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The role of wild birds in the transmission of avian influenza for Australia: an ecological perspective

John P. Tracey[A,D], *Rupert Woods*[B], *David Roshier*[C], *Peter West*[A] *and Glen R. Saunders*[A]

[A]Vertebrate Pest Research Unit, NSW Agriculture, Forest Road, Orange, NSW 2800, Australia.
[B]Australian Wildlife Health Network, PO Box 20, Mosman, NSW 2088, Australia.
[C]Johnstone Centre, School of Science and Technology, Charles Sturt University, Locked Bag 588, Wagga Wagga, NSW 2678, Australia.
[D]To whom correspondence should be addressed. Email: john.tracey@agric.nsw.gov.au

Abstract. Waterbirds, particularly Anatidae, are natural reservoirs for low-pathogenic avian influenza and have been implicated as the primary source of infection in outbreaks of highly pathogenic avian influenza. An understanding of the movements of birds and the ecology of avian influenza viruses within the wild bird population is essential in assessing the risks to human health and production industries. Marked differences in the movements of Australian birds from those of the Northern Hemisphere emphasises the danger of generalising trends of disease prevalence to Australian conditions. Populations of Anatidae in Australia are not migratory, as they are in the Northern Hemisphere, but rather display typical nomadic traits, sometimes moving large distances across continental Australia in response to flooding or drought. There is little known regular interchange of anatids between Australia and Asia. In contrast, species such as shorebirds and some seabirds are annual migrants to Australia along recognised flyways from breeding grounds in the Northern Hemisphere. Movement into Australia by these species mainly occurs into the north-west and along the east coast over the Pacific Ocean. These species primarily arrive during the Australian spring and form large aggregations along the coastline and on inland wetlands. Other Australian migratory species (passerines, bee-eaters, dollar-birds, cuckoos, doves) regularly move to and from Asia through the Torres Strait Islands. The disease status of these birds is unknown. The movements of some species, particularly anatids and ardeids, which have ranges including Australia and regions where the virus is known to occur, have been poorly studied and there is potential for introduction of avian influenza subtypes via this route. Avian influenza viruses are highly unpredictable and can undergo reassortment to more pathogenic forms. There is insufficient knowledge of the epidemiology and transmission of these viruses in Australia and broad-scale surveillance of wild birds is logistically difficult. Long-term studies of anatids that co-habit with Charadriiformes are recommended. This would provide an indication of the spatial and temporal patterns of subtypes entering Australia and improve our understanding of the ecology of endemic viruses. Until such time as these data become available, Australia's preparedness for avian influenza must focus on biosecurity at the wild bird–poultry interface.

Introduction

The biology and ecology of avian influenza viruses have previously been reviewed (Alexander 1993). Influenza viruses are members of the Family Orthomyxoviridae and are characterised into Types A, B or C on the basis of the antigenic character of the internal nucleoprotein antigen. Avian influenza is an infectious disease of birds caused by Type A strains of the influenza virus (WHO Expert Committee 1980). Only influenza A viruses have been isolated from avian species. The disease occurs worldwide and was first identified in Italy more than 100 years ago (Alexander 1987). Avian influenza viruses normally do not infect species other than birds, but have been recorded infrequently in a range of other animal species, including humans (Hinshaw *et al*. 1981; Alexander 1982; Claas *et al*. 1998; Katz 2003).

Influenza A viruses are divided into subtypes determined by haemagglutinin (H) and neuraminidase (N) antigens. At present, 15 H subtypes and 9 N subtypes have been identified. Each virus has one of each subtype in any combination (Animal Health Australia 2003). The reservoir for all avian influenza virus haemagglutinin (H) and neuraminidase (N) subtypes is aquatic birds, particularly waterfowl (Suss *et al*. 1994), in which they multiply in the gastrointestinal tract, producing large amounts of virus (Webster *et al*. 1978; Hinshaw *et al*. 1980) usually without producing clinical signs (Kida *et al*. 1980). In this environment, new combinations of H and N genes are generated and dispersed (Scholtissek *et al*. 1993). This process of exchanging genes between virus strains is called reassortment within influenza viruses and occurs when single cells of the host become coinfected with

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two genetically different viruses (Hinshaw *et al*. 1980). In wild waterbird hosts, the H and N subunits appear to be stable, and do not mutate (Sharp *et al*. 1997), as they do when the viruses infect domestic poultry and mammals. New virus combinations multiply readily in avian species and in chickens and turkeys a proportion have a propensity to mutate and produce severe disease, which, in turn, produces epizootics in poultry enterprises (Animal Health Australia 2003).

Infection in birds causes a wide spectrum of symptoms, and viruses can be divided into two groups according to their pathogenicity (Office International Epizooties 2001). Some forms of these viruses, known as highly pathogenic avian influenza (HPAI), can cause severe illness and mortality approaching 100% (Alexander 1993; Swayne and Suarez 2000). However, most strains of the virus are non-virulent, do not produce clinical signs, or cause only mild respiratory or reproductive disease. These are known as low-pathogenic avian influenza (LPAI) viruses, which are commonly isolated from wild birds, particularly Anseriformes (swans, ducks and geese) (e.g. Slemons and Easterday 1972; Stallknecht and Shane 1988). HPAI viruses, however, are not maintained by wild bird populations, but are occasionally isolated from wild birds during outbreaks in domestic poultry (Nestorowicz *et al*. 1987). The ability of LPAI to mutate into HPAI (Perdue *et al*. 1998), particularly in poultry, and the diversity of viruses circulating in wild bird populations (e.g. Webster *et al*. 1992) emphasises the potential importance of wild birds as a primary source of infection.

Epizootics of avian influenza may occur when a HPAI virus (with either a H5 or H7 haemagglutinin) is introduced to a naïve poultry population. Severe pandemics in humans occur when a major ‘antigenic shift’ has occurred such as when the haemagglutinin is changed. Severe disease epidemics occur when there is ‘drift’ with significant antigenic change in the haemagglutinin gene (Animal Health Australia 2003). The presence of avian influenza viruses in wild birds thus has significance primarily for its potential to infect domestic poultry and humans, within which it can then undergo reassortment to produce pathogenic forms (Webster *et al*. 1971, 1973). In addition, if humans are concurrently infected with both human and avian strains of influenza there is an increased risk of a new subtype emerging, which could result in the direct transmission between humans with the possibility of a pandemic (Webster 1998; Snacken *et al*. 1999; Baigent and McCauley 2003; Katz 2003).

There have been five known outbreaks of avian influenza in commercial bird flocks in Australia. Outbreaks occurred in 1976 (Turner 1976), 1985 (Barr *et al*. 1986) and 1992 (Selleck *et al*. 1997) in Victoria, in 1994 in Queensland (Westbury 1998), and in 1997 in Tamworth, New South Wales (Selleck *et al*. 2003). Viruses identified have all been of subtype H7 (H7N7, H7N3 and H7N4). The 2003–04 Asian epidemic of HPAI (subtype H5N1) commenced in August 2003 and by March 2004 was confirmed in China, Cambodia, Indonesia, Japan, Laos, South Korea, Taiwan, Thailand and Vietnam. H5N1 has also caused disease and death in humans (Claas *et al*. 1998; Subbarao *et al*. 1998; Yuen *et al*. 1998) via direct avian-to-human transmission.

The potential transmission of the H5N1, and other influenza A viruses from Asia to other countries via wild birds is of concern. Many bird species are known to undertake movements between Asia and Australia; the species involved, their movement behaviour, ecology and susceptibility to disease are all of importance when assessing the risk of introducing foreign disease into Australia. The objectives of this paper are to review the movements of wild birds between Asia and Australia, investigate their role in the transmission of avian influenza, and suggest ways in which Australia’s management of avian influenza viruses associated with wild birds can be improved.

Movements of birds between Australia and Asia

Movements of wild birds into Australia from Asia occurs every year with the arrival of large flocks of migratory shorebirds and the movement of other species between the archipelagos of south-east Asia and northern Australia. Moreover, some species have distributions that extend to New Guinea and parts of south-east Asia where avian influenza is known to occur (Fig. 1). Bird species known to travel between Asia and Australia are listed in the Appendix and discussed below.

Ducks, geese and magpie geese (Anseriformes)

Avian influenza has been isolated from species of ducks and geese (Anatidae) more than from any other avian family, but is unknown in magpie geese (Anseranatidae). Members of the Anatidae are ubiquitous throughout Australia but, unlike their Northern Hemisphere counterparts (e.g. Hestbeck *et al*. 1991), most populations do not undertake predictable migrations associated with seasonal changes in resource availability (see Kingsford and Norman 2002 for review). Instead, movements of waterfowl in Australia are less predictable and many populations are nomadic, moving large distances in response to prevailing climatic conditions such as flooding or drought (Lawler and Briggs 1991). This is particularly characteristic of species that occur in arid and semi-arid regions where resources are localised, ephemeral and affected by aseasonal stochastic processes (Halse and Jaensch 1989; Lawler *et al*. 1993; Roshier *et al*. 2001*a*). The movement and distribution of most waterbirds across the Australian continent is therefore largely determined by the distribution of surface waters in the dryland river systems and the many ephemeral lakes and water-bodies of inland Australia (Briggs 1992; Lawler *et al*. 1993; Kingsford 1995; Roshier *et al*. 2001*b*, 2002). Several species are wide-ranging and dispersive over most of the Australian continent, and are known to occur on the islands immediately to the north or have a geographic range that extends from northern Australia to parts of south-east Asia.

Movements of waterfowl from Australia to Asia have not been well studied but are thought to be irregular and to occur mainly from northern Australia. Banding records have confirmed the occurrence of these movements by Grey Teal (*Anas gracilis*) (Frith 1982). Grey Teal are among the most dispersive of Australian waterfowl and are widespread on inland wetlands and sheltered estuarine and marine waters (Marchant and Higgins 1990). Grey Teal are capable of moving thousands of kilometres over several weeks (Frith 1959, 1963) and have been recorded moving from south-eastern Australia to Western Australia and New Zealand (Frith 1957; Mills 1976; Frith 1982). In northern Australia, Grey Teal numbers peak in the dry season and are virtually absent in the wet season (December–April) (Marchant and Higgins 1990). Grey Teal numbers in northern Australia fluctuate markedly, with the greatest concentrations occurring after irruptions of southern populations (Frith 1982). When Grey Teal occur in large numbers on the northern coastal wetlands they are usually in poor condition and are regarded as not good eating by the traditional owners (Peter Kristofferson, personal communication), suggesting that their occurrence in northern Australia is, in part, driven by adverse conditions elsewhere. This species is known to be a dry-season visitor to islands in the Torres Strait (Draffan *et al*. 1983) and may be a frequent traveller between New Guinea and northern Australia.

The range of other waterfowl that extend to the flood-plains of New Guinea include the Magpie Goose (*Anseranas semipalmata*), Wandering Whistling-duck (*Dendrocygna arcuata*), Plumed Whistling-Duck (*Dendrocygna eytoni*), Rajah Shelduck (*Tadorna radjah*), Cotton Pygmy-Goose (*Nettapus coromandelianus*), Green Pygmy-Goose (*Nettapus pulchellas*), Pacific Black Duck (*Anas superciliosa*) and Hardhead (*Athya australis*) (see Marchant and Higgins 1990; Wetlands International 2002). Most of these species are dispersive, with little being known about the nature and extent of their movements (see Marchant and Higgins 1990). Only the Cotton Pygmy-Goose is regarded as sedentary, while the Plumed Whistling-duck is regarded as a partial migrant within Australia, with few records from New Guinea where it is a vagrant (Marchant and Higgins 1990). The range of the Wandering Whistling-duck includes northern Australia, New Guinea, and Pacific, Indonesian and Philippine Islands (Marchant and Higgins 1990; Wetlands

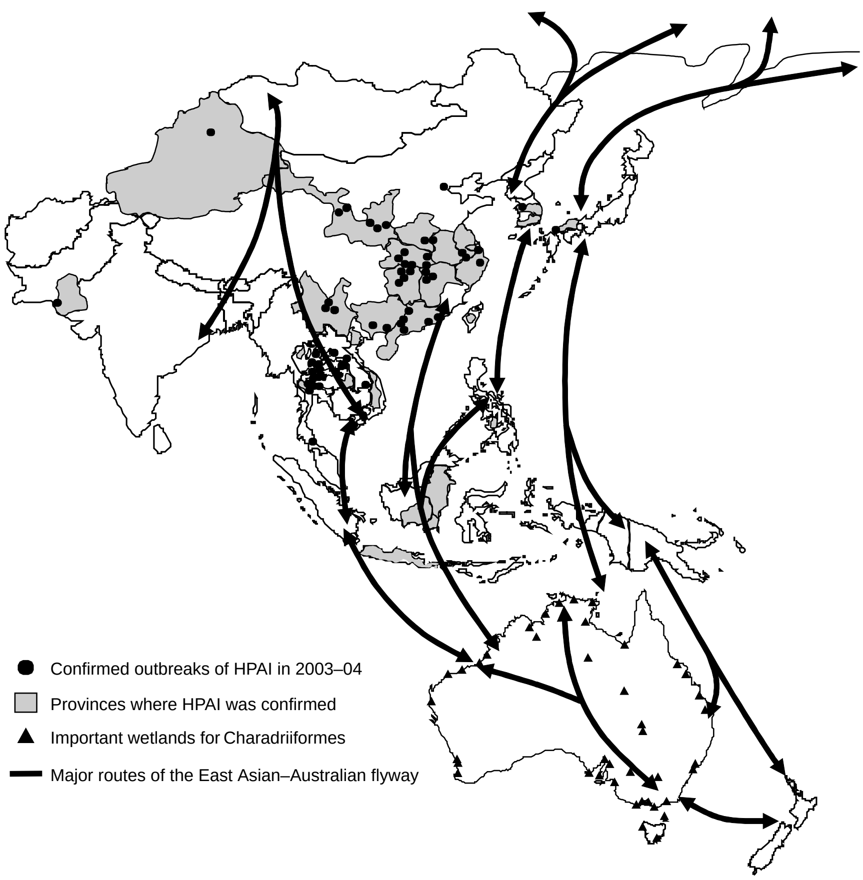

Fig. 1. Major routes of the East Asian–Australian flyway in relation to the 2003–04 epizootic of highly pathogenic avian influenza (HPAI). Source: Wetlands International (Oceania) and Avian Influenza Map for Asia: situation on 18/02/04.

International 2002). The eastern Indonesian and northern New Guinea populations are taxonomically distinct from those in Australia and southern New Guinea (Wetlands International 2002; Dickinson 2003), which suggests that the Australian subspecies does not extend north of New Guinea. Australian populations of Rajah Shelduck (*Tadorna radjah rufitergum*) are also taxonomically distinct from those that occur in New Guinea and the Moluccas Islands of Indonesia (Marchant and Higgins 1990; Wetlands International 2002; Dickinson 2003). The Australian subspecies is known to occur in the Torres Strait throughout the year and may move infrequently between Australia and southern New Guinea (Draffan *et al*. 1983). The range of the Pacific Black Duck includes southern Sumatra, Java, Sulawesi, New Guinea, New Britain and islands of the south-west Pacific Ocean (Marchant and Higgins 1990). There are three recognised subspecies, *superciliosa* (Australia, southern New Guinea, New Zealand), *rogersi* (Indonesian region) and *pelewensis* (northern New Guinea and islands of the south-west Pacific) (Marchant and Higgins 1990; Dickinson 2003). Pacific Black Duck are largely sedentary on permanent wetlands or in regions that are well watered, although they are dispersive from inland wetlands in summer. Birds banded at Griffith in southern New South Wales have been recovered as far afield as Tasmania, Queensland and New Zealand, but more than half of all banded birds were recovered within 100 km of the point of release (Frith 1959). Historically, Hardhead are known to occur in New Guinea and parts of Indonesia (Marchant and Higgins 1990) but the most recent worldwide survey of waterbird populations does not recognise a population outside Australia, apart from that of the subspecies *Aythya australis extima* on Vanuatu and New Caledonia (Wetlands International 2002; Dickinson 2003).

Although the movements of most Australian waterbirds are largely unpredictable or poorly known, some seasonal movement patterns are known for northern-distributed species. Magpie Geese, for example, spread out onto floodplains of northern Australia during the wet season then retreat to remnant wetlands in the dry season (Morton *et al*. 1990*b*). Similar patterns are evident for Wandering Whistling-duck and Green Pygmy-Goose (Marchant and Higgins 1990). Magpie Geese and Wandering Whistling-duck have been recorded moving across Torres Strait into New Guinea (Ashford 1979; Draffan *et al*. 1983), and Green Pygmy-Goose are a dry-season visitor to the Torres Strait (Marchant and Higgins 1990).

Shorebirds (Charadriiformes)

Shorebirds (Scolopacidae and Charadriidae) migrate annually between the Northern and Southern Hemispheres via known routes or flyways (Thomas 1970; Tulp *et al*. 1994). There are about 3 million birds, from 35 species, that regularly migrate from Australia each year (Wetlands International 2002). Most depart from Australia in March to breeding areas, some as far as north-eastern Siberia and Alaska, although some juvenile birds will remain in Australia (Lane 1987). Migrants return in September and spend late spring and summer in coastal and inland Australia (e.g. Tulp *et al*. 1994) (Fig. 1; Appendix). Larger species migrate further and over greater continuous distances, some travelling to China before stopping. Smaller species and juveniles that migrate have 'stop-over' areas in Asia and south-east Asia, and travel shorter distances. Eight major flyway routes have been defined for waders based on biological and geopolitical considerations (Asia-Pacific Migratory Waterbird Conservation Committee 2001). The East Asian–Australasian flyway is of relevance to Australia and highlights the importance of major routes into Australia in the north-west and along the central-east coastline (Fig. 1). Major 'stop-over' locations for these flights include sites throughout Asia, including provinces where HPAI has been confirmed during the 2003–04 outbreaks (Fig. 1). Interchange between Australia and Asia has been confirmed through sightings of flagged birds and recoveries of banded individuals (e.g. McClure 1998). Avian influenza is found occasionally in Charadriiformes (Table 1), with frequent occurrence of the virus in some species during particular seasons. Of particular relevance is that Charadriiformes can congregate in extremely large concentrations on coastal floodplains and mainland wetlands (Morton *et al*. 1993), where they regularly interact with Anatidae (Morton *et al*. 1990*a*).

Grebes (Podicipediformes)

Grebes are distinct from any other group of waterbirds (Sibley and Ahlquist 1990), differing in morphology and behaviour as they are totally reliant on wetlands for food (Fjeldsa 1988), protection (Hobbs 1958) and nesting (Dann 1981). Movements of grebes are poorly known. Most species are nomadic (Hobbs 1956; Masters and Milhinch 1974), with some migratory patterns suggested in northern populations (Marchant and Higgins 1990). They are capable of travelling over large distances (Marchant and Higgins 1990) but these movements are usually restricted to the Australian mainland. Movements into Asia are unknown but likely to be rare, despite evidence of breeding in the Torres Strait (Draffan *et al*. 1983). Australasian (*Tachybaptus novaehollandiae*) and Great-crested (*Podiceps cristatus*) Grebes are mainly solitary, although large flocks of several hundred can congregate in estuaries during winter (Wheeler 1947). Hoary-headed Grebes (*Poliocephalus poliocephalus*) are more gregarious, with flocks up to several thousand (Fjeldsa 1983), and up to 400 nests on a single wetland (Frith 1976).

Albatrosses, petrels and shearwaters (Procellariiformes)

Procellariiformes spend most of their time on the open sea and only return to land to breed, mostly on off-shore islands. Their nesting sites in the Southern Ocean are among the remotest locations on Earth. Many species in this order are capable of extraordinarily long journeys across open water and some migrate to Australian waters in vast numbers. For example, Short-tailed Shearwaters (*Puffinus tenuirostris*) breed from October to February in south-eastern Australia and migrate in their millions to the north Pacific during March (Marshall and Serventy 1961; Serventy 1961). Many other shearwaters have similar movement patterns and breed in Australian waters in our summer (Harper and Kinsky 1978). By contrast, Streaked Shearwater (*Calonectris leucomelas*) migrate from breeding islands off Japan and Korea and arrive in northern Australia in March (Gibson 1975; McClure 1998).

Procellariiformes are generally restricted to the islands and open waters of the Pacific and Southern Oceans and are rarely observed closer than the continental shelf. Petrels, in particular, are seldom observed from the mainland and breed on Pacific islands considerable distances from the shoreline (Warham 1990). The Shy Albatross (*Diomedea cauta*) is the only albatross to breed in Australia, also on off-shore islands (Harper and Kinsky 1978). Many species of this order regularly travel between Australia and Asia and some are known to carry avian influenza (Downie and Laver 1973).

Cormorants, darter and pelicans (terrestrial Pelecaniformes)

Cormorants, pelicans and the darter are nomadic and highly dispersive, travelling large distances to exploit temporary resources wherever they occur (Llewellyn 1983; Dorfman and Kingsford 2001). Nesting of most species is colonial and frequently occurs with other species (Norman 1974; Vestjens 1977), increasing the likelihood of transmission of avian influenza between individuals and across species. Pelicans (*Pelecanus conspicillatus*) have been recorded moving into Papua New Guinea from South Australia (Marchant and Higgins 1990), with large numbers recorded arriving in the Torres Strait (Draffan *et al*. 1983). Members of this order have worldwide distributions. The Darter (*Anhinga melanogaster*) has populations of four subspecies distributed across Australia, New Guinea, south-east Asia, India and Africa (Dickinson 2003), including the Australian subspecies *Anhinga melanogaster novaehollandiae*. This subspecies is

Table 1. The relative occurrence of avian influenza in families of birds known to move between Australia and Asia

Families were classified according to the relative occurrence of avian influenza between species using a subjective increasing scale (Unknown, Extremely Rare, Rare, Occasional, Common), derived from information in Downie and Laver (1973) (1); Downie *et al*. (1977) (2); Hanson (2003) (3); Iftimovici *et al*. (1980) (4); Kawaoka *et al*. (1988) (5); Lipkind *et al*. (1982) (6); Mackenzie *et al*. (1984) (7); Mackenzie *et al*. (1985) (8); Nestorowicz *et al*. (1987) (9); Peroulis and O'Riley (2004) (10); Romvary and Tanyi (1975) (11); Slemons *et al*. (1973) (12); and Stallknecht and Shane (1988) (13)

Order	Family	Common Family	Relative occurrence of avian influenza	Source
Anseriformes	Anseranatidae	Magpie Geese	Unknown	7
	Anatidae	Waterfowl	Common	7, 8, 10, 13
Procellariiformes	Procellariidae	Shearwaters/Petrels	Rare	1, 2, 7
	Hydrobatidae	Storm Petrels	Unknown	
Pelecaniformes	Phaethontidae	Tropicbirds	Unknown	
	Sulidae	Boobies/Gannets	Unknown	
	Phalacrocoracidae	Cormorants	Rare	4
	Pelecanidae	Pelicans	Unknown	
	Fregatidae	Frigatebirds	Unknown	
Ciconiiformes	Ardeidae	Herons/Bitterns	Rare	4
	Threskiornithidae	Ibises	Rare	4
Gruiformes	Rallidae	Rails	Unknown	
Charadriiformes	Scolopacidae	Turnstones/Sandpipers/Phalaropes	Occasional	3, 5, 7
	Charadriidae	Plovers	Occasional	13
	Glareolidae	Pratincole	Unknown	
	Laridae	Gulls/Terns	Occasional	7, 8, 13
Columbiformes	Columbidae	Pigeons/Doves	Extremely Rare	11
Cuculiformes	Cuculidae	Cuckoos	Unknown	
Coraciiformes	Halcyonidae	Kingfishers	Unknown	
	Meropidae	Bee-eaters	Extremely Rare	12
	Coraciidae	Dollarbird	Unknown	
Passeriformes	Meliphagidae	Honeyeaters	Unknown	
	Dicruridae	Drongoes	Unknown	
	Campephagidae	Cuckoo Shrikes	Unknown	
	Oriolidae	Orioles	Unknown	
	Sturnidae	Starlings	Extremely Rare	6, 9

confined to Australia and New Guinea and is recognised by some authors as a distinct species (see Wetlands International 2002). Movements of Darter are poorly known but they are dispersive and banding studies have recorded movements of over 2000 km within Australia (Marchant and Higgins 1990). Great Cormorants (*Phalacrocorax carbo*) have a worldwide distribution, with the Australian subspecies *Phalacrocorax carbo novaehollandiae* confined to Australia and New Zealand (Dickinson 2003). Some authors recognise two subspecies for Australia and New Zealand (Wetlands International 2002). All four common cormorant species in Australia – Great Cormorant, Pied Cormorant (*Phalacrocorax varius*), Little Pied Cormorant (*Phalacrocorax melanoleucos*) and Little Black Cormorant (*Phalacrocorax sulcirostris*) – are dispersive, with some individuals (*P. carbo*) recorded moving beyond the Australian mainland after large breeding events inland (Marchant and Higgins 1990). Flocks of Great and Little Black Cormorants have reached the islands of the Torres Strait and New Guinea (Geering *et al*. 1998), but movements off southern Australia are more common. The Little Pied and Little Black Cormorants are sympatric across much of their ranges in Australia, eastern Indonesia, south-west Pacific, New Guinea and New Zealand, while the Pied Cormorant is confined to Australia and New Zealand (see Wetlands International 2002). The Little Pied Cormorant has three subspecies and the Australian subspecies extends to Indonesia and Melanesia. Populations of the Little Black Cormorant are now considered to be a single species whose range extends from southern Australia and New Zealand into New Guinea and eastern Indonesia (Dickinson 2003). The nature and extent of cormorant movements between Australia and the northern parts of their range is largely unknown but likely to be infrequent.

Gannets, boobies, tropicbirds and frigatebirds (pelagic Pelecaniformes)

As partial migrants, some species of this order regularly pass through the oceans of Asia and south Asia, especially during autumn (Marchant and Higgins 1990). As is the case for Procellariiformes, they are marine species and breed on offshore islands (Nelson 1978). Mainland sightings have been associated with summer cyclones blowing individuals inland (Morris 1979). Boobies occur most commonly in tropical and subtropical waters and gannets prefer southern-temperate waters (Nelson 1978; Brooke 2004).

Egrets, heron, night heron, bitterns, stork, ibis, spoonbill (Ciconiiformes)

Egrets, Little Bittern (*Ixobrychus minutus*), ibis, White-faced Heron (*Egretta novaehollandiae*) and Royal Spoonbills (*Platalea regia*) are nomadic but also considered occasional dry-winter (June–August) migrants to New Guinea (Hancock and Elliott 1978; Finch 1982; Draffan *et al*. 1983). Little is known of the nature and extent of movements of species of this order. Great Egret (*Ardea alba*), Rufous Night-heron (*Nycticorax caledonicus*) and White-faced Heron are known to be dispersive (Marchant and Higgins 1990). Banding records have confirmed some interchange of Little Egret (*Egretta garzetta*) and Great Egret between Australia and New Guinea (Blakers *et al*. 1984; Marchant and Higgins 1990). Striated Herons (*Butorides striatus*) are generally sedentary, although some Asian populations undertake a regular migration (e.g. to Christmas Island: Stokes *et al*. 1987). This species is highly differentiated taxonomically into 29 distinct subspecies or populations and there is little apparent movement between populations (see Marchant and Higgins 1990; Wetlands International 2002). Large influxes of Rufous Night-heron in wetlands can occur after flooding (Hanscombe 1915), with infrequent and erratic movements into New Guinea (Anon. 1977; Schodde and Mason 1980; Draffan *et al*. 1983). Flocks of 50–100 Straw-necked Ibis (*Threskiornis spinicollis*) and 20–500 Australian White Ibis (*Threskiornis molucca*) have been observed in the Torres Strait (Draffan *et al*. 1983). Australian White Ibis nestlings banded in Australia and recovered in New Guinea confirm occasional movements further north (Carrick 1962). The Glossy Ibis (*Plegadis falcinellus*) has a wide distribution that includes Australia, south-east Asia, Africa and the east coast of North America (Wetlands International 2002; Dickinson 2003). Glossy Ibis are thought to be partial migrants in eastern Australia but movements elsewhere are thought to be erratic in response to rainfall (Marchant and Higgins 1990). Black-necked Storks (*Ephippiorhynchus asiaticus*) are sedentary and have not been recorded moving north of the Australian mainland, except the occasional record in the Torres Strait (Draffan *et al*. 1983).

Other non-passerines

A variety of other non-passerines regularly move between Asia and Australia. These include Rainbow Bee-eaters (*Merops ornatus*), Dollar-birds (*Eurystomus orientalis*), Brush (*Cuculus variolosus*) and Channel-billed (*Scythrops novaehollandiae*) Cuckoos, Common Koels (*Eudynamis scolopacea*), Superb Fruit Doves (*Ptilinopus superbus*), Pied Imperial Pigeons (*Ducula bicolor*) and Sacred (*Todiramphus sanctus*), Forest (*Halcyon macleayii*) and Buff-breasted Paradise (*Tanysiptera sylvia*) Kingfishers. Most of these conduct regular migrations into Asia for the winter months (March–August).

The main flyway route for these species is via the Torres Strait islands and New Guinea (Higgins 1999; Griffioen and Clarke 2002). Some species remain in New Guinea throughout winter (April–August) (e.g. Schodde *et al*. 1975) while others continue further north. For example, Rainbow Bee-eaters travel through to Micronesia and Japan (Blakers *et al*. 1984); Common Koels to Indonesia and as far north as the Philippines (Rand and Gillard 1967; Blakers *et al*. 1984); Channel-billed Cuckoos to southern Indonesia, the Bismarck

Archipelago and New Guinea (Hindwood 1953; Mason 1981; Draffan *et al*. 1983); and Sacred Kingfishers to Timor, New Guinea, the Solomon islands and parts of Indonesia (Rand and Gillard 1967; Bell 1981; McClure 1998). Some species display only partial migration, with individuals remaining in Australia throughout the year. This can vary with latitude, where southern populations of some species (e.g. Brush Cuckoos, Forest Kingfishers) are more migratory. All these species are observed migrating in flocks that are two orders of magnitude smaller than those of Charadriiformes (Lord 1956; Hobbs 1961;Warham 1962; Gill 1970; Lavery and Grimes 1974; Draffan *et al*. 1983).

Passerines

Few passerines are known to move between Asia and Australia. Those species that have been recorded moving between the continents include Metallic Starlings (*Aplonis metallica*), Cicada Birds (*Coracina tenuirostris*), Spangled Drongos (*Dicrurus bracteatus*), Olive-backed Orioles (*Oriolus sagittatus*) and Brown-backed Honeyeaters (*Ramsayornis modestus*). Metallic Starlings, Cicada Birds and Spangled Drongos regularly migrate to south-east Asia during the winter months through islands of the Torres Strait (Barnard 1911; Campbell and Barnard 1917; Griffioen and Clarke 2002). Southern populations of the Cicada Bird migrate north to New Guinea in autumn (Bell 1982*a*; Draffan *et al*. 1983), while northern populations are partial migrants. Spangled Drongos exhibit more varied movements, with some individuals conducting similar northward movements, while others move south during winter (Mayr and Rand 1937; Bell 1982*b*). Metallic Starlings, which are restricted to northern Queensland, roost and nest colonially in large numbers, with flocks of up to 5000 observed prior to migration (Blakers *et al*. 1984). Migrating Spangled Drongos usually form flocks of ~20 (Draffan *et al*. 1983), but larger flocks have been observed over Thursday Island (Blakers *et al*. 1984). Movements of Olive-backed Orioles and Brown-backed Honeyeaters into Asia are uncommon and irregular, apparently fluctuating with the availability of ripe fruit or nectar (Officer 1964; Gill 1970; Storr 1973; Draffan *et al*. 1983).

Occurrence of avian influenza in wild birds

A large number and variety of influenza viruses are maintained in wild bird populations. Avian influenza viruses have been isolated from more than 88 species of wild birds from 12 orders, comprising most of the major families (see Stallknecht and Shane 1988; Alexander 2000 for review). The first isolation from wild birds occurred in South Africa from Common Terns (*Sterna hirundo*) in 1961 (Becker 1966). An increase in surveillance during the late 1970s revealed ducks and geese (Anseriformes) as the main reservoir of the viruses, where prevalence exceeded 60% in some studies (e.g. Hinshaw *et al*. 1980). Overall isolation rates estimated from over 20000 samples indicate ~15% of Anseriformes and ~2% of all other species are infected with the virus at any one time (Stallknecht and Shane 1988; Alexander 2000). However, many of these studies are based on regular samples of Anseriformes only and may be unrepresentative of region and species. In other studies Charadriiformes (shorebirds, plovers and lapwings) (Kawaoka *et al*. 1988) and spoonbills (Astorga *et al*. 1994) have also been found to have a high prevalence of the virus, with isolation rates of up to 20% and 32% respectively. In Australia, prevalence of the virus is found to be much lower (Mackenzie *et al*. 1984, 1985; Peroulis and O'Riley 2004). Isolation rates and subtypes vary considerably over time, region and between species (Kawaoka *et al*. 1988; Sharp *et al*. 1993). This has been identified for Charadriiformes, where sampling along the Atlantic coast and the Gulf of Mexico revealed 78% of isolates from Ruddy Turnstones (*Arenaria interpres*), with concentrations of the virus during one season (spring) and in one location (Delaware Bay) (Hanson 2003). Species of Anatini (Anseriformes) also exhibit higher prevalence of avian influenza than other species of the same order (Stallknecht and Shane 1988). Other species normally not associated with the maintenance of avian influenza viruses are also occasionally infected (Table 1) (Stallknecht and Shane 1988). This has also occurred during outbreaks of HPAI, for example, Starlings (*Sturnus vulgaris*) (Nestorowicz *et al*. 1987), ratites (Selleck *et al*. 2003) and flamingos, falcons and crows during the 2003–04 Asian epidemic.

Seasonal infection patterns have emerged in Anseriformes, with the greatest prevalence during late autumn and winter (Sinnecker *et al*. 1982; Halvorson *et al*. 1985). This trend is consistent with the timing of outbreaks of human influenza, but differs from the spring epidemics evident in Charadriiformes (Hanson 2003). Movements and age of birds also appear to be important and are correlated with seasonal effects. For example, a significantly higher prevalence of the virus was recorded for juvenile mallards before migrating south for the winter (Deibel *et al*. 1985; Hinshaw *et al*. 1985, 1986).

Most subtypes (H1, H3, H4, H5, H6, H7[1], H11, H12) have been detected in Australian wild birds (Downie and Laver 1973; Downie *et al*. 1977; Mackenzie *et al*. 1984, 1985; Nestorowicz *et al*. 1987; Peroulis and O'Riley 2004). In Australia, no quantitative links have been made to wild birds during the five previous HPAI outbreaks in poultry. In addition Australian isolates of HPAI have been found to be distinct from those in other parts of the world, including Asia (Banks and Alexander 1997; see also Rohm *et al*. 1995 for an international perspective), which suggests an endemic rather than exotic source of infection. However, there is circum-

[1]Upon examination this isolate showed no serological reactivity against H7 antisera and was corrected to H15 (Rohm *et al*. 1996).

stantial evidence that waterfowl may have been involved in previous outbreaks, and sampling has been limited and on one occasion may have occurred too long after the epidemic (Westbury 1998; Selleck *et al*. 2003). Direct and indirect contact with waterfowl has been reported and has been suggested as a potential cause of initial infection (Westbury 1998). During the 1997 outbreak in Tamworth, New South Wales, HPAI was isolated from an adjacent Emu (*Dromaius novaehollandiae*) farm that was suggested to have played a role in the transmission of the virus (Selleck *et al*. 2003). Some evidence also suggests the transmission of HPAI can occur between domestic poultry and passerine birds, following reports of the virus infection in starlings (Nestorowicz *et al*. 1987; Westbury 1998).

The unpredictability inherent in avian influenza viruses, the variation in prevalence between species (e.g. Becker 1967), and temporal and spatial variation in virus occurrence makes generalisations across families difficult. However, to allow targeted surveillance, four prevalence classes have been identified to describe the relative occurrence of avian influenza virus (Table 1). Information contained in Table 1 was derived from information gathered from within Australia (Downie and Laver 1973; Downie *et al*. 1977; Mackenzie *et al*. 1984, 1985; Nestorowicz *et al*. 1987; Peroulis and O'Riley 2004) and review publications of studies conducted in the Northern Hemisphere (Stallknecht and Shane 1988; Stallknecht 1998; Hanson 2003). Of the 27 families known to move between Australia and Asia (Appendix), avian influenza infection is suggested to commonly occur in Anatidae and occasionally in Charadriidae (plovers, dotterels and lapwings), Laridae (skuas, jaegers, gulls and terns) and Scolopacidae (snipe, godwits, curlews, sandpipers, stints and phalaropes) (Table 1). The virus is rarely isolated from species of Ardeidae (herons, egrets, night-herons and bitterns), Threskiornithidae (ibis and spoonbills) and Procellariidae (petrels, shearwaters and prions), and may be extremely rare or unknown in the other 18 families (Table 1).

Transmission

Examining the spread of avian influenza is difficult, hence most information on transmissibility is based on laboratory experiments (Alexander 1993). Factors contributing to virus transmission are complex, and variability exists between subtypes, bird species and environmental factors.

Subtypes of avian (Type A) influenza are identified by the combination of H (haemagglutinin) and N (neuraminidase) proteins (Office International Epizooties 2001) and are important when considering the potential for transmission and mutation. All 15 subtypes are known to infect birds but in nearly all cases, only subtypes with H5 and H7 are known to mutate to the highly pathogenic form (cf. Laudert *et al*. 1993; Office International Epizooties 2001). HPAIs have been documented to arise from LPAI viruses (Perdue *et al*. 1998), but are not normally known to change subtypes during an outbreak. However, evidence suggests that recombination can occur when birds are infected with multiple subtypes (Webster *et al*. 1973; Sharp *et al*. 1997; Hoffmann *et al*. 2000). Further, some evidence indicates that viruses which are better adapted to avian populations have a demonstrated ability to prevent infections of other strains (Sharp *et al*. 1997). This may imply that wild birds that currently maintain well adapted LPAI viruses are less likely to transmit HPAI.

In most cases mutation into highly virulent viruses takes place only in domestic poultry, which occurs after their exposure to LPAI viruses. The only known outbreak of HPAI in wild birds occurred in Common Terns in 1961 (Becker 1966). Wild birds are implicated as important in this initial stage of transmission, but are not considered to be reservoirs of highly pathogenic strains. In comparison to wild birds, which do not normally show symptoms of disease, poultry are highly susceptible to H5 and H7 subtypes. Hence, subtypes that do not appear to affect wild birds have caused fatal diseases in poultry and other domestic birds. Birds that become exposed and survive infection may excrete virus for up to 14 days, orally and in faeces (Kida *et al*. 1980). While this, in theory, may provide opportunity for wild birds to spread the virus over a large distance, there is no documented evidence of this occurring for HPAI viruses. In most cases, secondary spread of HPAI has been associated with human activity, including live poultry markets (Panigrahy *et al*. 2002), rather than wild bird hosts (Wells 1963; Alexander 1993; Westbury 1998; Swayne and Suarez 2000).

Water is a likely medium for the transfer of non-virulent avian influenza and partially explains the high prevalence of the virus in Anseriformes and Charadriiformes, species of which congregate in large numbers in wetlands. The virus can remain infective in freshwater lakes for 4 days at 22°C, over 30 days at 0°C (Webster *et al*. 1978), or up to 200 days at 17°C at higher concentrations (Stallknecht *et al*. 1990*b*). This indicates a potential role in the transfer of the virus to poultry via contaminated water supplies sourced from dams, wetlands and other waterbird refuges. The duration of infectivity of water is also shown to decrease with increased salinity and pH (Stallknecht *et al*. 1990*a*), which may have implications for the maintenance of the virus in shorebirds and seabirds, and the management of water used in poultry production.

In some studies, a high prevalence of the virus and antibodies have been recovered from the eggs of waterbirds (Narayan *et al*. 1969; Romvary *et al*. 1980; Cappucci *et al*. 1985). Breeding areas of Charadiiformes often involve large numbers of eggs at specific sites (Lane 1987; Pringle 1987), which may provide an opportunity for sampling for avian influenza. However, the role of eggs in the transmission or maintenance of the virus is unknown.

Avian influenza in Australia

The role of wild animals in the introduction, maintenance and transmission of disease is largely dependent on a range of ecological factors, including the distribution and density of susceptible wild animal disease hosts (Animal Health Australia 2003). The risks associated with wild birds introducing H5N1 or other subtypes of avian influenza are virtually impossible to quantify with current information. There is insufficient knowledge of the epidemiology and transmission of avian influenza viruses and a lack of reliable information on the interchange of many birds between Asia and Australia, particularly of the Anatidae and Ardeidae. Moreover, avian influenza viruses are highly unpredictable and have a documented propensity for mutation. Review of current knowledge of bird movements and avian influenza in Australia is important for identifying the focus for future research and targeting species, timing and regions for surveillance.

In total, 99 bird species are known to move between Asia and Australia (Appendix). Of these, 63 undertake frequent migration, 20 travel occasionally and 16 rarely visit. Shorebirds (Charadriiformes) regularly migrate to Asia, but are mainly aggregated along Australian coastlines and at specific inland wetlands. In contrast, ducks and geese (Anseriformes) and other nomadic waterbirds are widely distributed but rarely move from the Australian mainland. Pelagic birds (Procellariiformes and Pelecaniformes) are annual or partial migrants, and are occasionally known to carry the virus but are rarely observed inside the continental shelf. Other migratory species of northern and north-eastern Australia travel through the Torres Strait Islands during winter but are unlikely to carry avian influenza. The risk to Australia appears to be in the association between shorebirds, which potentially harbour avian influenza viruses, and Australian ducks and geese. If infected, these ducks and geese could potentially spread virus to poultry farms as they disperse from coastal areas. If affected, poultry would then have the ability to transmit virus to humans. However, to date the transmission of avian influenza from poultry to humans is rare and has been associated with only a small number of viruses, mainly of Asian origin (Horimoto and Kawaoka 2001; Baigent and McCauley 2003; Katz 2003).

By definition, HPAI has the potential for very serious and rapid spread, irrespective of borders, which is of serious socio-economic and public health consequence, and is of importance in the international trade of livestock and livestock products. In Australia, current procedures for the management of incursions of HPAI within the poultry industry involve eradication. The five previous outbreaks of HPAI in the Australian poultry industry were eradicated by 'stamping out', a procedure involving the destruction of all potentially susceptible birds (Animal Health Australia 2003). However, the destruction of wild birds is unlikely to be effective, useful or practical in preventing the spread of the virus. Management of the virus should instead focus on ensuring that wild birds do not come into contact with domestic birds, either by direct contact or by way of contaminated water (Animal Health Australia 2003).

The Australian poultry industry is small in comparison to that of many other countries, including Hong Kong and China (Animal Quarantine Policy Branch 2001). The main areas within Australia for poultry production are usually sufficiently isolated from one another (Animal Health Australia 1996) to provide some protection against widespread transmission of exotic disease. Where poultry (and susceptible animals) exhibit a contiguous or near-contiguous population, the risk of widespread disease transmission may increase substantially.

There are no surveillance or vaccination programs currently in place for endemic avian influenza in poultry. The chances of detecting avian influenza viruses in shorebirds appears small; however, in other studies, the chance of detection increases 5-fold if waterbirds that are in contact with shorebirds are targeted for surveillance (Suss *et al*. 1994). A number of potential models could be used for surveillance of wild birds. Surveillance may be more effective if set up where waterbirds have a greater risk of interacting with poultry, such as around free-range poultry establishments, 'backyard' operations, or where biosecurity measures are lacking. The interaction between these farms and other commercial operations is also important in understanding the persistence of avian influenza viruses and their contact with poultry. Surveillance in remote aggregations of waterbirds in Australia may therefore be less important than where concentrations of domestic poultry occur, for example, near capital cities and key regional areas of New South Wales, Victoria and Queensland (Animal Quarantine Policy Branch 2001).

As a result of their large population sizes, surveillance of wild birds is logistically difficult, and large sample sizes are required to provide statistically meaningful results. A more useful option might be to focus avian influenza work in wild birds on long-term, longitudinal studies in waterfowl, which share habitat with shorebirds, an approach that has been used elsewhere with very good results (Suss *et al*. 1994). This would give an indication of the spatial and temporal patterns of subtypes entering Australia, and could act to significantly improve understanding of the ecology of these viruses within Australia.

Conclusions

An understanding of the ecology of the viruses within the wild bird population is essential in assessing the risks to human health and production industries. Long-term surveys for viruses in wild birds are required to improve our understanding of the prevalence of LPAI viruses and the role they play in the transmission of avian influenza to poultry and humans. These surveys should target anatids where there are highest densities of Charadriiformes, and could be strategically coordinated between field naturalist societies, research groups (such as the Australian Wader Study Group) and government authorities. For detecting the introduction of exotic viruses, sampling should focus on coastal floodplains of the north-west, along the central-east coastline and other important wetlands for Charadriiformes (Fig. 1). Knowledge of the interface between anatids and domestic poultry is needed for assessing the risks of virus transfer. The optimal time for sampling would occur when shorebirds first arrive in Australia (August–October). This period also coincides with suggestions that higher prevalence of avian influenza for these species occurs in spring. More accurate information is required on the movements of waterbirds (particularly Anatidae and Ardeidae) between Asia and Australia. This would aid our understanding of the importance of wild birds in introducing foreign subtypes of avian influenza as well as their potential to transmit other viruses, including Japanese encephalitis and Newcastle disease. Until such time as these data become available, Australia's preparedness against HPAI must focus on biosecurity at the wild bird–poultry interface.

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Appendix. Movements, abundance, and distribution of birds with Australian and Asian distributions

Information in this table is derived from Blakers *et al*. (1984), Marchant and Higgins (1990, 1993), Higgins and Davies (1996); Higgins (1999); Kingsford and Norman (2002) and Higgins and Peter (2003). For consistency, categories of Kingsford and Norman (2002) were used where possible. Aust.–Asia movements are categorised as Regular, Occasional, Rare, Unknown. Movements: Sedentary (S), Nomadic (N), Partial Migrant (PM), Annual Migrant (AM). Abundance: Abundant (A), Locally Abundant (LA), Common (C), Locally Common (LC), UnCommon (UC), Vagrant (V), Rare (R). Ecological information: Good, Moderate, Poor. Distribution: Continental, Northern (N), Eastern (E), Southern (S), Western (W), Pelagic and Coastal. Nomenclature follows Christidis and Boles (1994). Asterisks indicate isolations of avian influenza virus

Taxon	Aust.–Asia movements	Movements	Timing of movement to Australia	Australian abundance	Ecological information	Australian distribution
Anseriformes						
Anatidae						
Plumed Whistling-Duck (*Dendrocygna eytoni*)*	Rare	N	Variable	LA	Moderate	N/SE
Wandering Whistling-Duck (*Dendrocygna arcuata*)	Regular	N	Variable	LA	Poor	N/NE
Radjah Shelduck (*Tadorna radjah*)	Rare	N	Variable	MC	Poor	N
Cotton Pygmy-Goose (*Nettapus coromandelianus*)	Occasional	S	Variable	UC	Poor	NE
Green Pygmy-Goose (*Nettapus pulchellus*)	Occasional	S	Variable	C	Poor	N
Pacific Black Duck (*Anas superciliosa*)*	Rare	S-N	Variable	A	Good	Continental
Northern Shoveler (*Anas clypeata*)*	Rare	AM	Aug, Sep	V	Poor	SW/SE
Grey Teal (*Anas gracilis*)*	Occasional	N	Variable	A	Good	Continental
Northern Pintail (*Anas acuta*)*	Rare	AM	Aug, Sep	V	Poor	SW
Garganey (*Anas querquedula*)*	Rare	AM-N	Aug, Sep	R-UC	Poor	N
Hardhead (*Aythya australis*)	Rare	N	Variable	LA-C	Moderate	Continental
Anseranatidae						
Magpie Goose (*Anseranas semipalmata*)	Regular	N	Variable	LA-C	Good	N
Procellariiformes						
Procellariidae						
Streaked Shearwater (*Calonectris leucomelas*)	Regular	AM	May, Jun	UC	Poor	Pelagic
Wedge-tailed Shearwater (*Puffinus pacificus*)*	Occasional	AM	Aug, Sep	A	Poor	Pelagic
Flesh-footed Shearwater (*Puffinus carneipes*)	Occasional	AM	Sep, Oct	A	Poor	Pelagic
Sooty Shearwater (*Puffinus griseus*)	Occasional	AM	Sep, Oct	MC	Poor	Pelagic
Short-tailed Shearwater (*Puffinus tenuirostris*)	Regular	AM	Aug, Sep	A	Poor	Pelagic
Hydrobatidae						
Matsudaira's Storm-Petrel (*Oceanodroma matsudairae*)	Regular	AM	Jul, Aug	UC	Poor	Pelagic
Pelecaniformes						
Phaethontidae						
Red-tailed Tropicbird (*Phaethon rubricauda*)	Regular	N	Variable	LA	Poor	Pelagic
White-tailed Tropicbird (*Phaethon lepturus*)	Regular	N	Variable	UC	Poor	Pelagic
Sulidae						
Masked Booby (*Sula dactylatra*)	Regular	PM	Sep, Oct	LA	Poor	Pelagic
Red-footed Booby (*Sula sula*)	Regular	PM	Jun, Jul	LA	Poor	Pelagic
Brown Booby (*Sula leucogaster*)	Regular	PM	Variable	LA	Poor	Pelagic
Anhingidae						
Darter (*Anhinga melanogaster*)	Rare	N	Variable	MC	Moderate	Continental
Phalacrocoracidae						
Little Pied Cormorant (*Phalacrocorax melanoleucos*)	Occasional	N	Variable	A	Good	Continental
Little Black Cormorant (*Phalacrocorax sulcirostris*)	Occasional	N	Variable	A	Good	Continental
Great Cormorant (*Phalacrocorax carbo*)*	Rare	N	Variable	A	Good	Continental
Pelecanidae						
Australian Pelican (*Pelecanus conspicillatus*)	Occasional	N	Variable	LA-C	Good	Continental
Fregatidae						
Great Frigatebird (*Fregata minor*)	Regular	N	Variable	LA	Poor	Pelagic
Lesser Frigatebird (*Fregata ariel*)	Regular	N	Variable	LA	Poor	Pelagic
Ciconiiformes						
Ardeidae						
White-faced Heron (*Egretta novaehollandiae*)	Occasional	S-N	Variable	C	Moderate	Continental
Little Egret (*Egretta garzetta*)	Occasional	S-N	Variable	C	Good	N/E/SE
Eastern Reef Egret (*Egretta sacra*)	Occasional		Variable	C	Poor	Coastal
White-necked Heron (*Ardea pacifica*)	Rare	N	Variable	MC	Moderate	Continental

(*continued*)

Appendix. (*continued*)

Taxon	Aust.–Asia movements	Movements	Timing of movement to Australia	Australian abundance	Ecological information	Australian distribution
Pied Heron (*Ardea picata*)	Regular	S-N	Dec, Feb	LA-C	Moderate	N
Great Egret (*Ardea alba*)	Occasional	N	Variable	C	Good	Continental
Intermediate Egret (*Ardea intermedia*)	Rare	PM-N	Unknown	C	Moderate	N/E/SE
Cattle Egret (*Ardea ibis*)	Rare	PM	Unknown	LA-C	Moderate	SW/N/E/SE
Striated Heron (*Butorides striatus*)	Rare	S	Variable	LC	Poor	Coastal
Nankeen Night Heron (*Nycticorax caledonicus*)	Occasional	N-S	Variable	C	Poor	N/E/SE/W
Little Bittern (*Ixobrychus minutus*)	Occasional	AM	Aug	UC	Poor	SW/SE/E
Black Bittern (*Ixobrychus flavicollis*)	Unknown	S-N	Variable	LC-UC	Poor	N/E
Threskiornithidae						
Glossy Ibis (*Plegadis falcinellus*)*	Occasional	N	Variable	LA	Moderate	Continental
Australian White Ibis (*Threskiornis molucca*)	Occasional	S-N	Variable	LA-C	Good	Continental
Straw-necked Ibis (*Threskiornis spinicollis*)	Occasional	S-N	Variable	C	Good	Continental
Royal Spoonbill (*Platalea regia*)	Occasional	S-N	Variable	C	Moderate	N/E/SE/W
Gruiformes						
Rallidae						
Spotless Crake (*Porzana tabuensis*)	Unknown	S-N	Unknown	C-UC	Poor	SW/SE
White-browed Crake (*Porzana cinerea*)	Unknown	S	Unknown	LC	Poor	N
Purple Swamphen (*Porphyrio porphyrio*)	Unknown	N	Unknown	C	Moderate	SW/E
Charadriiformes						
Scolopacidae						
Latham's Snipe (*Gallinago hardwickii*)	Regular	AM	Aug	LC	Poor	SE/E
Swinhoe's Snipe (*Gallinago megala*)	Regular	AM	Aug	MC	Poor	SE/E
Black-tailed Godwit (*Limosa limosa*)	Regular	AM	Sep, Oct	MC	Moderate	Continental
Bar-tailed Godwit (*Limosa lapponica*)	Regular	AM	Sep, Oct	C	Moderate	Continental
Little Curlew (*Numenius minutus*)	Regular	AM	Oct	LA-MC	Moderate	N
Whimbrel (*Numenius phaeopus*)	Regular	AM	Sep, Oct	MC	Poor	Coastal
Eastern Curlew (*Numenius madagascariensis*)	Regular	AM	Sep, Oct	MC	Moderate	Coastal
Marsh Sandpiper (*Tringa stagnatilis*)	Regular	AM	Oct, Nov	MC-UC	Moderate	Continental
Common Greenshank (*Tringa nebularia*)	Regular	AM	Oct, Nov	C	Moderate	Continental
Wood Sandpiper (*Tringa glareola*)	Regular	AM	Jul, Oct	MC-UC	Moderate	Continental
Terek Sandpiper (*Xenus cinereus*)	Regular	AM	Sep, Oct	MC-UC	Moderate	Coastal
Common Sandpiper (*Actitis hypoleucos*)	Regular	AM	Sep, Oct	MC-UC	Moderate	Continental
Grey-tailed Tattler (*Heteroscelus brevipes*)	Regular	AM	Sep, Oct	C	Poor	Coastal
Wandering Tattler (*Heteroscelus incanus*)	Regular	AM	Nov	UC	Poor	Coastal
Ruddy Turnstone (*Arenaria interpres*)*	Regular	AM	Sep, Oct	MC	Moderate	Continental
Asian Dowitcher (*Limnodromus semipalmatus*)	Regular	AM	Sep, Oct	R	Poor	Coastal
Great Knot (*Calidris tenuirostris*)	Regular	AM	Sep, Oct	LA-UC	Moderate	Coastal
Red Knot (*Calidris canutus*)*	Regular	AM	Sep, Oct	C	Poor	Coastal
Sanderling (*Calidris alba*)	Regular	AM	Sep, Oct	MC	Poor	Coastal
Red-necked Stint (*Calidris ruficollis*)*	Regular	AM	Sep, Oct	A-C	Moderate	Continental
Long-toed Stint (*Calidris subminuta*)	Regular	AM	Aug	UC	Moderate	Continental
Pectoral Sandpiper (*Calidris melanotos*)	Occasional	AM	Oct, Nov	UC	Poor	Continental
Sharp-tailed Sandpiper (*Calidris acuminata*)	Regular	AM	Sep, Oct	C	Moderate	Continental
Curlew Sandpiper (*Calidris ferruginea*)	Regular	AM	Sep, Oct	A-C	Moderate	Continental
Broad-billed Sandpiper (*Limicola falcinellus*)	Regular	AM	Sep, Oct	MC-UC	Poor	Coastal
Jacanidae						
Comb-crested Jacana (*Irediparra gallinacea*)	Rare	S	Variable	C	Poor	N/NE
Charadriidae						
Grey Plover (*Pluvialis squatarola*)	Regular	AM	Sep, Oct	MC	Moderate	Coastal
Lesser Sand Plover (*Charadrius mongolus*)	Regular	AM	Sep, Oct	MC	Poor	Coastal
Greater Sand Plover (*Charadrius leschenaultii*)	Regular	AM	Sep, Oct	UC	Moderate	Coastal
Oriental Plover (*Charadrius veredus*)	Regular	AM	Oct, Nov	LA-UC	Poor	N/SE
Masked Lapwing (*Vanellus miles*)	Unknown	S–N	Unknown	C	Good	N/E/SE
Glareolidae						
Oriental Pratincole (*Glareola maldivarum*)	Regular	AM	Nov	LA-UC	Moderate	N/W
Australian Pratincole (*Stiltia isabella*)	Regular	AM	Aug, Sep	C-UC	Moderate	Continental

(*continued overleaf*)

Appendix. (*continued*)

Taxon	Aust.–Asia movements	Movements	Timing of movement to Australia	Australian abundance	Ecological information	Australian distribution
Laridae						
Lesser Crested Tern (*Sterna bengalensis*)	Unknown	S	Unknown	C	Poor	Coastal
Crested Tern (*Sterna bergii*)	Unknown	S	Unknown	C	Poor	Coastal
Roseate Tern (*Sterna dougallii*)	Regular	S–N	Variable	C-UC	Poor	Coastal
Black-naped Tern (*Sterna sumatrana*)	Unknown	S–N	Unknown	LC	Poor	Coastal
Common Tern (*Sterna hirundo*)*	Regular	AM	Sep, Oct	MC	Good	Coastal
Little Tern (*Sterna albifrons*)	Regular	AM	Variable	MC-UC	Moderate	Coastal
Bridled Tern (*Sterna anaethetus*)	Regular	AM	Jan, Feb	C	Poor	Coastal
Sooty Tern (*Sterna fuscata*)*	Regular	AM	Variable	A	Moderate	Coastal
Whiskered Tern (*Chlidonias hybridus*)	Regular	AM–N	Sep, Oct	A-C	Moderate	Continental
White-winged Black Tern (*Chlidonias leucopterus*)	Regular	AM–N	Sep, Oct	MC-UC	Poor	Continental
Columbiformes						
Columbidae						
Superb Fruit-Dove (*Ptilinopus superbus*)	Regular	N	Sep, Oct	UC	Moderate	E
Pied Imperial-Pigeon (*Ducula bicolor*)	Regular	AM	Aug, Sept	C-MC	Moderate	N
Cuculiformes						
Cuculidae						
Brush Cuckoo (*Cacomantis variolosus*)	Regular	AM	Sep, Oct	MC	Moderate	N/E
Common Koel (*Eudynamys scolopacea*)	Regular	PM	Sep, Oct	MC	Moderate	N/E
Channel-billed Cuckoo (*Scythrops novaehollandiae*)	Regular	PM	Sep, Oct	MC	Moderate	N/S
Coraciiformes						
Halcyonidae						
Buff-breasted Paradise-Kingfisher (*Tanysiptera sylvia*)	Regular	AM	Sep, Oct	UC	Moderate	NE
Forest Kingfisher (*Todiramphus macleayii*)	Regular	AM	Sep, Oct	C	Good	NE/E
Sacred Kingfisher (*Todiramphus sanctus*)	Regular	AM	Sept, Oct	C	Good	Continental
Meropidae						
Rainbow Bee-eater (*Merops ornatus*)	Regular	AM	Sept, Oct	C	Good	Continental
Coraciidae						
Dollarbird (*Eurystomus orientalis*)	Regular	AM	Sept, Oct	MC	Good	N/E
Passeriformes						
Meliphagidae						
Brown-backed Honeyeater (*Ramsayornis modestus*)	Occasional	S	Sept, Oct	LC	Poor	NE
Dicruridae						
Spangled Drongo (*Dicrurus bracteatus*)	Regular	S–AM	Sep, Oct	C	Moderate	NE
Campephagidae						
Cicadabird (*Coracina tenuirostris*)	Regular	AM	Sep, Oct	UC-MC	Poor	NE
Oriolidae						
Olive-backed Oriole (*Oriolus sagittatus*)	Occasional	PM-AM	Sep, Oct	C-MC	Moderate	N/E
Sturnidae						
Metallic Starling (*Aplonis metallica*)	Regular	AM	Sep, Oct	C-LC	Moderate	NE