery 1970*a*; Frith 1982; Blakers *et al.* 1984; Marchant and Higgins 1990, 1993, 1996;

Table 2. Numbers of waterbird species and abundance of waterbirds on ten wetlands of two different types, five natural (N) and five reservoirs (D), between 1983 and 2000
Data are from aerial surveys of waterbirds in eastern Australia (Kingsford *et al.* 1999*b*)

Name	Type	Location		Area	No. of	No. of species		Abundance			Density[A]
		Latitude	Longitude	(ha)	surveys	Mean	Range	Mean	s.e.	Median	
Burrendong Dam	D	32°36′	149°09′	6059	17	11.8	7–16	3804	1888.06	820	0.14
Coolmunda Dam	D	28°26′	151°14′	1640	16	22.8	12–30	4575	1131.95	3717	0.44
Cordeaux Reservoir	D	34°22′	150°46′	634	11	2.7	1–6	21	5.65	13	0.02
Dartmouth Dam	D	36°35′	147°34′	5125	17	<1.0	0–1	3.05	2.94	0	<0.001
Lake Moondara	D	20°35′	139°33′	1715	17	24.8	17–31	12618	3122.74	8777	5.12
Jack Smith Lake	N	38°29′	147°00′	1461	16	11.4	4–23	3268	999.09	1629	1.11
Lake Galilee	N	22°29′	145°46′	10747	10	20.1	1–35	175438	146868.28	23258	2.16
Lake Hope	N	28°24′	139°19′	3164	7	18.7	2–27	11753	4287.87	7565	2.39
Lake Mumbleberry	N	24°29′	138°39′	1292	4	19.8	19–22	52997	17673.74	45545	35.17
Macquarie Marshes[B]	N	30°34′	147°33′	8480	17	15.3	8–26	12975	4873.23	5600	0.66

[A]No. (median) of waterbirds ha^{-1}.
[B]Northern part of the Macquarie Marshes.

Maddock 2000), except for cryptic or rare species (Table 1). But most information is based on presence or absence data (see Blakers *et al.* 1984). At the wetland level, distribution of waterbird species also varies (Halse *et al.* 1993*a*; Kingsford and Porter 1994) and mobile waterbirds may use the same or different wetlands at different times, making investigations of specific distribution difficult.

Abundance

Many parts of the continent support large numbers of waterbirds at different times. For example, floodplains in the Alligator Rivers Region of the Northern Territory (Bayliss and Yeomans 1990) can have more than 2.5 million waterbirds (Morton *et al.* 1990*a*, 1990*b*, 1993*a*, 1993*b*, 1993*c*) and up to one million or more waterbirds may occur during large floods on the Cooper Creek system (Kingsford *et al.* 1999*a*). Individual inland wetlands also often support large numbers of waterbirds (Table 2) (Kingsford 1995; Halse *et al.* 1998; Kingsford and Halse 1999) but their importance as habitat is often unpredictable. Studies of waterbird numbers over long periods on individual or a series of wetlands in Australia have consistently shown considerable temporal and spatial variation (Briggs 1977*a*; Gosper *et al.* 1983; Woodall 1985; Kingsford and Porter 1994; Halse *et al.* 1998; Roshier *et al.* 2001*a*). Frith's (1959*b*) statement that it 'has frequently been observed that the numbers of wild ducks in different localities usually vary greatly from year to year …' remains as true today as it did more than 40 years ago.

This model contrasts with the regular seasonal cycles, low variability in wetland availability and relatively strong philopatry of waterfowl (Anderson *et al.* 1992; Haffner 1997; Robertson and Cooke 1999) that make abundance of waterbirds reasonably predictable in the Northern Hemisphere. The spatial and temporal availability of Australian wetland habitat (Roshier *et al.* 2001*b*) and available food resources are probably the most important factors determining the abundance of waterbirds (Roshier *et al.*, in press). It is not surprising that waterbird abundance in Australia is generally unpredictable and interpretation of such data difficult (Briggs and Holmes 1988; Norman and Nicholls 1991; Kingsford 1996; Kingsford *et al.*1999*b*). Information on the abundance of species is categorised as 'good' in three of the more conspicuous orders (Table 1) on the basis of long-term surveys (Braithwaite *et al.* 1986; Briggs and Holmes 1988; Bayliss and Yeomans 1990; Morton *et al.* 1990*a*, 1990*b*; Norman and Nicholls 1991; Briggs *et al.* 1993; Kingsford *et al.* 1994*a*, 1999*b*; Halse *et al.* 1998).

There is one reasonably clear pattern at the regional or individual wetland scale: low numbers of waterbirds usually occur after flooding, when habitat is extensive and waterbird numbers have not increased by immigration or breeding. In contrast, there may be large concentrations of waterbirds during dry times, when birds are forced to move and concentrate on the remaining, more permanent wetlands, often in coastal areas (White 1987; Morton *et al.* 1990*a*, 1990*b*; Norman and Nicholls 1991; Maher and Braithwaite 1992; White 1993; Kingsford 1996).

Status

One waterbird species, the White Gallinule, *Porphyrio albus* (Lord Howe Island), and two subspecies, Lewin's Rail (south-western Western Australia) and Buff-banded Rail (Macquarie Island), are presumed extinct (Garnett and Crowley 2000). Another two species, the Australasian Bittern and Painted Snipe, and two subspecies, the Buff-Banded Rail (Cocos Island) and the Cape Barren Goose (south-western Australia) are considered vulnerable (Garnett and Crowley 2000; Appendix 1). Although low, Cape Barren Geese numbers in south-western Australia are stable (Halse *et al.* 1995). Two species, the Little Bittern and the Cotton Pygmy-goose, are considered near threatened at a national level (Garnett and Crowley 2000, Appendix 1) and a further 19 species of waterbirds are listed by one of the States or Territories as endangered, vulnerable or rare (Table 1, Appendix 1). Some other species appear to have declined in numbers in eastern Australia in the 50 years preceding Cowan's (1973) review, and subsequently, but the pattern for most species is not clear (Kingsford *et al.* 1999*b*, 2000). Nevertheless, numbers and composition have declined on individual wetlands (Briggs *et al.* 1994; Kingsford and Thomas 1995) and the ranges of some species have contracted (e.g. Magpie Goose, Cotton Pygmy-goose, Green Pygmy-goose, Black-necked Stork, Brolga). The causes of contractions are not well understood. Species in low numbers and restricted range are of most concern for conservation but there is usually poor information to determine whether populations are increasing or decreasing. Breeding populations of some species have also declined (e.g. Intermediate Egrets declined in coastal New South Wales by 98% between 1988 and 1998: Maddock 2000) while inland the impact of river regulation has affected breeding in this and other colonially nesting species (Kingsford and Johnson 1998; Leslie 2001). In contrast, a few waterbirds have increased in range and numbers (e.g. Australian White Ibis, Australian Wood Duck: Blakers *et al.* 1984) with the creation of new habitat and enhanced (sometimes artificial) food sources. Silver Gulls have increased in numbers around cities (Smith and Carlile 1992) and Cattle Egrets have benefited from the expansion of grazing lands (Maddock and Geering 1994; Maddock 2000), often into floodplains. Australian Wood Ducks have exploited newly created farm dams (Kingsford 1992), with associated improved pastures, and moved recently onto the urban lawns, golf courses and roadsides in Australia.

Movements

Movements of waterbirds reflect the predictablity of wetlands, food resources and breeding and moulting needs. Many Northern Hemisphere species, particularly waterfowl and high-latitude waders, make predictable migrations of considerable distances from breeding grounds to wintering areas (Gauthreaux 1982; Bellrose and Trudeau 1988; Rohwer and Anderson 1988; Hestbeck *et al.* 1991) whereas movements of Australian waterbirds are generally more complex and unpredictable. Thus early naturalists and observers suggested that Australian waterbirds, mainly waterfowl, moved into Victoria from elsewhere (e.g. Norman and Young 1980). Subsequently, others proposed models for movements of waterfowl from inland sites to the coast each summer (Downes 1954; Morgan 1954; Anon. 1960; Frith 1982; Gentilli and Beckle1983) and from north to south in the south-east (e.g. Pacific Black Duck and Australian Shelduck: Frith 1963; McKean and Braithwaite 1976). Many thousands of game species of waterfowl, banded in the 1950–70s, provided the first real evidence for considerable variation in movement of waterbirds in Australia (Frith 1959*c*, 1962, 1963, 1977; Norman 1970, 1971*a*, 1971*b*, 1979). Recoveries, usually from hunters, were multi-directional, with no clear obvious causal factors, but, with observations of influxes of waterfowl and a perception of regularity in the wetland wetting and drying cycles**,** aided model development. There was some inherent bias since hunting occurred predominantly in the south-east and south-west (Briggs *et al.* 1985*a*; Halse *et al.* 1993*b*), there was poor banding coverage in the inland (but see Lawler *et al.* 1993) and the regularity of major flooding was patently illusory. Waterbird counts on particular wetlands (e.g. Gosper *et al.* 1983; Woodall 1985), resightings of marked birds (Jessop and Minton 1995; Geering *et al.* 1998) and studies of spatial and temporal variability of wetlands (Kingsford *et al.* 2001; Roshier *et al.* 2001*a*, 2001*b*) have improved understanding of movements of Australian waterbirds.

Movements vary from predictable to highly variable or nomadic. The most regular movements of Australian waterbirds are those of wading species that migrate between Australia and the Northern Hemisphere. They arrive in spring and fly down the coast or central Australia, returning to breed in the Northern Hemisphere in autumn (Thomas 1970; Lane 1987; Tulp *et al.* 1994). Their movements may be less predictable when they follow the temporary inland wetlands (Kingsford and Porter 1993; Kingsford *et al.* 1999*a*). A few individuals remain in Australia, adding to the complexity (Lane 1987). Movements of many tropical waterbirds are also predictable, driven by the seasonal wet and dry: they spread out onto inundated floodplains during the wet season and then retreat to remnant wetlands in the dry season (Morton *et al.* 1990*a*). Availability of food and nesting sites influence such movements (Bayliss and Yeomans 1990; Morton *et al.* 1990*a*, 1990*b*, 1993*a*, 1993*b*). Fluctuations in waterbird numbers in nearby Papua New Guinea reflect regular movement from tropical Australia (Halse *et al.* 1996; Geering *et al.* 1998), presumably also in response to the relative availability of habitat and food resources.

Along the east coast of Australia some waterbirds respond to predictable seasonal factors. Cattle Egrets move south during the winter from their normal breeding sites (Chalmers 1972; Maddock 1990, McKilligan *et al.* 1993; Maddock and Geering 1993; Maddock 2000; see Fig. 1) using favourable winds around low- and high-pressure weather systems (Maddock and Bridgman 1992; Bridgman *et al.* 1997, 1998). Other waterbirds (Pacific Black Duck, Black Swan, Purple Swamphen, Dusky Moorhen and Comb-crested Jacana) also move into coastal regions during the spring (Gosper *et al.* 1983). Such regularity is mediated by rainfall events within the species' ranges.

In contrast, there is little semblance of predictability in waterbird movements into or out of inland Australia (Frith 1982; Briggs 1992), like most desert birds (Davies 1984). Irregular climate and consequent flooding cycles create large areas of wetland habitat anywhere (Chapman and Lane 1997; Kingsford and Halse 1999; Roshier *et al.* 2001*a*, 2001*b*, in press), resulting in considerable variation in local or regional numbers. Floods on inland rivers produce 'boom' conditions (Kingsford *et al.* 1999*a*), resulting in massively increased habitat (Kingsford *et al.* 2001) and attracting waterbirds from the south-eastern part of the continent (Matheson 1978). While shallow waters on floodplains rarely last more than a few months, they can be extremely productive for all feeding groups of waterbirds (e.g. piscivores, herbivores and invertebrate feeders), often resulting in breeding (Lawler and Briggs 1991; Kingsford and Porter 1993; Kingsford *et al.* 1999*a*).

Dry periods inevitably follow extensive inland flooding, forcing waterbirds to move. Banding studies and resighting of patagially tagged birds have demonstrated that this dispersal can be at a continental scale, often exceeding 1000 km. With numbers often increased by recruits following breeding, movement can be rapid (Frith 1957*a*; Llewellyn 1983) to nearby (Kingsford 1996) or more distant, semi-permanent or permanent wetland habitat. For example, large colonies of ibis and egrets in the Macquarie Marshes disperse as the wetland dries to coastal locations and the tropics (Carrick 1962; McKilligan 1975; Geering *et al.* 1998). Similarly, Australian Pelicans were rare around Brisbane when Lake Eyre in central Australia was full in 1974–76 but became numerous again in 1978–79 when it dried (Woodall 1985) and similarly in northern Australia (Draffan *et al.* 1983). Black-tailed Native-hens rapidly built up in numbers in south-eastern Australia after the wet years inland in 1973 and 1974 (Matheson 1978). Sometimes waterbird movement occurs between landmasses. For example, Pacific Black Duck dispersed from Victoria to New Zealand (Norman 1973) and Grey Teal banded in Victoria reached Western Australia, New Guinea and New Zealand (F. I. Norman, unpublished data). Influxes of Grey Teal to New Zealand from Australia also sometimes occur after dry periods in Australia (Mills 1976; Frith 1982). Australian Pelicans banded on the Coorong, South Australia, have moved to Papua New Guinea (Marchant and Higgins 1990). The extent of movements from inland habitats may depend on the unpredictable availability of intervening wetlands (Roshier *et al.* 2001*a*, 2001*b*, in press) and so may not have a defined direction.

Movement patterns vary among Australian waterbirds, not only in time but in extent, reflecting differing use of wet-

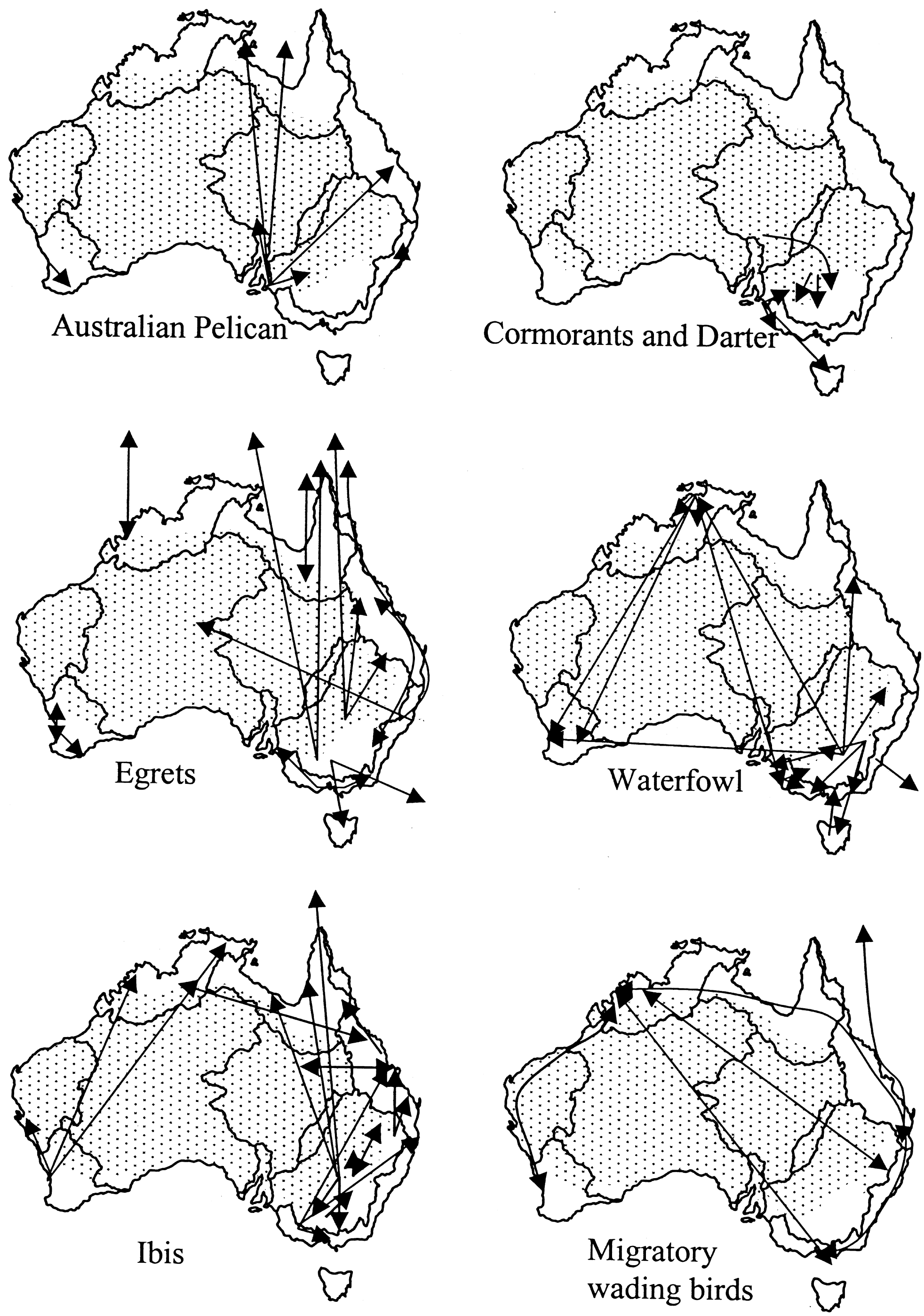

Fig. 1. Movement patterns for waterbird groups for which data are available, based on banding studies and patagial tagging (Frith 1957a, 1963; Carrick 1962; McKilligan 1975; Llewellyn 1983; Marchant and Higgins 1990; Geering *et al.* 1998). Dotted area signifies arid Australia (<500 mm annual rainfall) with the continent divided into 12 main river basins (see Kingsford 2000*a*).

lands (Gosper *et al.* 1983) and perhaps dispersive capabilities. While there is some understanding of this, relatively little is known about what causes the differences between and within species. In general, species that exploit temporary aquatic habitats move further than more sedentary species. With comparative banding and recovery effort, 50% of recoveries of Pacific Black Duck and Australian Shelduck, 40% of Australian Wood Duck and 22% of Hardhead recoveries were within 100 km of banding sites in Victoria (Norman 1970, 1971*a*, 1971*b* 1973). About 19% of Hardhead recoveries were further than 500 km, compared with 3% and 8% for Australian Wood Duck and Australian Shelduck respectively. Similarly, recoveries of banded Grey Teal were more distant than those of Pacific Black Duck (Frith 1959*c*, 1963) and Great Cormorants moved further than either of the species of small cormorant (Llewellyn 1983). There is also considerable variability in movement patterns within species (Frith 1959*c*). Band recoveries decrease with distance from the banding sites (Frith 1959*c*, 1962, 1963; Norman 1970*a*, 1970*b*, 1971, 1979; Llewellyn 1983) and movement patterns may vary with age in ibis, with young ibis moving further than older birds (McKilligan 1975).

For some waterbird species, breeding habitat may be limited and its availability and extent govern movements. For example, Intermediate Egrets regularly move to and from the Macquarie Marshes (R. Jones, personal communication) and female Chestnut Teal often return to breed each year, in the same or nearby artificial nest boxes in Victoria (F. I. Norman, unpublished data). For other species, availability of food governs movements; for example, Cape Barren Geese disperse from breeding islands to nearby mainland feeding areas when moist vegetation dries and remain until moist vegetation reappears after rain (Dorward *et al.* 1980). Other examples of predictable movements relate to moulting requirements. In south-eastern Australia, Australian Shelducks move from breeding areas to large semi-permanent or permanent wetlands and Black Swans to a marine embayment to moult each year (McKean and Braithwaite 1976; Norman 1983). Other physiological factors may also regulate movements. Some species, such as Black Swan, Grey or Chestnut Teal, move from freshwater habitats to forage in tidally influenced marine areas (Lavery 1972*a*; Norman 1983) but they may need access to fresh water (e.g. Baudinette *et al.* 1982) because their nasal glands are not sufficiently acclimated to release accumulated salt.

Current knowledge of movement patterns for many species remains rudimentary, particularly for those using habitats in inland Australia. For the six orders of waterbirds considered, knowledge of movements was categorised as ‘moderate’ for Anseriformes and Ciconiiformes, but ‘poor’ for the other orders (Fig. 1, Table 1). Some progress is underway, with demonstrations of wetland connectivity across inland Australia (Roshier *et al.* 2001*a*, 2001*b*, in press) and long-term counts on individual wetlands. Without indices of wetland connectivity and relationship for different waterbird species, the timing and extent of movements will remain unknown. Some advances will be achieved with satellite tracking movements of substantial numbers of individuals but such studies will inevitably be biased by costs and small sample size (see Bridgman *et al.* 1997).

In summary, we propose a general model for the movements of waterbirds in Australia. Waterbird movements in Australia are dynamic, with habitat, food and breeding requirements determining whether waterbirds move, when they do and how far. These factors may act at local (Kingsford 1996), regional or continental scales (Roshier *et al.* 2001*a*, 2001*b*, in press). Since wetlands can dry or flood at any time within a species’ range, particularly inland, different proportions of the population of a species (e.g. Grey Teal) may be affected at different temporal and spatial scales. No doubt, wetland connectivity provides the means for dispersal to produce continental-wide movements in some species (McKilligan 1975; Roshier *et al.* 2001*a*).

Mortality and survival

As with all species, the future of populations of Australian waterbird species depends on a balance between recruitment and mortality. Hunting is a most obvious mortality factor and there have been numerous estimates of survival based on calculations of mortality of game waterfowl, using band returns (Frith 1963; Norman 1970*a*, 1971; Briggs *et al.* 1983; Halse *et al.* 1993*b*). Most studies have shown that waterfowl seldom survive more than about three years, although they may live more than 10 years in captivity. Separating hunting mortality from other forms of survival is difficult and little information exists regarding its additive or compensatory nature (see below — Threatening Processes). In other waterbirds, mortality rates have only been estimated for Cattle Egrets where predation and accidental death were the major causes of mortality; they have a mean life expectancy of 2.6 years, although one individual lived for 11.1 years (McKilligan *et al.* 1993).

Diseases are a significant cause of mortality in populations of waterbirds outside Australia (Brand *et al.* 1988; Aguirre *et al.* 1991; Wobeser 1992) but details of their impact are not well known in Australia, probably because of limited research effort. Large numbers of waterbirds sometimes do die (e.g. on Lake Cowal) although the cause of these deaths has seldom been determined. Botulism is reasonably common in Australia, causing high mortality of waterbirds at a local level (Woodall 1982; Galvin *et al.* 1985; Harrigan 1987), although there has been relatively little research on the extent of its impact in Australia and relatively little effort or facilities for investigating its impact (Harrigan 1987). The protozoan *Giardia* naturally occurs in some Straw-necked Ibis (Forshaw *et al.* 1992; McRoberts *et al.* 1996), and *Haemaproteus nettionis* and *Plasmodium relictum* occurred at low levels in waterfowl (Bennett *et al.* 1977) but their effects are not known.

Moulting

Renewal of feathers in waterbirds is an important stage in life cycles, generally timed not to conflict with breeding or migration (Brooke and Birkhead 1991). Most information about moult in waterfowl comes from Northern Hemisphere studies that indicate relatively little variability among the Anatinae (Hohman *et al.* 1992). In these waterfowl, predictable moulting patterns, usually after dispersal from breeding areas or during parental care, reflect predictable seasons (Brooke and Birkhead 1991; Hohman *et al.* 1992; Hobson *et al.* 2000). As with other facets of life cycles, there is scarce information on moulting in Australian waterbirds (Table 1); although the sequences may be similar to counterparts elsewhere, the timing is highly variable.

Most Australian waterbirds renew their primary (wing) feathers irregularly (Marchant and Higgins 1990) although waterfowl (except Magpie Geese: Johnsgard 1978), grebes and Eurasian Coot shed them simultaneously and, in Australia, become flightless for 2–5 weeks (Lavery 1972*b*; Braithwaite 1981*a*). Pacific Black Duck usually moult wing feathers in late summer but the timing is more variable in Grey Teal (Braithwaite 1976*b*). Some ducks may moult primary feathers when caring for their young (Lavery 1972*b*) or when reproductively active (Braithwaite 1976*a*, 1981*a*), unlike their related species. Some individuals may postpone their annual wing moult to conserve energy during dry periods (Lavery 1972*b*; Kingsford 1986*a*), as do some species in South America and on the Falkland Islands (Summers 1983; Summers and Mantin 1985).

Two body moults each year are common in waterfowl, a basic or eclipse plumage and an alternate plumage, but there is probably considerable variability. Usually the basic plumage is dull whereas the latter, timed before the breeding season, tends to have more elaborate colouration (Hohman *et al.* 1992). Australian waterfowl exhibit similar plumages (Kingsford 1986*a*; Marchant and Higgins 1990) and many other Australian waterbirds have breeding and non-breeding plumages (Marchant and Higgins 1990) but relatively little is known of moulting patterns (Table 1). Elaborate feathers develop on the necks and heads of some species and are used in courtship (e.g. Royal Spoonbill, Intermediate Egret: Marchant and Higgins 1990).

Feeding ecology

Australian waterbirds may be considered herbivores (e.g. Black Swan, Australian Wood Duck), invertebrate feeders (e.g. Black-winged Stilt, Pink-eared Duck), piscivores (e.g. Australian Pelicans) or omnivores that feed on both plant and animal material (e.g. Chestnut Teal**:** Norman and Mumford 1982). The basic diets of most waterbirds are known (summaries provided in Barker and Vestjens 1989; Marchant and Higgins 1990, 1993, 1996) and categorised as 'good' for four orders of waterbirds but only 'moderate' for the other two (Table 1); nevertheless, detailed understanding of feeding ecology for most Australian waterbirds remains poor.

Morphological, behavioural and physiological factors and availability of food impose constraints on what species of waterbird use a wetland but various species can occupy the same wetland and use different resources (Norman *et al.* 1979). For example, Australian Pelicans have specialised bills and flock behaviour for feeding on fish and Pink-eared Ducks have highly specialised spatulate bills that sift plankton (Marchant and Higgins 1990). Diets can also reflect differences in bill size, as between spoonbill species (Vestjens 1975*a*) or male and female Whiskered Terns (Dostine and Morton 1989*a*). Closely related species of waterbirds may use different habitats but consume the same or different prey (Carrick 1959; Miller 1979; Dostine and Morton 1988). Thus chicks of Cattle and Intermediate Egrets were fed different prey because adults used different foraging habitats (Baxter and Fairweather 1989). Diet requirements affect behaviour and use of habitat. Thus herbivorous waterbirds have to feed for extended periods (Kingsford 1986*b*; Briggs 1990) because of the indigestibility of fibrous plant material (Marriot and Forbes 1970; Dawson *et al.* 2000).

The composition and abundance of waterbird communities on a wetland often reflects the availability of food (Kingsford and Porter 1994; McDougall and Timms 2001) and so herbivorous species damage rice-growing areas (Frith 1957b) and fish-eating birds can collect around fish farms. Food items are usually consumed in relation to their availability, varying with time and location. Hence the proportions of fish and crustaceans in diets of cormorants and darters change (Vestjens 1975*a*; Miller 1979; Dostine and Morton 1988, 1989*b*) and the considerable spatial and temporal variation in cormorant abundance on particular semi-permanent wetlands presumably reflects food availability (Dorfman and Kingsford 2001). Herbivores and invertebrate feeders also eat what is available (Dostine and Morton 1989*c*; Kingsford 1989*a*) and the feeding area for a grazing species, like the Australian Wood Duck, may be bordering pastures (Kingsford 1986*b*) rather than the wetland itself.

This simplistic assertion that diet reflects availability is overlaid with the complexity of differences in availability of foods to one or more species, reflecting wetting and drying cycles of wetlands in their range. Abundant food for waterbirds usually coincides with flooding patterns or rainfall, producing wetland habitat (Maher 1984; Maher and Carpenter 1984; Briggs *et al.* 1985*b*; Crome and Carpenter 1988; Kingsford 1989*b*; Boulton and Lloyd 1992; Puckridge *et al.* 2000). In contrast, food abundance is low during dry periods (Kingsford 1989*a*; Whitehead and Saalfeld 2000) and waterbirds may take whatever foods are available, disperse or die. For example, about 200 Black Swans died when aquatic macrophytes declined at Lake Altibouka in arid

Australia (Kingsford and Porter, unpublished data). Australian Pelicans also sometimes stay and die (Barnard 1927), demonstrating the inevitable energetic conflict between moving to another habitat or remaining where decreasing resources may become abundant. During dry periods, diet may even switch from herbivory to insectivory (e.g. Australian Wood Ducks: Kingsford 1989*a*) or waterbirds may move from fresh to saline areas, changing their diet (e.g. Chestnut Teal: Norman 1983; Grey Teal: Lavery 1972*a*).

Interactions between waterbirds' diet and breeding energetics are critical to understanding population processes, including survival, but details for Australian species are poor. Factors governing the presence and abundance of dietary items are equally important but, similarly, are poorly understood even though these may drive the distribution and abundance of waterbirds. For example, the patchy occurrence of Pink-eared Duck, an obligatory plankton feeder, probably reflects the temporary abundance of major food taxa in temporary or permanent wetlands (Frith 1957*a*; Kingsford 1996). For some species, prey may be more accessible in shallow temporary wetlands than deep waters of permanent wetlands (e.g. Black-necked Stork: Dorfman *et al.* 2001). Where food availability is most variable, waterbirds need to balance the increasing risk that a particular food source may be depleted with the increased benefit of its future availability. Migratory waders must change their diet to suit differences in prey composition and availability at an international scale while for species with a continental range, the availability of food varies correspondingly. In summary, Australian waterbirds are probably no different to counterparts elsewhere in their response to food availability but they may be forced to disperse more extensively to capitalise on temporary but productive food sources.

Reproductive ecology

The reproductive ecology of Australian waterbirds is similar to that of waterbirds elsewhere, except for considerable flexibility in the timing and extent of breeding periods. Many Australian waterbirds can breed at any time of the year, contrasting markedly with the more restricted pattern of their Northern Hemisphere counterparts, where breeding is highly structured and seasonal, and responsive to photoperiod (Murton and Kear 1973; Batt *et al.* 1992). Light was discounted early as a stimulus for breeding in Australian waterbirds because the erratic breeding pattern is much more closely tied to rainfall 'and its effects on the breeding habitat and food' (Frith 1982). Factors thought to stimulate breeding in Australian waterbirds generated some early debate but this primarily related to differing emphases about food availability (Frith 1982; Crome 1986; Fullagar *et al.* 1988).

For most Australian waterbirds, breeding occurs when food resources are approaching, or are at, a maximum (Carrick 1962; Braithwaite and Frith 1969; McKilligan 1975, 1984; Miller 1980; Braithwaite 1982; Llewellyn 1983; Crome 1986; Kingsford 1989*b*; Maddock and Baxter 1991; Whitehead and Saalfeld 2000). Plentiful food allows waterbirds to build up body reserves before breeding (Briggs 1991*a*, 1991*b*; McKilligan 2001), with egg-laying being primarily dependent on available nutrients (Braithwaite 1977; Miller 1980; Briggs 1991*b*). For example, the availability of nutritious and abundant vegetation determines when herbivorous waterbirds such as Black Swans and Australian Wood Ducks breed (Braithwaite 1976*a*, 1982; Kingsford 1989*b*). Thus, female Australian Wood Ducks and Chestnut Teal put on body fat during times of high food availability and convert this into reproductive effort (Norman and Hurley 1984; Briggs 1991*a*), while changes in food availability may account for seasonal differences in clutch size of Black Swans (e.g. Braithwaite 1977). Studies of how breeding varies with climate in different parts of Australia have been critical to current understanding of reproductive ecology.

In Australia's tropics, predictable breeding coincides with the summer wet season (Lavery 1970*b*; McKilligan 1975; Frith 1982; Whitehead and Saalfeld 2000; Chatto 2000; Maddock 2000) whereas, in southern temperate areas, breeding generally occurs in the spring, after winter rains have filled wetlands and increasing temperatures (and, incidentally, day length) lead to increased food availability (McKilligan 1975; Braithwaite 1976*a*; Frith 1982; Halse and Jaensch 1989; Kingsford 1989*b*). In contrast, breeding may be initiated at any time in the arid zone (Carrick 1962; Braithwaite and Frith 1969), following flooding (McKilligan 1975; Lawler and Briggs 1991; Maher and Braithwaite 1992; Kingsford and Johnson 1998; Ley 1998; Briggs and Thornton 1999). Breeding may not occur for decades. For example, the endorheic Lake Eyre receives water from Cooper Creek, one of its major river systems, only about every 12.5 years, while Lake Blanche, where many species breed, is supplied by Strzelecki Creek and fills only every 14 years (Kingsford *et al.* 1999*a*).

Rainfall and subsequent flooding affect timing and duration of reproductive effort, and its success, among and within waterbird species. Some Australian waterbirds breed after heavy rains (Lavery 1970*b*; Maddock and Baxter 1991; McKilligan 2001). Thus, egret colonies re-established on the north coast of New South Wales, when heavy rainfall followed a dry period (Geering 1993) and Australian Wood Ducks bred in autumn and spring with sufficient rainfall (Kingsford 1989*b*). Wetlands fill, liberating nutrients that allow rapid increases in productivity, ultimately providing food that may initiate and support breeding. At Lake Yamma Yamma, on Cooper Creek in central Australia, for example, fish biomass increased from 7 t during dry periods in remnant waterholes to 13000 t during the 1990 flood (S. Bunn and P. Davies, personal communication), stimulating about 20000 Australian Pelicans to establish a colony.

In contrast, prolonged dry periods may stop or extensively modify breeding of waterbirds. In dry years, waterbirds breed later, produce fewer clutches and smaller eggs, have higher nest densities and lower reproductive success, and there is increased intraspecific nest parasitism (e.g. Magpie Goose: Whitehead and Saalfeld 2000; Australian Wood Ducks: Kingsford 1989*b*; Briggs 1991*c*; tropical waterfowl: Lavery 1970*b*; Great, Little and Intermediate Egrets: Maddock 1986; Straw-necked Ibis and Intermediate Egrets: Kingsford and Johnson 1998; Kingsford and Auld, unpublished data). Pacific Black Duck laid during a dry period but no young survived (Fullagar *et al.* 1988) and Little Cormorants had reduced sperm counts and did not lay in a dry year (Miller 1980). If habitat availability or food resources are not sustained, breeding events fail (e.g. Black Swans: Braithwaite 1982; Australian Pelicans: Llewellyn 1983; Kingsford and Porter 1993) or their success is reduced by predation when nests become accessible as a result of lowered water levels (Australian Pelicans: Vestjens 1977). Similarly, Straw-necked Ibis abandoned their almost fledged chicks on Lake Altiboulka, following rapid recession of a natural flood. Although proximate factors for such abandonment are probably associated with falling water levels, ultimate factors are probably related to food availability. A bizarre example illustrates how there can be sequential breeding related to food availability. Nesting of Australian Pelicans on Lake Wyara in south-western Queensland began and partly failed, leaving some dead and starving chicks. Black Swans then nested, using dead pelican chicks as nesting material (Kingsford, unpublished). Breeding by the Australian Pelicans probably coincided with high levels of fish populations while Black Swans nested later as the water cleared and aquatic macrophytes became abundant.

Apart from abundant food, waterbirds also require suitable nest sites for breeding which may be specialised (Marchant and Higgins 1990, 1993, 1996). Many Australian waterfowl are obligate nesters in tree hollows (Frith 1982), breeding on or near wetlands with trees of appropriate age to provide such hollows (e.g. Australian Wood Duck: Kingsford 1992). For many herons, egrets, ibises and bitterns, dense vegetation is essential for breeding (Frith 1982; Marchant and Higgins 1990) and such areas are confined to relatively few wetlands around Australia (McKilligan 1975; Cowling and Lowe 1981; Marchant and Higgins 1990; Baxter 1994; Kingsford and Johnson 1998; Chatto 2000; Leslie 2001). Other species breed on islands, only provided by some lakes (e.g. Banded Stilt: Burbidge and Fuller 1982; Australian Pelicans, Silver Gulls, Caspian and Gull-billed Terns: Waterman and Read 1992; Kingsford and Porter 1993, 1994; Kingsford *et al.* 1999*a*). Many breeding sites (islands and densely vegetated swamps) are used again by individual colonially breeding waterbirds (Llewelyn 1983; Maddock and Geering 1993; McKilligan *et al.* 1993; Geering *et al.* 1998) though not always (Maddock and Geering 1993; Baxter 1994).

Basic information about reproductive ecology of many waterbird species is known (Marchant and Higgins 1990, 1993, 1996) but is categorised as only 'moderate' for two orders and 'poor' for the other four, particularly for cryptic species (Halse and Jaensch 1989; Marchant and Higgins 1990, 1993, 1996) (Table 1). But detailed information is confined to only a few species (Magpie Geese: Whitehead and Tschirner 1991*a*; Whitehead 1998, 1999; Whitehead and Saalfeld 2000; Black Swans: Braithwaite 1977, 1981*a*, 1981*b*, 1982; Chestnut Teal: Norman 1982; Norman and Mumford 1982; Norman and Hurley 1984; Norman and McKinney 1987; Norman and Brown 1988; Australian Shelduck: Riggert 1977; Australian Wood Duck: Kingsford 1989*a*, 1989*b*, 1990*a*, 1990*b*; Briggs 1991*a*, 1991*b*, 1991*c*; some cormorants: Norman 1974; Miller 1979, 1980; ibises: Carrick 1962; McKilligan 1975; Lowe 1983; egrets: Baxter 1994; Maddock 1984, 2000). These studies have variously identified different roles of males and females during breeding, body condition of the sexes, incubation periods, sibling rivalry, egg sizes, egg laying sequences, intraspecific parasitism, clutch sizes, renesting attempts, within season variations and reproductive success.

In summary, the breeding ecology of most species of waterbirds in Australia exhibits a plasticity reflective of spatial and temporal availability of habitat and food resources. This is true of waterbirds in the rest of the world but food distribution and abundance is probably more seasonally predictable elsewhere than on the Australian continent. Further weight comes from observations that some captive Australian waterfowl in the Northern Hemisphere conform to the model of highly structured breeding while others can breed at any time (e.g. Murton and Kear 1973, 1976). To reinforce this, some observations highlight the capacity for a rapid breeding response in Australian waterbirds: Grey Teal may engage in reproductive behavioural displays after a single heavy downpour of rain (Braithwaite 1976*b*). There is considerable variation in gonadal state of Australian waterfowl (Frith 1959*d*; Braithwaite and Frith 1969) to the point where the Pink-eared Duck, the extreme nomadic species (Frith 1982), is always capable of breeding (Braithwaite 1969). Straw-necked Ibis move to breeding areas after rain (McKilligan 1975) and Rufous Night Herons can even breed while in juvenile plumage (Braithwaite and Clayton 1976). Extended favourable periods may also allow waterbirds to produce more than one or two clutches in a season (Braithwaite 1981*a*; Fullagar *et al.* 1988), leading to major increases in waterbird numbers (Cowan 1973).

Behaviour

The vagaries of the continent's climate have shaped patterns of abundance, movements and reproductive ecology. Here we examine its effect on comfort, feeding, courtship, parental care and other behaviours. Knowledge of behaviours of most groups of Australian waterbirds is categorised as 'moderate' for three orders, 'good' in Anseriformes, but 'poor' for the Gruiformes and Charadriformes (Table 1).

Comfort behaviours (sensu McKinney 1965) are reasonably stereotypical in waterfowl and appear to be similar for Australian species (Marchant and Higgins 1990). Johnsgard (1965) and Frith (1982) summarised existing information about courtship and mating behaviour for waterfowl that was later updated for all waterbirds in Marchant and Higgins (1990, 1993, 1996). Observations of captive waterfowl have provided good information about stereotyped behaviour such as courtship behaviour (Johnsgard 1965; Fullagar and Carbonell 1986) with further details from studies in the wild (Vestjens 1975*b*, 1977; Braithwaite 1981*b*; Kingsford 1986*b*). Courtship displays of Australian waterbirds also resemble those of waterbirds elsewhere (Johnsgard 1965; Marchant and Higgins 1990, 1993, 1996; McKinney 1992) but their mating systems exhibit more variability. Polygynous mating systems exist for some Australian species, such as the Tasmanian Native-hen (Gibbs *et al.* 1994) and Purple Swamphen (Craig 1979, 1980) and Magpie Geese have more than one male or female involved in nesting (Whitehead 1999). Most Australian waterbirds are apparently monogamous but there is considerable variation among species. Some species are seasonally monogamous while others show more extended pair bonding: promiscuous mating systems (Musk Duck) and extra-pair copulations are additional reproductive strategies used by local species (McKinney *et al.* 1983; Marchant and Higgins 1990, 1993, 1996). Plasticity of pair bonds and the extent of parental care of Australian waterfowl, compared with similar taxa elsewhere (Norman and McKinney 1987; Kingsford 1990*a*, 1990*b*; Oring and Sayler 1992), may reflect the influence of the continent's ecology. Long-term pair bonds are more common in Australian dabbling ducks than in their Northern Hemisphere counterparts (Fullagar *et al.* 1988), and Australian Wood Ducks have long-term pair bonds and biparental care (Kingsford 1990*a*, 1990*b*), unlike close relatives in the Northern Hemisphere (Kingsford 1986*b*). This strategy may be particularly important in exploiting new and variable habitats where a long period of courtship behaviour may reduce successful reproduction (Fullagar *et al.* 1988). Australia also has the only two waterfowl species that feed their young (Musk Duck and Magpie Goose: Oring and Sayler 1992)

Relatively little is known about the activity budgets of Australian waterbirds apart from diurnal behaviour of some waterfowl species (Norman *et al.* 1979; Kingsford 1986*b*; Briggs 1990). These studies showed that waterbirds divided up their activities between loafing, swimming, feeding, comfort and locomotion (see also McKinney 1965). There appears to be nothing unusual about activity patterns of Australian waterbirds compared with counterparts elsewhere. In summary, there is some evidence that Australian waterfowl have mating systems that reflect the variability of the continent but otherwise their behaviour appears reasonably similar to species elsewhere.

Threatening processes

Major threatening processes affect freshwater ecosystems around the world (Allan and Flecker 1993) and offer a convenient framework for reviewing the threats to waterbird habitats and populations in Australia. These processes include habitat loss and degradation, and the potential problems caused by the spread of exotic species, over-exploitation, pollution and climate change.

Habitat loss and degradation

The loss and degradation of habitat is the greatest threat to the long-term survival of waterbirds. Irreversible loss of wetland continues in Australia at an alarming rate (Finlayson and Rea 1999), often driven by economic imperatives and government decisions (Kingsford 1999*a*). About 50% of floodplain wetlands have probably disappeared from the Murray–Darling Basin as a result of water resource development, including diversions for more intensive agriculture (Kingsford 2000*a*). Many wetlands along the eastern, south-eastern and south-western coasts have been drained for agriculture, urbanisation or flood mitigation (Riggert 1966; Goodrick 1970; Corrick and Norman 1980; Norman and Corrick 1988; Halse 1989; Blackman *et al.* 1996; Davis and Froend 1999). Coastal flood mitigation on the tropical east coast has probably reduced the habitats of Black-necked Storks, Comb-crested Jacana (Braithwaite 1975; Briggs 1977*b*) and Hardhead (Frith 1982) and other species.

Prolonged flooding in some wetlands used as irrigation storages (Kingsford 2000*a*) has killed floodplain vegetation and affected waterbird communities; permanently flooded wetlands (e.g. Menindee Lakes) have little aquatic vegetation, their dead floodplain trees a reminder of past flooding regimes. Such flooding inevitably changes the diversity of waterbirds and the composition of breeding species. Egrets no longer breed in an impounded wetland because they need live trees (Briggs *et al.* 1994).

The storage of water in dams, and its subsequent diversion upstream, denies water to floodplain wetlands (Kingsford 2000*a*). The Macquarie Marshes, for example, have been reduced in area covered by flood water by at least 40–50%, with a consequent decrease in numbers of waterbirds and their diversity, and the frequency and extent of breeding of colonial waterbirds (Kingsford and Thomas 1995; Kingsford and Johnson 1998). Similar changes have affected waterbirds in the Barmah–Millewa forest on the Murray River (Leslie 2001) and are likely to be widespread (Kingsford 2000*a*) wherever major impoundments regulate rivers to divert water, reducing available wetland habitat for waterbirds. Numbers of nests of colonial waterbirds are positively related to areas of River Red Gum, *Eucalyptus camaldulensis*, flooded for at least four months (Briggs *et al.* 1997). Reduced flooding has inevitable consequences and even when birds breed, reducing flows can cause abandonment of nests (Carrick 1962). Such impacts were well recognised many years ago (Downes 1954; Frith 1974; Norman 1981) but until recently there has been relatively little imperative to mitigate them.

Other factors, symptomatic of anthropogenic impact on wetlands and rivers, may also affect the habitat of waterbirds. They include increasing levels of salinity (Murray–Darling Basin Ministerial Council 1999) and cyanobacterial blooms (Bowling and Baker 1996). Salinity can cause profound changes in aquatic fauna (Hart *et al.* 1990) and flora (Froend *et al.* 1987) and influence distribution and abundance of waterbirds (Halse 1987), but the impacts of cyanobacteria on waterbird habitat are not known. Water releases from major dams are often unseasonally cold and remain depressed for many hundreds of kilometres, affecting the food resources and habitat of waterbirds (Lugg 1999). Grazing by livestock changes aquatic vegetation (Robertson 1997; Jansen and Robertson 2001), and the cropping of cereals on arid-zone lakes as floods recede (Briggs and Jenkins 1997) have ecological impacts. Additionally, harvesting of trees on floodplains may also reduce breeding sites for hole-nesting species of waterfowl.

Spread of exotic species

Interactions between exotic species, other than humans, and Australian waterbirds are varied. The Mallard, *Anas platyrhynchos*, is the only alien species of duck currently established in Australia. Variants are common on the wetlands of parks in major capital cities and in rural towns, hybridising with Pacific Black Duck and posing a potentially serious problem for the genetic security of the local species. Restricted pairing and stable populations were considered to render the threat unimportant in Sydney (Braithwaite and Miller 1975). But, in southern South Australia, 3165 Pacific Black Duck, 1422 Mallards and 684 hybrids or feral ducks were counted on 484 wetlands, representing an increase in numbers and distribution since 1970 (Paton *et al.* 1992). Mallards occur on Norfolk Island and have even invaded subantarctic Macquarie Island and hydridised (Hermes *et al.* 1986; Norman 1987, 1990). The species could be spreading slowly from urban centres, without detection, and may prove to be a future intractable problem for wildlife authorities. Mallard have ably demonstrated invasive potential by colonising all of New Zealand, replacing Pacific Black Duck (Todd 1979).

European Carp, *Cyprinus carpio*, change the aquatic vegetation of wetlands and their water quality (Koehn *et al.* 2000) and may affect food or habitat quality for some waterbirds, as may other exotic fish species. Carp may also be a source of food for piscivores (Miller 1979) for a limited time before they grow too big. Similarly, exotic vegetation can change the habitat of waterbirds. Thus Para Grass, *Brachiaria mutica*, Olive Hymenachne, *Hymenachne amplexicaulis*, and Aleman, *Echinochloa polystachya*, Grasses were introduced into tropical wetlands as improved pasture for cattle (Rea and Storrs 1999). These alien species have reduced habitat availability and affected reproduction in Magpie Geese by reducing the production of seeds of native annual plants (Whitehead and Saalfeld 2000). The wattle *Mimosa pigra* has also invaded tropical wetlands and formed a thick cover across them (Cook *et al.* 1996), probably limiting areas in which waterbirds can breed and feed. Other examples of weeds include Alligator Weed, *Alternananthera philoxeroides*, at Barrenbox Swamp and Water Hyacinth, *Eichornia crassipes*, in the Gwydir wetlands and willows. The spread of alien flora through aquatic ecosystems is a major threatening process and its insidious nature has substantial potential to seriously modify habitats for local waterbirds.

Pigs, foxes, cats, dogs and dingos prey on waterbirds, particularly while breeding (e.g. ibis and Australian Pelicans**:** Vestjens 1977; Lowe 1983). The potentially serious Cane Toad, *Bufo marinus*, does not apparently affect most waterbirds (Covacevich and Archer 1975). During nesting, competition for nest sites with the introduced Common Starlings, *Sturnus vulgaris*, House Sparrows, *Passer domesticus*, Common Mynah, *Acridotheres tristis*, and Bees, *Apis mellifera*, may be a problem for waterfowl that nest in tree holes (Norman 1982).

Hunting

Hunting may affect the survival of waterfowl populations. Humans have hunted waterbirds, particularly waterfowl, for thousands of years in Australia and aborigines still harvest Magpie Geese, and other species, and their eggs in the Northern Territory (Dexter and Bayliss 1991). Others hunt waterfowl for recreation (Cairns and Kingsford 1995), and the numbers involved in this activity may be considerable.

Recreational hunting may cause significant but localised mortality but does not appear to affect the populations of species themselves (Whitehead *et al.* 1988; Halse *et al.* 1993*b*; Briggs *et al.* 1993). In south-western Western Australia, where waterfowl were hunted intensively, nearly 60% of Pacific Black Duck, and 40% of Grey Teal mortality was caused by hunting but elsewhere hunting probably accounted for less than 25% (Halse *et al.* 1993*b*). Other estimates, where hunting mortality equated to natural mortality, are similar (Norman and Powell 1981; Briggs *et al.* 1983; Halse *et al.* 1993*b*). Thus, in Victoria in the 1950s and 1960s, about 46% of banded Australian Wood Ducks and 56% of Hardhead had died within a year and about 89% within four years, suggesting a mean life expectancy of just over a year (Norman 1970, 1971*a*, 1971*b*). Similarly, more than 50% of Pacific Black Duck and Grey Teal banded in south-eastern Australia had died within the first year and by the fourth year most (95%) had died (Frith 1963). Mortality in young male Grey Teal was about 10% higher than in adult males and, in Pacific Black Duck, declined with age although this was not so for Grey Teal (Frith 1963). While it is not known whether hunting mortality is compensatory or additive, there was no evidence that hunting reduced survival rates (Halse *et al.* 1993*b*). Recreational hunting has declined in the last decade around Australia as licence requirements, identification tests and fees have increased and community values have changed (Cairns and Kingsford 1995; Kingsford *et al.* 1999*b*) and some States no longer allow recreational hunting. However, ducks are still shot as pests on agricultural crops grown in the south-east of the continent (Frith 1957*b*), with some 200 000 waterfowl killed each year on rice crops in New South Wales (Curtin and Kingsford, unpublished data). In some years, relatively large numbers of protected waterbirds (including Freckled Duck) were shot during opening weekends of annual seasons (e.g. Norman and Norris 1982; Norman and Horton 1993) but this has not occurred recently.

Pollution

One byproduct of hunting is the wasted lead shot that is deposited in wetlands and then ingested by waterbirds. Subsequent poisoning may cause death (Koh and Harper 1988; Harper and Hindmarsh 1990; Smith *et al.* 1995; Whitehead and Tschirner 1991*b*). While widescale die-offs that occur elsewhere (e.g. Pain 1992) have not been reported in Australia, high levels of lead have been reported in Australian waterfowl tissues (Wickson *et al.* 1992; Norman *et al.* 1993) and its cumulative impact is of concern (Kingsford *et al.* 1994*b*). In 1996, recommendations were made to phase out use of lead shot throughout Australia, replacing it with alternatives such as steel and bismuth (Australian and New Zealand Environment Conservation Council 1996), but this has not yet been implemented by all States.

Many of Australia's rivers have well established irrigation areas where pesticides are used. Run-offs into rivers have been implicated in the deaths of fish populations (Fairweather 1999) but not, apparently, those of waterbirds. In North America, irrigation drainage waters with pollutants have seriously contaminated wetlands (Lemly *et al.* 1993), affecting reproductive success of waterbirds (Ohlendorf *et al.* 1989). In Australia, organochlorines at levels exceeding those recommended for human consumption were prevalent in wings of waterfowl shot in eastern Australia (Olsen *et al.* 1980) but little is known about the impacts of these pesticides on health or reproduction of local waterbirds. Many Straw-necked Ibis chicks died from chlorpyrifos poisoning in 1995 (National Parks, unpublished data) in the Macquarie Marshes although its source was not identified. Given the persistence of organochlorines, there may be long-term problems associated with contamination of wetlands and watercourses and consequent impacts on waterbird populations. There is at least one record of pollution killing waterbirds when raised cyanide levels in a tailings dam near Parkes in New South Wales resulted in the death of almost 2000 waterbirds (National Parks and Wildlife Service, unpublished data). Relatively little is known about impacts of heavy metals (but see Bacher and Norman 1984).

Climate change

Changes in climate could affect the distribution of local wetlands and hence waterbirds. However, inherent variation in Australia's climate may make any long-term, systematic impact difficult to discern above shorter-term, background variation. Accepting the reality of an increase in global temperatures, the consequent decreases projected for the amounts of water in the rivers of the Murray–Darling Basin will probably mean that the areas of wetland will decline further, affecting waterbird breeding and feeding. For tropical wetlands, major changes could occur as floodplain wetlands potentially become inundated by seawater (Woodroffe and Mulrennan 1991; Eliot *et al.* 1999). Such changes may affect the Magela Creek, the Alligator Rivers region and Mary River plains (Woodroffe and Mulrennan 1993) in northern Australia, one of the country's most important wetland habitats for waterbirds (Morton *et al.* 1990*a*). In addition, saline mudflats could replace freshwater wetlands, extensively changing the waterbird communities involved (Eliot *et al.* 1999).

Conservation measures

The most serious threatening process for Australian waterbirds is the loss of habitat. A measure of reducing habitat loss is the protection of wetlands through establishment of conservation reserves and listing them as wetlands of international importance under the terms of the Ramsar Convention (Davis 1994), or identifying wetlands of national importance (Australian Nature Conservation Agency 1996). These are only initial steps for effective conservation.

Resumption of major parts of the continent for nature conservation is clearly not practical or politically viable but a site-based approach of reservation of individual blocks of land does not work well for waterbirds that use most of the continent. Conservation is exacerbated because Australian waterbirds may have separate habitats for differing parts of their life cycle. Hence non-breeding habitats may be different to breeding and moulting habitats and locations of breeding sites may themselves change. For example, colonial waterbirds can eventually kill the trees that they nest in, necessitating movement (Baxter 1994). Without conservation of habitats outside an officially recognised reserve system (Woinarski *et al.* 1992), the long-term future of waterbird species cannot be assured. This inevitably implies an intensive and well focussed management of floodplain systems (Whitehead *et al.* 1990; Whitehead and Saalfeld 2000) and river management that should include private land (or leasehold) as well as public areas. One option is the establishment of a network of the major wetland areas (e.g. lakes and swamps), formally and informally recognised, for waterbirds throughout Australia. This could then form the basis for private or public agreements to protect the water resources that maintain such wetlands (Kingsford *et al.* 1998, 2001). Establishment of terminal wetlands on major river systems as Ramsar sites offers another mechanism for future conservation of wetlands because upstream river regulation or extractions will affect the terminal wetland. This will trigger ancillary obligations and potential punitive measures under the Commonwealth's Environment Protection and Biodiversity Conservation legislation (EPBC Act 2000) if ecological characteristics are affected.

Actual conservation will depend on social demand (and demonstration of impacts) and will rely on a combination of appropriate legislation, a suitable reserve system and appropriate management on and off the reserves. Ecological sustainability of wetlands is primarily dependent on a water supply that is seldom protected (Kingsford and Halse 1999): protection of flows at the catchment scale is critically important and a major challenge for the survival of waterbirds and their habitats (Kingsford *et al.* 1998). Wetland loss and development of water resources are formidable issues, closely tied to future economic development in Australia (Kingsford 2000*a*). Unless policies protecting rivers are implemented (Kingsford 2000*b*), habitats for waterbirds will continue to disappear.

Conclusions

Australian waterbirds are different from their counterparts in other parts of the world. Much of their ecology is shaped by the spatial and temporal variability of wetland habitats that seldom resemble the predictable habitats of their counterparts in the Northern Hemisphere (Cowan 1973). Distribution, abundance, movements and ultimately survival depend on local, regional and continental wetland availability. Feeding and reproductive ecology vary considerably, depending on the location of a species on the continent and the abundance of food resources, perhaps at a scale beyond local or regional. Moulting behaviour and timing remains largely unknown for most waterbirds but appears to exhibit more variability than elswhere. In contrast, behaviour and morphology of Australian waterbirds resemble those of other waterbirds. The variability described for the ecology of Australian waterbirds is present in other parts of the Southern Hemisphere (e.g. South Africa: Siegfried 1970) and may be present elsewhere but not expressed because predictable seasons govern life cycle stages.

While detailed understanding of waterbird ecology in Australia remains in its infancy (Table 1), what is known has contributed much to an understanding of biotic and abiotic interactions on the continent. Basic research on individual species, particularly rare and cryptic species and those harvested, will continue to improve this. Technology (e.g. satellite tracking) may eventually help identify where species move and in response to what factors but habitat loss remains the most serious problem affecting the conservation of Australian waterbirds. Long-term data on abundance of waterbirds will be essential to understand the impacts of humans against a background of considerable climatic variability. They are a useful focus for wetland and river conservation (Kingsford and Halse 1999). There is also considerable information available about their biology, perhaps more than that for other aquatic fauna and flora (Cullen and Lake 1995). Birds, including waterbirds, are followed by many interest groups and there are international agreements and conventions that focus on their conservation. In one sense, they are also one of the easier elements of a wetland ecosystem to census or measure. With aerial surveys, many wetlands can be monitored (Kingsford 1999*b*; Kingsford *et al.* 1999*b*), providing long-term data on the health of wetlands and the species involved (Kingsford and Thomas 1995; Kingsford and Johnson 1998; Leslie 2001). With such data, real changes may be effected for the management of water resources for all aquatic flora and fauna. Whatever these may be, it will need to be cognisant that the ecology of Australian waterbirds is a product of unpredictable climate, river flows and wetland availability.

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Appendix 1. Nomenclature and taxonomy follows Christidis and Boles (1994) for 93 waterbird species (13% of all species in Australia and its territories, not including vagrants, introduced or extinct species) considered in this paper

Main distribution is categorised as continental (C), northern (N), eastern (E), southern (S), western (W) or combinations of these (adapted from Blakers *et al.* 1984). Ecological information is available for each species on a relative scale: G, good; M, moderate; P, Poor. Status is defined (following Garnett and Crowley 2000) as extinct (E), vulnerable (V) or near threatened (NT); letters in parentheses identify the Commonwealth, States or Territories (C, Commonwealth; N, New South Wales; NT, Northern Territory; Q, Queensland; S, South Australia; T, Tasmania; V, Victoria; W, Western Australia) where species are thought to be critically endangered, endangered, vulnerable or rare by State Governments

Order	Common name	Specific name	Main distribution	Information	Status
Anseriformes	Magpie Goose	*Anseranas semipalmata*	N	G	(N,S)
	Plumed Whistling-Duck	*Dendrocygna eytoni*	N/NE	M	
	Wandering Whistling-Duck	*Dendrocygna arcuata*	N/SE	P	
	Blue-billed Duck	*Oxyura australis*	SW/SE	M	(N,S)
	Musk Duck	*Biziura lobata*	SW/SE	M	(S)
	Freckled Duck	*Stictonetta naevosa*	C	M	(N, NT, Q, S, V)
	Black Swan	*Cygnus atratus*	C	G	
	Cape Barren Goose	*Cereopsis novaehollandiae*	S	G	V[A] (S, W)
	Australian Shelduck	*Tadorna tadornoides*	SW/SE	G	
	Radjah Shelduck	*Tadorna radjah*	N	P	(Q)
	Australian Wood Duck	*Chenonetta jubata*	W/S/E	G	
	Cotton Pygmy-goose	*Nettapus coromandelianus*	NE	P	NT (N, Q)
	Green Pygmy-goose	*Nettapus pulchellus*	N	P	
	Pacific Black Duck	*Anas superciliosa*	C	G	
	Australasian Shoveler	*Anas rhynchotis*	SW/E	M	(S)
	Grey Teal	*Anas gracilis*	C	G	
	Garganey	*Anas querquedula*	N	P	
	Chestnut Teal	*Anas castanea*	SW/SE	G	
	Pink-eared Duck	*Malacorhynchus membranaceus*	C	M	
	Hardhead	*Aythya australis*	C	M	
Podicipediformes	Australasian Little Grebe	*Tachybaptus novaehollandiae*	C	M	
	Hoary-headed Grebe	*Poliocephalus poliocephalus*	C	M	
	Great Crested Grebe	*Podiceps cristatus*	C	M	(S, T)
Pelecaniformes	Darter	*Anhinga melanogaster*	C	M	
	Little Pied Cormorant	*Phalacrocorax melanoleucos*	C	G	
	Pied Cormorant	*Phalacrocorax varius*	C	G	
	Little Black Cormorant	*Phalacrocorax sulcirostrus*	C	G	
	Great Cormorant	*Phalacrocorax carbo*	C	G	
	Australian Pelican	*Pelecanus conspicillatus*	C	M	
Ciconiiformes	White-faced Heron	*Egretta novaehollandiae*	C	P	
	Little Egret	*Egretta garzetta*	N/E/SE	G	(V)
	White-necked Heron	*Ardea pacifica*	C	P	
	Great-billed Heron	*Ardea sumatrana*	N	P	
	Pied Heron	*Ardea picata*	N	P	
	Great Egret	*Ardea alba*	C	G	(V)
	Intermediate Egret	*Ardea intermedia*	N/E/SE	G	(S,V)
	Cattle Egret	*Ardea ibis*	N/E/SE	G	
	Striated Heron	*Butorides striatus*	N/E	P	
	Nankeen Night Heron	*Nycticorax caledonicus*	C	M	
	Little Bittern	*Ixobrychus minutus*	W/E	P	NT (S, V)
	Black Bittern	*Ixobrychus flavicollis*	N/E	P	(N, V)
	Australasian Bittern	*Botaurus poiciloptilus*	W/SE	P	V (N,V, S)
	Glossy Ibis	*Plegadis falcinellus*	N/E/SE	M	(S)
	Australian White Ibis	*Threskiornis molucca*	C	G	
	Straw-necked Ibis	*Threskiornis spinicollis*	C	G	
	Royal Spoonbill	*Platalea regia*	N/E/SE	M	
	Yellow-billed Spoonbill	*Platalea flavipes*	C	M	
	Black-necked Stork	*Ephippiorhynchus asiaticus*	N/E	M	(N,Q)
Gruiformes	Sarus Crane	*Grus antigone*	NE	P	
	Brolga	*Grus rubicunda*	N/SE	M	(N, S, V)
	Red-necked Crake	*Rallina tricolor*	NE	P	
	Buff-banded Rail	*Gallirallus philippensis*	E/SW/N	P	V[B]

Appendix 1. Continued

Order	Common name	Specific name	Main distribution	Information	Status
	Lewin's Rail	*Rallus pectoralis*	SE	P	E[C] (Q, V, W)
	Bush-hen	*Gallinula olivacea*	N/NE	P	(N)
	Baillon's Crake	*Porzana pusilla*	SE	P	(S)
	Australian Spotted Crake	*Porzana fluminea*	SE	P	
	Spotless Crake	*Porzana tabuensis*	SW/SE	P	
	White-browed Crake	*Porzana cinereus*	N	P	
	Chestnut Rail	*Eulabeornis castaneoventris*	NW	P	
	Purple Swamphen	*Porphyrio porphyrio*	SW/E	M	
	Dusky Moorhen	*Gallinula tenebrosa*	SW/E	M	
	Black-tailed Native-hen	*Gallinula ventralis*	C	M	
	Tasmanian Native-hen	*Gallinula mortierii*	SE	G	
	Eurasian Coot	*Fulica atra*	C	M	
Charadriiformes	Latham's Snipe	*Gallinago hardwickii*	SE/E	P	(S)
	Swinhoe's Snipe	*Gallinago megala*	SE/E	P	
	Black-tailed Godwit	*Limosa limosa*	C	M	(N)
	Bar-tailed Godwit	*Limosa lapponica*	C	M	
	Marsh Sandpiper	*Tringa stagnatilis*	C	M	
	Common Greenshank	*Tringa nebularia*	C	M	
	Wood Sandpiper	*Tringa glareola*	C	M	
	Common Sandpiper	*Actitis hypoleucos*	C	M	
	Ruddy Turnstone	*Arenaria interpres*	C	M	
	Red-necked Stint	*Calidris ruficollis*	C	M	
	Long-toed Stint	*Calidris subminuta*	C	M	
	Sharp-tailed Sandpiper	*Calidris acuminata*	C	M	
	Curlew Sandpiper	*Calidris ferruginea*	C	M	
	Painted Snipe	*Rostratula benghalensis*	SE/E	P	V (N, Q, S, V)
	Comb-crested Jacana	*Irediparra gallinacea*	N/NE	M	(N)
	Black-winged Stilt	*Himantopus himantopus*	C	G	
	Banded Stilt	*Cladorhynchus leucocephalus*	SW/S	G	
	Red-necked Avocet	*Recurvirostra novaehollandiae*	SE/SW	M	
	Red-capped Plover	*Charadrius ruficapillus*	C	M	
	Double-banded Plover	*Charadrius bicinctus*	E/SE.	M	
	Black-fronted Dotterel	*Elseyornis melanops*	C	M	
	Hooded Plover	*Thinornis rubricollis*	S	M	NT (C, S, V)
	Red-kneed Dotterel	*Erythrogonys cinctus*	C	M	
	Masked Lapwing	*Vanellus miles*	N/E/SE	G	
	Silver Gull	*Larus novaehollandiae*	C	G	
	Gull-billed Tern	*Sterna nilotica*	C	M	
	Caspian Tern	*Sterna caspia*	C	M	
	Whiskered Tern	*Chlidonias hybridus*	C	M	
	White-winged Black Tern	*Chlidonias leucopterus*	C	P	

[A]Subspecies *Cereopsis novaelandiae grisea* (Recherche Cape Barren Goose)
[B]Subspecies *Gallirallus philippensis andrewsi* (Vulnerable), *Gallirallus philippensis macquariensis* (Extinct)
[C]Subspecies *Rallus pectoralis clelandi*