

Research, part of a Special Feature on [Risk mapping for avian influenza: a social-ecological problem](#)
Will Wallace's Line Save Australia from Avian Influenza?

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ABSTRACT. Australia is separated from the Asian faunal realm by Wallace's Line, across which there is relatively little avian migration. Although this does diminish the risk of high pathogenicity avian influenza of Asian origin arriving with migratory birds, the barrier is not complete. Migratory shorebirds, as well as a few landbirds, move through the region on annual migrations to and from Southeast Asia and destinations further north, although the frequency of infection of avian influenza in these groups is low. Nonetheless, high pathogenicity H5N1 has recently been recorded on the island of New Guinea in West Papua in domestic poultry. This event increases interest in the movements of birds between Wallacea in eastern Indonesia, New Guinea, and Australia, particularly by waterbirds. There are frequent but irregular movements of ducks, geese, and other waterbirds across Torres Strait between New Guinea and Australia, including movements to regions in which H5N1 has occurred in the recent past. Although the likelihood of avian influenza entering Australia via an avian vector is presumed to be low, the nature and extent of bird movements in this region is poorly known. There have been five recorded outbreaks of high pathogenicity avian influenza in Australian poultry flocks, all of the H7 subtype. To date, Australia is the only inhabited continent not to have recorded high pathogenicity avian influenza since 1997, and H5N1 has never been recorded. The ability to map risk from high pathogenicity avian influenza to Australia is hampered by the lack of quantitative data on the extent of bird movements between Australia and its northern neighbors. Recently developed techniques offer the promise to fill this knowledge gap.

Key Words: *avian influenza; Australia; bird migration; risk mapping.*

INTRODUCTION

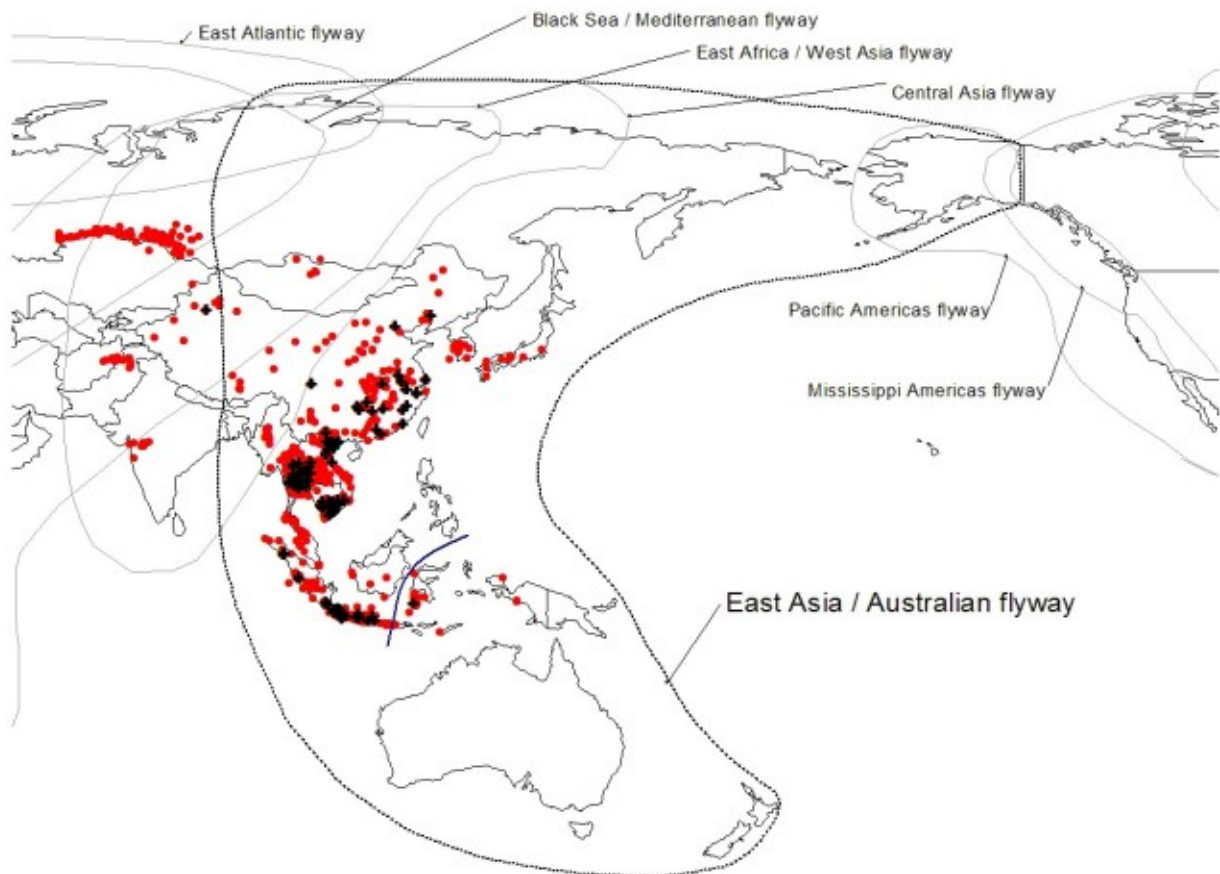
The isolation of the Australian biota from the remainder of the world is well known to every beginning student of biogeography. Wallace's Line, passing through the Indonesian archipelago between Bali and Lombok, forms a distinct boundary between the Asiatic and Australian faunal realms (Fig. 1). Although the separation between faunal realms is not absolute, there is remarkably little avian migration across the line (Dingle 2004). Some 34 species of shorebirds (Scolopacidae and Charadriidae) regularly migrate from the northern hemisphere to spend the northern winter in Australia along with 19 others, of which there are less than 10 recorded as vagrants (Christidis and Boles 2008), as do several shearwater species, notably the Short-tailed Shearwater (*Puffinus tenuirostris*) (see Fig. 1). Only 10 species of land birds from Eurasia regularly migrate to the Australo-Papuan region, of

which only two swifts, Fork-tailed Swift (*Apus pacificus*) and White-throated Needletail (*Hirunapus caudacutus*), penetrate far into continental Australia on a regular basis (Dingle 2004).

The longevity and geographic extent of highly pathogenic avian influenza (HPAI) epizootics, in particular H5N1, in poultry since 1997 continue to have serious socioeconomic consequences at a global level. Whether wild birds are implicated in the dissemination of H5N1 is debatable. It is sometimes argued that migratory birds are unlikely to be responsible for large-scale movements of HPAI, on the basis that "dead birds don't fly" (Williams 2005). However, Type A influenza occurs at high prevalence in many ducks and geese worldwide (Olsen et al. 2006), and recent experimental work suggests that mallard (*Anas platyrhynchos*) are capable of excreting high titres of H5N1 without showing clinical signs of disease

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Fig. 1. Epizootics (red dots) and human cases (+) of highly pathogenic avian influenza (HPAI) in the East Asian–Australasian Flyway (dashed line) 2003–2008. Wallace’s Line (solid line). Source: OIE 2006, Wetlands International 2006, FAO 2007, WHO 2008a,b.



(Keawcharoen et al. 2008). Although migratory birds may not be likely to regularly transfer HPAI over large distances, it is a possibility that can not be dismissed.

Incidents of HPAI continue to occur regularly in close proximity to the northern part of Australia in Indonesia. More human deaths from H5N1 have been reported in Indonesia than in any other country (WHO 2008b), with cases also recorded in domestic poultry from much of Indonesia (WHO 2008a). These Indonesian outbreaks were first documented by the WHO in poultry in February 2004 and humans in July 2005 (WHO 2008c), although there

are reports of a possible earlier Indonesian record in poultry in 2003 (Algers et al. 2008). More recently, H5N1 caused at least 93 deaths in chickens in three villages in West Papua on the island of New Guinea, which is on the Australian side of Wallace's Line, in July 2006 (OIE 2006; Fig. 2). No human cases were reported. Despite the close proximity of New Guinea, Australia remains the only continent, with the exception of Antarctica, that has not had a reported occurrence of HPAI of any type since 1997 (Sims and Turner 2008). In this paper we discuss why this might be the case and identify knowledge gaps that must be filled to adequately map avian influenza risk in Australia.

AVIAN INFLUENZA IN AUSTRALIAN WILD BIRDS

A wide range of low pathogenicity strains of avian influenza (LPAI) have been reported in wild bird species within Australia, including all H types except H10, H14, and H16 (Downie and Laver 1973, Downie et al. 1977, Mackenzie et al. 1984, Mackenzie et al. 1985, Nestorowicz et al. 1987, Rohm et al. 1996, Peroulis and O'Riley 2004, Tracey et al. 2004, Turner 2004, Hurt et al. 2006). Tracey et al (2004) and Sims and Turner (2008) provide an overview of these reports. Recent evidence supports the belief that the prevalence of avian influenza in wild birds in Australia is much lower than found elsewhere (Olsen et al. 2006). Since 2004, over 16,000 wild birds have been sampled for avian influenza in Australia, primarily ducks and shorebirds (Animal Health Australia 2006, 2007a, Haynes et al., *in press*). Only 1% of these have tested positive for avian influenza using real-time polymerase chain reaction (PCR), and subtypes were only identified from 0.3%; all of low pathogenicity (Haynes et al., *in press*). With the exception of H7 from a starling, which was likely to have been infected from poultry during the 1985 epizootic (Nestorowicz et al. 1987), HPAI has never been detected in wild birds in Australia, and H5N1 (LPAI or HPAI) has also not yet been detected.

Anseriformes and Charadriiformes are consistently identified as the primary reservoir of LPAI (Stallknecht and Shane 1988, Hanson 2003, Stallknecht and Brown 2008), which is consistent with detections from Australia's wild birds. Of importance, both LPAI H5 and LPAI H7 have been detected from wild anatids across New South Wales, Victoria, and Tasmania (Haynes et al., *in press*), which are potential sources of endemic strains of HPAI in poultry. Other subtypes detected have included H3N2 and H4N2 from ducks in Victoria, H4N8 from Rednecked Stints (*Calidris ruficollis*) on the central coast of New South Wales, H11N9 from Sharp-tailed Sandpipers (*C. acuminata*) on the central coast of New South Wales, and H13N6 from a 3–4-wk-old Silver Gull (*Larus novaehollandiae*) in Tasmania (Animal Health Australia 2006).

PREVIOUS OUTBREAKS OF HIGH PATHOGENICITY AVIAN INFLUENZA IN AUSTRALIA

Five outbreaks of high pathogenicity avian influenza have been recorded in commercial bird

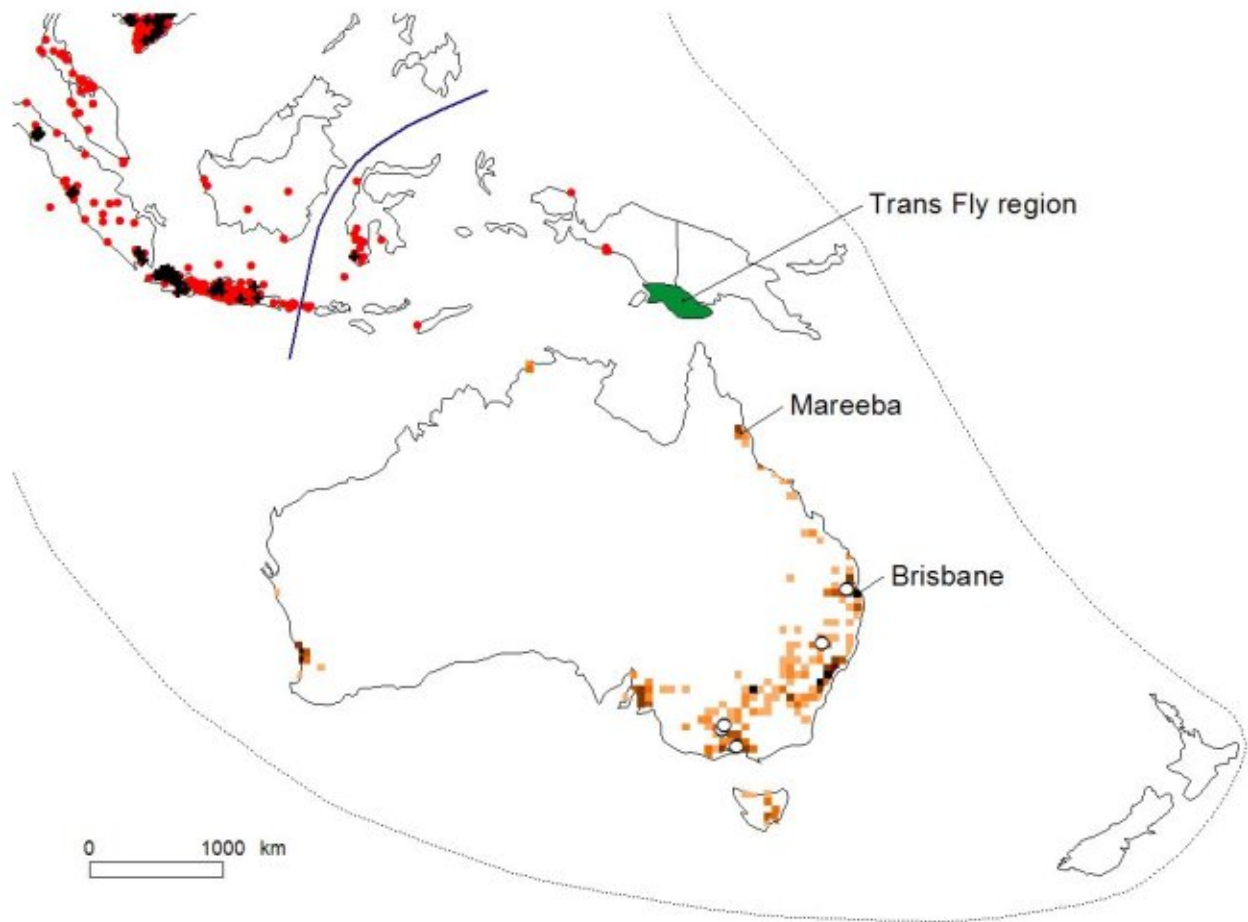
flocks in Australia (Tracey et al. 2004, Sims and Turner 2008), the earliest in 1976 and the most recent in 1997 (see Fig. 2). All of these were of the H7 subtype. The source of the earlier epizootics was not clearly identified, although domestic ducks were implicated in outbreaks in 1976 and 1992 because low virulence H7N7 was identified in ducks on farms adjacent to those on which the high pathogenicity strains were discovered. The 1997 outbreak was the most serious, affecting three farms in New South Wales, causing large-scale mortality amongst domestic chickens (Selleck et al. 2003). The role of wild birds in these outbreaks is controversial. In at least four of the five outbreaks, there was close association of the flocks in which the outbreaks occurred with wild waterfowl (Bunn 2004). However, the H7 subtype identified in the poultry flock was not recovered from any wild birds in the vicinity (Arzey 2004a,b). Bunn (2004) notes that this has also been the case in numerous outbreaks internationally, and this fact does not necessarily infer that wild birds are not implicated in the origin of the outbreaks.

The particular H7 lineage responsible for all the Australian outbreaks is described by Turner (2004) as a distinct subset of the Eurasian lineage, suggesting to him that it may have been imported via the East Asian-Australasian Flyway. However, Arzey (2005) emphasizes the unique nature of the lineage, suggesting that continual interchange with the Eurasian flyways does not occur. Interestingly, the same virus strain was also isolated from farmed emu chicks from one of the farms involved in the 1997 outbreak (Selleck et al. 2003), although it did not produce signs of clinical disease in these animals. Because the emus were housed in open pens, they had the opportunity for contact with wild birds and may have been the source of the entire outbreak.

MIGRATORY PATHWAYS BETWEEN ASIA AND AUSTRALIA

There are large-scale annual migrations of shorebirds along the East Asian-Australasian Flyway (Fig. 1). Many of these birds come from areas in which highly pathogenic avian influenza cases have been confirmed in the recent past. Further, their migration routes bring them down the heavily populated east coast of Australia in which there are large flocks of commercial poultry (Fig. 2). However, despite the fact that avian influenza has been recorded from shorebirds, no cases of

Fig. 2. Previous epizootics of HPAI in Australia (open circles) in relation to Wallace's Line (solid line), poultry density (heads km⁻²: squares, color gradation from fawn to black in steps 17–10, 10–50, 50–100, 100–200, 200–500, 500–1000, 1000–2500), and important wetlands for Charadriiformes (solid triangles). Source: Poultry density modified from Wetlands International (2006) and FAO (2007).



HPAI have been recorded from any of the shorebirds that migrate down the Australian coast. Similarly, although AI has been found in numerous species of shorebirds in North America, highly pathogenic strains have not been found (Krauss et al. 2007). The risk of introduction of HPAI from this route is therefore probably very low. The primary role of wild birds in avian influenza in Australia is in maintaining low pathogenicity strains. These include H5 and H7 subtypes, which may mutate into high pathogenicity strains when introduced into poultry. It is this process that is thought to have occurred in the five high pathogenicity H7 subtype outbreaks described in Fig. 2.

Given the potential for ducks and geese to be responsible for long distance movements of H5N1 and the presence of the virus strain in the Indonesian archipelago, the possibility of H5N1 introduction by Anseriformes is of concern. Several species in this order are found both in northern Australia and in the southern parts of Indonesia and New Guinea (see Fig. 3) and may move between Australia and its northern neighbors. These include Wandering Whistling-Duck (*Dendrocygna arcuata*), Pacific Black Duck (*Anas superciliosa*), Grey Teal (*Anas gracilis*), Green Pigmy Goose (*Nettapus pulchellus*), and Magpie Goose (*Anseranas semipalmata*) (Beehler et al. 1986, Marchant and Higgins 1990).

In addition, the Plumed Whistling-Duck (*Dendrocygna eytoni*), which is widely distributed across northern Australia, occurs in small numbers in the Trans-Fly region of New Guinea, and the Spotted Whistling-Duck (*Dendrocygna guttata*), which is primarily occurs in New Guinea, is a vagrant to Cape York (Barrett et al. 2003). Movements of these species between Australia, the southern parts of New Guinea, and the Indonesian archipelago are poorly understood. None of them are known to have regular migrations from Australia to beyond the southern parts of New Guinea into Indonesia, but they are highly dispersive.

A large number of waterbirds, including egrets, ibis, pelicans, and ducks move between the Trans-Fly region of New Guinea and northern Australia (Halse et al. 1996, Dingle 2004). This region has large areas of savannah very similar to those in northern Australia and is described as a small piece of Australia isolated in southern New Guinea by Beehler et al. (1986). This region is the most likely point of exchange between Australian birds and potentially infected individuals from elsewhere in the Indonesian archipelago. Here waterbirds that are predominantly Asian or New Guinean in origin mix with species that are predominantly Australian. The Trans-Fly region is almost 1000 km from the most recent outbreak of H5N1 in West Papua reported in 2006 (see Fig. 2). However, the number of birds moving, and the frequency with which they move between the Trans-Fly and Australia or through the region to elsewhere in New Guinea and the Indonesian archipelago is poorly known (Dingle 2004, Tracey et al. 2004). Further, whether H5N1 is now endemic in a wild bird reservoir in West Papua is unknown. If a wild bird were to act as a vector for AI into Australia, the little evidence that exists suggests that this region is a possible pathway for movement of the virus.

Geering et al. (1998) report the recovery in Dasa Majur, West Papua, quite close to the villages where H5N1 has been reported (see Fig. 4), of an Intermediate Egret *Ardea intermedia* that had been banded at Campbell's Island on the Murray River in southern Australia. Recent mortalities of Little (*Egretta garzetta*) and Great (*Ardea alba*) Egrets from HPAI H5N1 in Hong Kong (Hong Kong Information Services Department 2007, 2008) demonstrate that egrets are susceptible to H5N1 and may well be capable of carrying H5N1. What is entirely unknown is whether movements of egrets

in the reverse direction from West Papua to southern Australia occur and whether these movements are at all common.

MOVEMENTS AND MAINTENANCE OF AVIAN INFLUENZA WITHIN AUSTRALIA

Even if HPAI were to arrive in Northern Australia in migrating waterbirds, population density of humans, and thus of domestic poultry, is very low in this region. Whether it would be able to spread into areas where it was capable of affecting poultry flocks and hence humans is unclear. Most movements of waterbirds across inland Australia are driven by irregular rainfall events (Kingsford and Norman 2002), and changes in distribution and abundance of waterbirds may occur at regional and subcontinental scales during these events (Roshier et al. 2001, 2002). During these events, dense mixed-species flocks gather on ephemeral water bodies (up to 20 species at densities in excess of 35 ha⁻¹, Kingsford and Norman 2002), with the potential for cross-species transmission. Many of the species listed above as moving between the Trans-Fly area of New Guinea and northern Australia are essentially tropical in distribution, for example the Green Pigmy Goose, the Wandering Whistling-Duck, and the Magpie Goose (see Fig. 3) and, with the exception of the poultry production areas in Mareeba in northern Queensland and around Brisbane (see Fig. 2), mostly do not overlap in distribution with major poultry production regions. However, some species occasionally move in small numbers into southern regions of Australia in response to rainfall and flooding events, as occurred in 2007 when Magpie Geese bred in the Riverina for the first time in many decades (Mike Schultz, *personal communication*). Wandering Whistling-Ducks have also been recorded as far south as Victoria and south western, Western Australia (Barrett et al. 2003). Numerous other species of waterbirds are known to be highly dispersive within Australia and could form links between the northern wetlands and southern wetlands close to major poultry production areas. Another potential concern is that avian influenza, although only low pathogenicity strains to date, has been found in White Ibis (Epstein et al. 2006), which have increased dramatically in the last few years, particularly in association with humans. These might form a potential direct transfer route between

Fig. 3. Distribution of (a) Magpie Goose (*Anseranas semipalmata*), (b) Wandering Whistling-Duck (*Dendrocygna arcuata*), (c) Cotton Pygmy Goose (*Nettapus coromandelianus*), (d) Pacific Black Duck (*Anas superciliosa*), (e) Grey Teal (*Anas gracilis*), and (f) Radjah Shelduck (*Tadornis radjah*) in Southeast Asia and Australasia. Source: Frith 1982, Wetlands International 2006. Wallace's Line (solid line). Sources differ on the distribution and degree of range overlap in Wallacea of Grey Teal and the closely related Indonesian Teal (*Anas gibberifrons*) (cf., Kear and Hulme 2005).

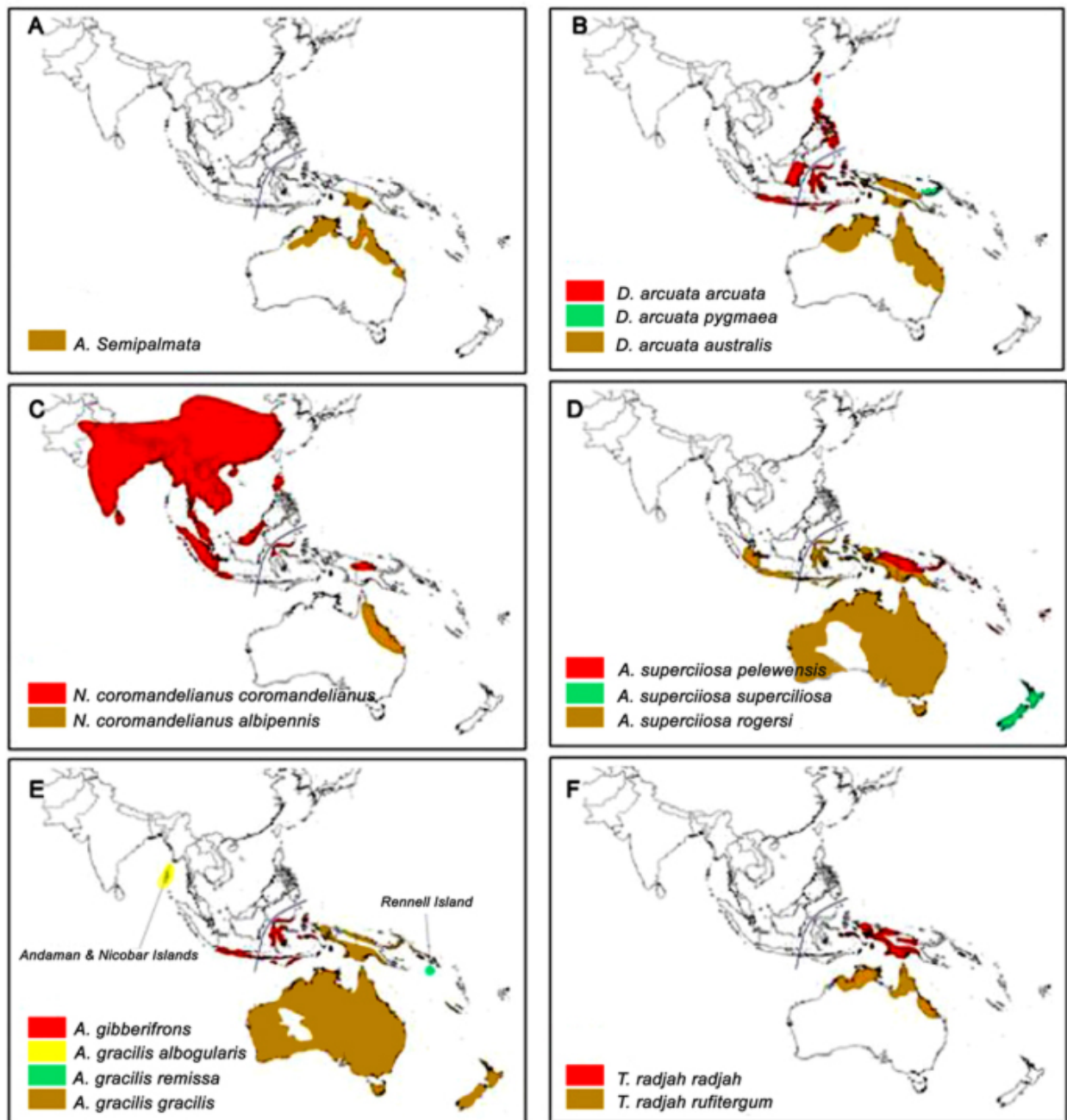
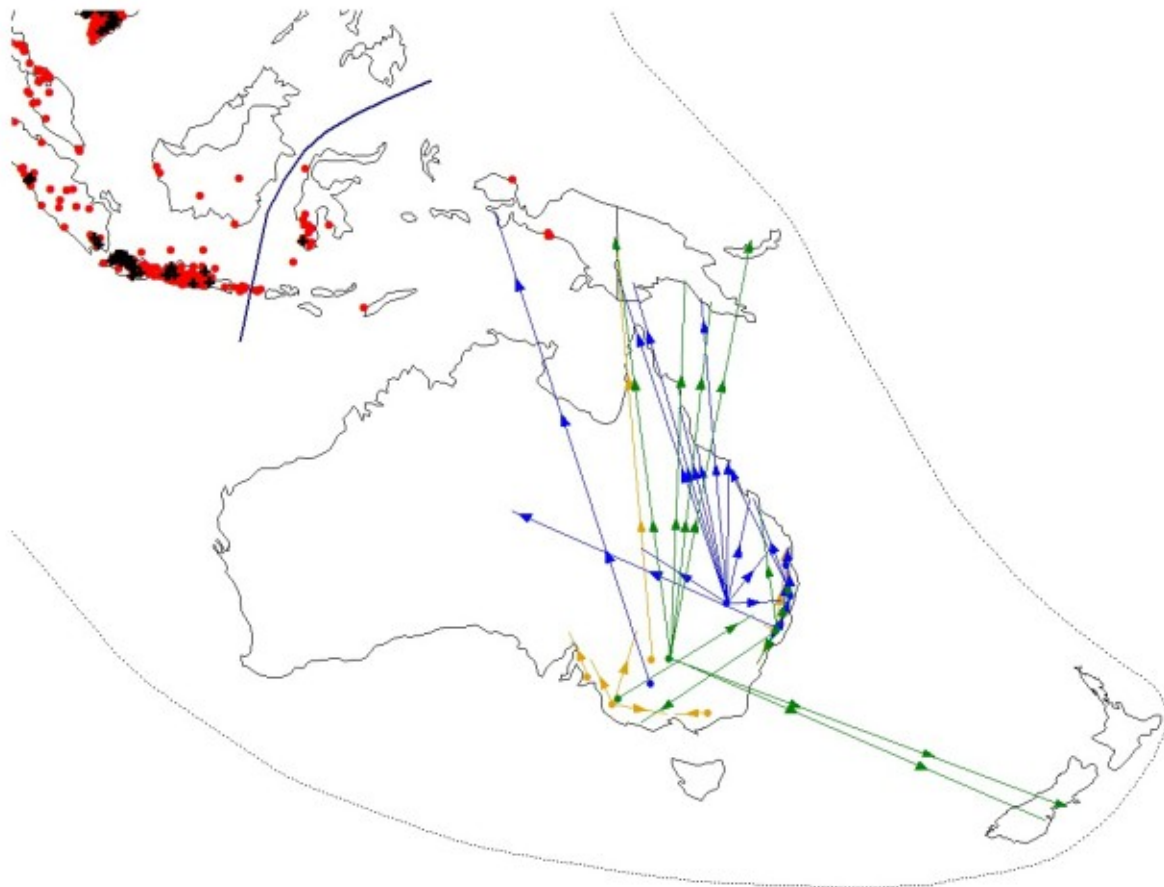


Fig. 4. Movements of banded Great (*Ardea alba*) (orange arrows), Intermediate (*Ardea intermedia*) (green arrows), and Little (*Egretta garzetta*) (blue arrows) Egret in Australasia in relation to epizootics (red dots) and human cases (+) of HPAI. Wallace's Line (solid line). Source: Geering et al. 1998, OIE 2006, Wetlands International 2006, FAO 2007, WHO 2008a,b.



the dispersive ducks and geese in northern Australia and high-density human populations in the southern part of the continent.

TOWARD RISK MAPPING FOR HPAI WITHIN AUSTRALIA: CRITICAL INFORMATION GAPS

Before risk mapping can be undertaken, it is necessary to determine to what the risk applies. A map of a risk to human health may be quite different from a map of risk to domestic poultry, which in turn may be very different from a map of risk to wild bird health.

Risk to human health

Human and avian influenza viruses are closely related and it is likely that some genetic material of all human influenza viruses originated in birds (e.g., Gamblin et al. 2004). However, only a small number of avian influenza viruses have been known to infect humans directly, including H5N1, H7N2, H7N3, H7N7 and H9N2. HPAI H5N1, in particular, has caused international public health concern because of its ability to cause death in humans. To date, H5N1 primarily causes zoonotic disease in poultry and unusually has caused mortality in wild birds (WHO 2008c). The transmission of HPAI H5N1 from infected poultry to humans is

inefficient, and serious infections in humans has typically only been associated with direct contact with sick or dying poultry. Although transmission of HPAI to humans via wild birds is possible (Guan et al. 2004, Sabirovic et al. 2007, Keawcharoen et al. 2008), and should not be dismissed (Flint 2007), the major risk factor for humans is contact with poultry during an epizootic. Therefore in Australia the most effective preventative measure from a human health perspective is to prevent and control epizootics in poultry, and in the event of an epizootic, to impose additional health precautions.

Risk to poultry

There are a number of possible explanations as to why has Australia not had an incident of HPAI since 1997, including (1) low prevalence of LPAI H5 or H7 in wild birds; (2) the absence of regular migratory movements of ducks and geese from Asia; (3) the significant decline in major waterbird breeding events during this period; (4) low poultry density; (5) enhanced biosecurity of commercial poultry operators, including limiting the contact with wild birds and the regular treatment of water; and (6) enhanced biosecurity of international and domestic trade of live wild birds, poultry, and poultry products.

The low prevalence of LPAI evident in Australia relative to other continents warrants consideration of the abundance, ecology, and movements of its wild avian hosts. Differences in prevalence between species and locations evident from overseas studies have been attributed to foraging behavior and movements (Munster et al. 2007). Prevalence of avian influenza in anatids of North America peaks with the concentration of first-year birds prior to migration (Hinshaw et al. 1985). In Australia movements and breeding events for waterbirds is related to surface waters and is considerably less predictable than for anatids in the northern and western hemispheres. Major breeding events for waterbirds have been few in Australia since the onset of drought in 2001, although several have recently occurred in early 2008 following major rains in eastern Australia. An obvious and consistent decline in abundance has been reported for many of Australia's Anseriformes and migratory and resident Charadriiformes (Nebel et al. 2008).

Although an outbreak of high pathogenicity avian influenza in wild birds would certainly trigger

concern, it is an outbreak in domestic poultry which would produce a large-scale management response. The Australian government veterinary emergency plan (AusVet plan) proposes a range of actions including preemptive slaughter of domestic poultry and movement controls if the disease is discovered in Australia (Animal Health Australia 2007b). The most logical basis for risk mapping is therefore a threat to domestic poultry populations, rather than to wild birds or humans.

The risk of HPAI emergence in poultry at any particular point in Australia will be a function of disease arrival in Australia, dispersal within Australia, and the presence of poultry farms. Of these three components, the distribution of poultry farms is clearly the best understood and most amenable to mapping. Large commercial farms are distributed, as might be expected, close to a large population centers, particularly along the eastern seaboard of Australia (Fig. 2). Significantly, there are no large-scale commercial farms in the far north of the continent, particularly in the Northern Territory and the northern part of Western Australia, in areas that are potentially subject to exposure to AI from waterbirds dispersing directly from Indonesia and other parts of Asia. At a trivial level, a risk map of risk from HPAI to domestic poultry in Australia would simply be the distribution of large poultry rearing areas as shown in Fig. 2, with those in the north of Australia being at a somewhat higher risk than those further south.

Although anecdotal information and limited band recovery data discussed above show that waterbirds do move between Australia, New Guinea and parts of the Indonesian archipelago, there is insufficient hard data on the frequency of such movements on which any form of quantitative risk map could be based. The potential role of Magpie Geese in avian influenza transmission in northern Australia is a critical question. The species is the sole representative of its family, so it should not necessarily be expected that its susceptibility to AI would be similar to other members of the Anseriformes. Magpie Geese do move between Australia and New Guinea, are present in large flocks and very high densities in northern Australia, and are widely dispersive. Although the numbers have decreased since European settlement along the densely populated eastern seaboard (Nye et al. 2007), they still can be found in this area in small numbers and therefore represent a potential route for AI to come into contact with domestic poultry

populations in southern Australia. Several thousand cloacal swabs and faecal samples have been taken from Magpie Geese in the northern Australia since 2004 and to date no avian influenza, either of high or low pathogenicity has been recorded (Animal Health Australia 2006, 2007a). Similarly, ibis and egrets are highly dispersive within Australia and some movements to and from New Guinea occur (Draffan et al. 1983, Taplin, *unpublished report*). The likelihood that ibis and egrets could act as a vector of high pathogenicity avian influenza in the Australian region is unknown.

FILLING THE KNOWLEDGE GAPS

Identifying research priorities for avian influenza is extremely complex and requires a broad range of expertise in areas of health sciences, diagnostics, virology, ecology, epidemiology, and disease control. Overarching research priorities in these areas have been identified by many others (see for example Sims 2006, FAO 2007, and Swayne 2008, other papers this issue). However significant knowledge gaps are apparent in host ecology that are essential for understanding and managing avian influenza in Australia. In assessing the likelihood of HPAI entering Australia from the north it is contemporary patterns of bird movement and populations with strong migratory connectivity that are of greatest interest. Populations and regions are connected ecologically when individuals seeking resources move between populations, (source and sink populations, sensu Pulliam and Danielson 1991) or move between breeding and nonbreeding ranges (migratory connectivity, sensu Webster et al. 2002). Connectivity may be strong or weak depending on whether all or part of the population undertakes migration, the nature and strength of environmental cues promoting movement, whether individuals are philopatric to sites or regions, and the existence of physical or climatic barriers to movement. Differences in connectivity may be reflected in population dynamics, individual breeding strategies, individual reproductive success, and differential selection pressures on parts of the population (Webster et al. 2002). The degree of connectivity, such as that found in closed local populations, partially connected populations (metapopulations) or broad-scale homogeneity (panmixis), results in recognizable patterns of genetic variation within and among populations. Highly variable molecular markers and advanced analytical techniques can be used on field samples

to infer the underlying connectivity pattern (Pearse and Crandall 2004). At the core of this is the power of using multiple genetic loci in better estimating past and present demographic parameters such as population size and migration rates relative to the power of estimates based on single loci. Multiple loci can readily overcome the problems of stochasticity and sampling inherent in the use of a single locus such as mitochondrial DNA (Edwards and Beerli 2000). One may also observe abrupt genetic change at geographic barriers such as a mountain range or strait, a geographic cline of differentiation, stepping stone gene flow in which migration occurs solely between neighboring populations, and sex-biased gene flow (Avisé 2000, Hellberg et al. 2002).

Compared to the massive bird banding programs, observational studies and use of radar in the northern Hemisphere, Australia has a much shorter and less successful history of following the movements of its migrant and nomadic species. The continent is simply too huge and the number of ornithologists too small for conventional methods to work for most species. In recent years the tools and methods for detecting contemporary connectivity have developed rapidly. They include satellite telemetry (Rodgers 2001), stable isotopes and trace elements in tissue to infer geographic origins (Rubenstein and Hobson 2004, Hobson 2005), avian parasites as population markers (Ricklefs et al. 2005), and genetic techniques that enable assignment of individuals to populations (e.g., Pritchard et al. 2000). These techniques can be used in combination to improve inference of population origins (Clegg et al. 2003).

Satellite telemetry

Tracking the movements of individual birds with transmitters (e.g., Beekman et al. 2002, Clausen et al. 2003, Fox et al. 2003, Petrie and Wilcox 2003, Miller et al. 2005) informs us directly of the frequency, timing, and extent of their movements. The only practical way of characterizing the real-time movements of nomadic waterfowl over large areas is to use satellite-based tracking systems that overcome many of the logistic problems associated with detecting movement from ground-based or aerial platforms (Roshier et al. 2006, 2008). The lightest solar-powered platform transmitter terminals (PTT) are less than 10 g currently and have a notional operating life of 5 yr or more. The light weight means that PTTs can be deployed on a wide

range of species, including many waterfowl, and have recently been deployed on 22 Wandering Whistling-Ducks at Lake Murray (7.22° S, 141.55° E, in the Western Province of Papua New Guinea (Roshier et al. *unpublished data*). In the 290 d since being released in August 2007, individual birds have moved up to 420 km southeast into the coastal areas of West Papua and south into the Trans-Fly region, which straddles the border between Papua New Guinea and West Papua.

Analyses of genetic structure in Australasian bird populations

Most Australian examples of the application of genetic methods to understanding population structure (Joseph and Omland, *unpublished data*) are from terrestrial birds. Rhymer et al. (2004) found that Pacific Black Duck *Anas superciliosa* populations of Australia and New Zealand do not fall into two discrete groups concordant with geography and attributed this to gene flow; alternatives involving current isolation, however, are nonetheless compatible with their data (Joseph and Omland, *unpublished data*), and multilocus data are necessary to discriminate between the alternatives. MtDNA has been favored in many studies for several reasons. It has a relatively fast mutation rate, is not subject to recombination, and it is inherited maternally, which reduces the effective population size. These criteria make it a useful population marker because population-specific variants accumulate relatively rapidly due to differentiation by the stochastic process of genetic drift. However, mtDNA may be less useful when populations have only recently diverged because even its rapid mutation rate may not have produced population specific markers (Pearse and Crandall 2004). In these cases, microsatellites from nuclear DNA are more effective for identifying the origin or kinship of individuals as they mutate more rapidly. Ultimately, the use of several loci of which just one would be mtDNA, leads to increased confidence in inferences about population differentiation.

Analyses of genetic differentiation between overseas and Australian populations of co-distributed waterbird species will inform us of current and historical connections between bird populations. A problem in interpretation is that if genetic differentiation is low, then either

movements between the regions and the populations occur on a regular basis, or the populations have been so recently separated that they have not assorted into separately defined genetic units. Recent inferential methods for resolving this problem (e.g., Hey and Nielsen 2004) used data from hypervariable loci such as the mtDNA control region and microsatellites.

Origins and structure of migrant populations in northern Australia

There are two main approaches for the biogeochemical analysis of tissues to infer geographic origins: analysis of stable isotope, and trace element composition (Hobson 2005, Hobson and Norris 2008). Analysis of stable isotope composition has been used to examine migration, food webs, diet, resource allocation to various tissues, and the effect of pollution (Hobson 1995, Chamberlain et al. 1997, Hobson 1999, Kelly 2000, Pain et al. 2004, Atkinson et al. 2005). In analyzing migratory connectivity, stable isotopes are useful in two ways: identifying geographic origins and/or population structure. If isotopic patterns exist within the range of the study species, then the location of the bird at the time various tissues were biologically active can be inferred from the analysis of isotope ratios in tissue samples (see review in Hobson 2005). In Australia the isotopic landscape for most elements is poorly known, and the potential for this work is untapped. For our purposes, this technique can tell us whether the geographical provenance of two or more individuals is the same even if we cannot directly observe them at their geographic origin. Tissues that have contrasting isotopic turnover rates have the potential to provide a more complete story of individual bird movements. For example, blood plasma, whole blood, and feathers provide insight into origins over the previous 3, 30, and 300 d, respectively (Hobson 2005). Stable isotopes of C and N can be used to distinguish tissues actively growing in mesic or xeric environments, and marine or terrestrial environments. Moreover, it is possible to identify those birds that are not in isotopic equilibrium with their current environment and therefore new arrivals (Marra et al. 1998).

Trace element composition in feather and other tissues is ultimately determined by diet. It provides spatial information when the uptake of trace elements into these tissues is influenced by surface

geology (reviewed by Hobson 2005). The elemental composition of feather has been shown to differ on fine geographical scales but may also show greater intrapopulation variation (Bortolotti et al. 1990). Although there may be difficulties in assignment of individuals to a population because of this variation, the technique can distinguish the origins of individuals and small groups with different migration or wintering behavior (e.g., Szep et al. 2003, also see review by Hobson 2005). The ability to differentiate between individuals with differing migration or wintering behavior adds another level of explanation in our quest to understand these migration systems.

CONCLUSIONS

Wallace's Line probably has protected Australia from the most recent H5N1 avian influenza epizootic. The absence of regular migratory movements of ducks and geese from Asia limits the vulnerability of Australia to outbreaks originating in Asia. Low pathogenicity AI is present in Australia, but at much lower prevalence than in many other parts of the world. Those outbreaks that have occurred in the past have probably resulted from mutations of low pathogenicity strains to high pathogenicity within Australia, rather than from the arrival of high pathogenicity strains from elsewhere. However, the relative isolation of Australia cannot be assumed to be a complete barrier against the arrival of high pathogenicity strains in wild birds. As well as the regular movements of shorebirds down the East Asian-Australasian Flyway, there is some evidence of irregular movements of ducks, geese, and other waterbirds from areas in Indonesia, particularly West Papua, in which H5N1 has been recently recorded. The difficulty in assessing and mapping this risk is that movement patterns of birds between Australia and its northern neighbors are poorly known. Filling these knowledge gaps is difficult because of the irregularity and unpredictability of these movements, together with enormous spatial scale over which they occur. A range of recent technological advances in assessing the extent of population separation and long-range migration means that the capacity to fill these knowledge gaps is now available.

Responses to this article can be read online at:
<http://www.ecologyandsociety.org/vol13/iss2/art41/responses/>

Acknowledgments:

H. McCallum's contribution was supported by a grant from the Australian Research Council (DP0451402), and J. Tracey acknowledges support from the Invasive Animal Cooperative Research Centre, and the Wildlife and Exotic Disease Preparedness Program.

LITERATURE CITED

- Algers, B., H. J. Blokhuis, D. M. Broom, P. Costa, M. Domingo, M. Greiner, D. Guemene, J. Hartung, F. Koenen, C. Müller-Graf, D. B. Morton, A. Osterhaus, D. U. Pfeiffer, R. Roberts, M. Sanaa, M. Salman, J. M. Sharp, P. Vannier, M. Wierup, and M. Wooldridge.** 2008. Animal health and welfare aspects of avian influenza and the risk of its introduction into the EU poultry holdings. Scientific Opinion of the Panel on Animal Health and Welfare. *The EFSA Journal* **715**:1-161.
- Animal Health Australia.** 2006. *Australian Wildlife Health Network. Animal Health Surveillance Quarterly Report* **11**:9-11. Available online at: <http://www.animalhealthaustralia.com.au/status/ahsq.cfm>.
- Animal Health Australia.** 2007a. *Australian Wildlife Health Network. Animal Health Surveillance Quarterly Report* **12**:9-10. Available online at: <http://www.animalhealthaustralia.com.au/status/ahsq.cfm>.
- Animal Health Australia.** 2007b. *Disease strategy: avian influenza. Version 3.2.* Australian Veterinary Emergency Plan (AUSVETPLAN), Edition 3. Available online at: http://www.animalhealthaustralia.com.au/programs/eap/ausvetplan_home.cfm.
- Arzey, G.** 2004a. The role of wild aquatic birds in the epidemiology of avian influenza in Australia. *Australian Veterinary Journal* **82**:377-378.
- Arzey, G.** 2004b. The role of wild aquatic birds in the epidemiology of avian influenza in Australia: Reply. *Australian Veterinary Journal* **82**:644-645.

- Arzey, G.** 2005. The role of wild waterfowl in the epidemiology of AI in Australia. *Australian Veterinary Journal* **83**:445-445.
- Atkinson, P. W., A. J. Baker, R. M. Bevan, N. A. Clark, K. B. Cole, P. M. Gonzalez, J. Newton, L. J. Niles, and R. A. Robinson.** 2005. Unravelling the migration and moult strategies of a long-distance migrant using stable isotopes: Red Knot (*Calidris canutus*) movements in the Americas. *Ibis* **147**:738-749.
- Avise, J. C.** 2000. *Phylogeography*. Harvard University Press, Cambridge, Massachusetts, USA.
- Barrett, G., A. Silcocks, S. Barry, R. Cunningham, and R. Poulter.** 2003. *New atlas of Australian birds*. CSIRO, Canberra, Australia.
- Beehler, B. M., T. K. Pratt, and D. A. Zimmerman.** 1986. *Birds of New Guinea*. Princeton University Press, Princeton, New Jersey, USA.
- Beekman, J. H., B. A. Nolet, and M. Klaassen.** 2002. Skipping swans: fuelling rates and wind conditions determine differential use of migratory stopover sites of Bewick's Swans *Cygnus bewickii*. *Ardea* **90**:437-460.
- Bortolotti, G. R., K. J. Szuba, B. J. Naylor, and J. F. Bendell.** 1990. Intrapopulation variation in mineral profiles of feathers of Spruce Grouse. *Canadian Journal of Zoology* **68**:585-590.
- Bunn, C. M.** 2004. The role of wild aquatic birds in the epidemiology of avian influenza in Australia. *Australian Veterinary Journal* **82**:644-644.
- Chamberlain, C. P., J. D. Blum, R. T. Holmes, X. H. Feng, T. W. Sherry, and G. R. Graves.** 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* **109**:132-141.
- Christidis, L., and W. E. Boles.** 2008. *Systematics and taxonomy of Australian birds*. CSIRO, Collingwood, Victoria, Australia.
- Clausen, P., M. Green, and T. Alerstam.** 2003. Energy limitations for spring migration and breeding: the case of Brent Geese *Branta bernicla* tracked by satellite telemetry to Svalbard and Greenland. *Oikos* **103**:426-445.
- Clegg, S. M., J. F. Kelly, M. Kimura, and T. B. Smith.** 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's Warbler (*Wilsonia pusilla*). *Molecular Ecology* **12**:819-830.
- Dingle, H.** 2004. The Australo-Papuan bird migration system: another consequence of Wallace's Line. *Emu* **104**:95-108.
- Downie, J. C., V. S. Hinshaw, and W. G. Laver.** 1977. The ecology of influenza: isolation of type A influenza viruses from Australian pelagic birds. *Australian Journal of Experimental Biology and Medical Science* **55**:635-643.
- Downie, J. C., and W. G. Laver.** 1973. Isolation of type A influenza virus from an Australian pelagic bird. *Virology* **51**:259-269.
- Draffan, R. D. W., S. T. Garnett, and G. W. Malone.** 1983. Birds of the Torres Strait: an annotated list and biogeographical analysis. *Emu* **83**:207-234.
- Edwards, S. V., and P. Beerli.** 2000. Perspective: gene divergence, population divergence, and the variance in coalescence time in phylogeographic studies. *Evolution* **54**:1839-1854.
- Epstein, J. H., J. McKee, P. Shaw, V. Hicks, G. Micalizzi, P. Daszak, A. M. Kilpatrick, and G. Kaufman.** 2006. The Australian White Ibis (*Threskiornis molucca*) as a reservoir of zoonotic and livestock pathogens. *EcoHealth* **3**:290-298.
- Flint, P. L.** 2007. Applying the scientific method when assessing the influence of migratory birds on the dispersal of H5N1. *Virology Journal* **4**:131-133.
- Food and Agriculture Organization of the United Nations (FAO).** 2007. *The global strategy for prevention and control of H5N1 highly pathogenic avian influenza*. FAO and the World Organisation for Animal Health (OIE), Rome, Italy. Available online at: http://www.fao.org/docs/eims/upload/210745/glob_strat_HPAI_apr07_en.pdf.
- Fox, A. D., C. M. Glahder, and A. J. Walsh.** 2003. Spring migration routes and timing of Greenland White-fronted Geese: results from satellite telemetry. *Oikos* **103**:415-425.

Frith, H. J. 1982. *Waterfowl in Australia*. Revised Edition. Angus and Robertson, Sydney, Australia.

Gamblin, S. J., L. F. Haire, R. J. Russell, D. J. Stevens, B. Xiao, Y. Ha, N. Vasisht, D. A. Steinhauer, R. S. Daniels, A. Elliot, D. C. Wiley, and J. J. Skehel. 2004. The structure and receptor binding properties of the 1918 influenza hemagglutinin. *Science* **303**:1838-1842.

Geering, D. J., M. Maddock, G. R. Cam, C. Ireland, S. A. Halse, and G. B. Pearson. 1998. Movement patterns of Great, Intermediate and Little Egrets from Australian breeding colonies. *Corella* **22**:37-46.

Guan, Y., L. L. M. Poon, C. Y. Cheung, T. M. Ellis, W. Lim, A. S. Lipatov, K. H. Chan, K. M. Sturm-Ramirez, C. L. Cheung, Y. H. C. Leung, K. Y. Yuen, R. G. Webster, and J. S. M. Peiris. 2004. H5N1 influenza: a protean pandemic threat. *Proceedings of the National Academy of Sciences* **101**:8156-8161.

Halse, S. A., G. B. Pearson, R. P. Jaensch, P. Kulmoi, P. Gregory, W. R. Kay, and A. W. Storey. 1996. Waterbird surveys of the Middle Fly River floodplain, Papua New Guinea. *Wildlife Research* **23**:557-569.

Hanson, B. A. 2003. *Temporal, spatial and species patterns of avian influenza viruses among wild birds*. Dissertation. University of Georgia, Athens, Georgia, USA.

Haynes, L., E. Arzey, C. Bell, N. Buchanan, G. Burgess, V. Cronan, C. Dickason, H. Field, S. Gibbs, P. M. Hansbro, T. Hollingsworth, A. C. Hurt, P. Kirkland, H. McCracken, J. O'Connor, J. P. Tracey, J. Wallner, S. Warner, R. Woods, and C. Bunn. 2008. Australian surveillance for avian influenza viruses in wild birds: July 2005 to June 2007. *Australian Veterinary Journal*, in press.

Hellberg, M. E., R. S. Burton, J. E. Neigel, and S. R. Palumbi. 2002. Genetic assessment of connectivity among marine populations. *Bulletin of Marine Science* **70**:273-290.

Hey, J., and R. Nielsen. 2004. Multilocus methods for estimating population sizes, migration rates and divergence time, with applications to the divergence of *Drosophila pseudoobscura* and *D. persimilis*. *Genetics* **167**:747-760.

Hinshaw, V. S., J. M. Wood, R. G. Webster, R. Deibel, and B. Turner. 1985. Circulation of influenza-viruses and paramyxoviruses in waterfowl originating from two different areas of North America. *Bulletin of the World Health Organization* **63**:711-719.

Hobson, K. A. 1995. Reconstructing avian diets using stable-carbon and nitrogen isotope analysis of egg components: patterns of isotopic fractionation and turnover. *Condor* **97**:752-762.

Hobson, K. A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* **120**:314-326.

Hobson, K. A. 2005. Using stable isotopes to trace long-distance dispersal in birds and other taxa. *Diversity and Distributions* **11**:157-164.

Hobson, K. A., and D. R. Norris. 2008. Animal migration: a context for using new techniques and approaches. Pages 1-20 in K. A. Hobson and L. I. Wassenaar, editors. *Tracking animal migration with stable isotopes*. Elsevier, New York, New York, USA.

Hong Kong Information Services Department. 2007. Little Egrets tests positive for H5N1 virus. Available online at: http://www.info.gov.hk/gia/general/200711/24/P200711240153_print.htm.

Hong Kong Information Services Department. 2008. Great Egret tested for H5 virus. Available online at: <http://www.info.gov.hk/gia/general/200802/05/P200802050255.htm>.

Hurt, A. C., P. M. Hansbro, P. Selleck, B. Olsen, C. Minton, A. W. Hampson, and I. G. Barr. 2006. Isolation of avian influenza viruses from two different transhemispheric migratory shorebird species in Australia. *Archives of Virology* **151**:2301-2309.

Kear, J., and M. Hulme. 2005. *Ducks, geese and swans*. Oxford University Press, Oxford, UK.

Keawcharoen, J., D. van Riel, G. van Amerongen, T. Bestebroer, W. E. Beyer, R. van Laveren, A. Osterhaus, R. A. M. Fouchier, and T. Kuiken. 2008. Wild ducks as long-distance vectors of highly pathogenic avian influenza virus (H5N1). *Emerging Infectious Diseases* **14**:600-607.

- Kelly, J. F.** 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* **78**:1-27.
- Kingsford, R. T., and F. I. Norman.** 2002. Australian waterbirds: products of the continent's ecology. *Emu* **102**:47-69.
- Krauss, S., C. A. Obert, J. Franks, D. Walker, K. Jones, P. Seiler, L. Niles, S. P. Pryor, J. C. Obenauer, C. W. Naeve, L. Widjaja, R. J. Webby, and R. G. Webster.** 2007. Influenza in migratory birds and evidence of limited intercontinental virus exchange. *PLoS Pathogens* **3**:167.
- Mackenzie, J. S., D. Britten, V. S. Hinshaw, and J. Wood.** 1985. Isolation of avian influenza and paramyxoviruses from wild birds in Western Australia. Pages 336-339 in A. J. Della-Porta, editor. *Veterinary viral diseases: their significance in south-east Asia and the western Pacific*. Academic Press, Sydney, Australia.
- Mackenzie, J. S., E. C. Edwards, R. M. Holmes, and V. S. Hinshaw.** 1984. Isolation of ortho- and paramyxoviruses from wild birds in Western Australia and the characterisation of novel influenza A viruses. *Australian Journal of Experimental Biology and Medical Science* **62**:89-99.
- Marchant, S., and P. J. Higgins.** 1990. *Handbook of Australian, New Zealand and Antarctic birds Volume 1. Part B. Australian pelican to ducks*. Oxford University Press, Melbourne, Australia.
- Marra, P. P., K. A. Hobson, and R. Holmes.** 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**:1884-1886.
- Miller, M. R., J. Y. Takekawa, J. P. Fleskes, D. L. Orthmeyer, M. L. Casazza, and W. M. Perry.** 2005. Spring migration of Northern Pintails from California's Central Valley wintering area tracked with satellite telemetry: routes, timing, and destinations. *Canadian Journal of Zoology* **83**:1314-1332.
- Munster, V. J., C. Baas, P. Lexmond, J. Waldenström, A. Wallensten, T. Fransson, G. F. Rimmelzwaan, W. E. P. Beyer, M. Schutten, B. Olsen, A. D. M. E. Osterhaus, and R. A. M. Fouchier.** 2007. Spatial, temporal, and species variation in prevalence of influenza A viruses in wild migratory birds. *PLoS Pathogens* **3**:61.
- Nebel, S., J. L. Porter, and R. T. Kingsford.** 2008. Long-term trends of shorebird populations in eastern Australia and impacts of freshwater extraction. *Biological Conservation* **141**:971-980.
- Nestorowicz, A., Y. Kawaoka, W. J. Bean, and R. G. Webster.** 1987. Molecular analysis of the hemagglutinin genes of Australian H7N7 influenza viruses: role of passerine birds in maintenance or transmission. *Virology* **160**:411-418.
- Nye, E. R., C. R. Dickman, and R. T. Kingsford.** 2007. A wild goose chase-temporal and spatial variation in the distribution of the Magpie Goose (*Anseranas semipalmata*) in Australia. *Emu* **107**:28-37.
- Olsen, B., V. J. Munster, A. Wallensten, J. Waldenström, A. D. M. E. Osterhaus, and R. A. M. Fouchier.** 2006. Global patterns of influenza A virus in wild birds. *Science* **312**:384-388.
- Pain, D. J., R. E. Green, B. Giessing, A. Kozulin, A. Poluda, U. Ottosson, M. Flade, and G. M. Hilton.** 2004. Using stable isotopes to investigate migratory connectivity of the globally threatened Aquatic Warbler *Acrocephalus paludicola*. *Oecologia* **138**:168-174.
- Pearse, D. E., and K. A. Crandall.** 2004. Beyond FST: analysis of population genetic data for conservation. *Conservation Genetics* **5**:585-602.
- Peroulis, I., and K. O'Riley.** 2004. Detection of avian paramyxoviruses and influenza viruses amongst wild bird populations in Victoria. *Australian Veterinary Journal* **82**:79-82.
- Petrie, S. A., and K. L. Wilcox.** 2003. Migration chronology of eastern-population Tundra Swans. *Canadian Journal of Zoology* **81**:861-870.
- Pritchard, J. K., M. Stephens, and P. Donnelly.** 2000. Inference of population structure using multilocus genotype data. *Genetics* **155**:945-959.
- Pulliam, H. R., and B. J. Danielson.** 1991. Sources, sinks, and habitat selection: a landscape perspective on population-dynamics. *American Naturalist* **137**:50-66.

- Rhymer, J. M., M. J. Williams, and R. T. Kingsford.** 2004. Implications of phylogeography and population genetics for subspecies taxonomy of Grey (Pacific Black) Duck (*Anas superciliosa*) and its conservation in New Zealand. *Pacific Conservation Biology* 10:57-66.
- Ricklefs, R. E., S. M. Fallon, S. C. Latta, B. L. Swanson, and E. Bermingham.** 2005. Migrants and their parasites: a bridge between two worlds. Pages 210-221 in R. Greenberg and P. P. Marra, editors. *Birds of two worlds: the ecology and evolution of migration*. Johns Hopkins University Press, Baltimore, Oregon, USA.
- Rodgers, A. R.** 2001. Recent telemetry technology. Pages 79-121 in J. J. Millspaugh and J. M. Marzloff, editors. *Radio tracking and animal populations*. Academic Press, San Diego, California, USA.
- Rohm, C., N. Zhou, J. Suss, J. Mackenzie, and R. G. Webster.** 1996. Characterization of a novel influenza hemagglutinin, H15: criteria for determination of influenza A subtypes. *Virology* 217:508-516.
- Roshier, D., M. Asmus, and M. Klaassen.** 2008. What drives long-distance movements in the nomadic Grey Teal *Anas gracilis* in Australia? *Ibis* 150:474-484.
- Roshier, D. A., N. I. Klomp, and M. Asmus.** 2006. Movements of a nomadic waterfowl, Grey Teal *Anas gracilis*, across inland Australia: results from satellite telemetry spanning fifteen months. *Ardea* 94:461-475.
- Roshier, D. A., A. I. Robertson, and R. T. Kingsford.** 2002. Responses of waterbirds to flooding in an arid region of Australia and implications for conservation. *Biological Conservation* 106:399-411.
- Roshier, D. A., A. I. Robertson, R. T. Kingsford, and D. G. Green.** 2001. Continental-scale interactions with temporary resources may explain the paradox of large populations of desert waterbirds in Australia. *Landscape Ecology* 16:547-556.
- Rubenstein, D. R. and K. A. Hobson.** 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution* 19:256-263.
- Sabirovic, M., S. Hall, J. Wilesmith, P. Grimley, N. Coulson, and F. Landeg.** 2007. Assessment of the risk of introduction of H5N1 HPAI virus from affected countries to the UK. *Avian Diseases* 51:340-343.
- Selleck, P. W., G. Arzey, P. D. Kirkland, R. L. Reece, A. R. Gould, P. W. Daniels, and H. A. Westbury.** 2003. An outbreak of highly pathogenic avian influenza in Australia in 1997 caused by an H7N4 virus. *Avian Diseases* 47:806-811.
- Sims, L. D.** 2006. *A risk-based approach to avian influenza virus research priorities*. Australian Biosecurity Cooperative Research Centre, Manunda, Queensland, Australia. Available online at: http://www1.abcrc.org.au/uploads/publication_250.pdf.
- Sims, L. D., and A. J. Turner.** 2008. Avian influenza in Australia. Pages 239-250 in D. E. Swayne, editor. *Avian Influenza*. Blackwell, Iowa City, Iowa, USA.
- Stallknecht, D. E., and J. D. Brown.** 2008. Ecology of avian influenza in wild birds. Pages 43-58 in D. E. Swayne, editor. *Avian Influenza*. Blackwell, Ames, Iowa, USA.
- Stallknecht, D. E., and S. M. Shane.** 1988. Host range of avian influenza virus in free-living birds. *Veterinary Research Communications* 12:125-141.
- Szep, T., A. P. Moller, J. Vallner, A. Kovacs, and D. Norman.** 2003. Use of trace elements in feathers of sand martin *Riparia riparia* for identifying moulting areas. *Journal of Avian Biology* 34:307-320.
- Swayne, D. E.** 2008. *Avian influenza*. Blackwell, Ames, Iowa, USA.
- Tracey, J. P., R. Woods, D. Roshier, P. West, and G. R. Saunders.** 2004. The role of wild birds in the transmission of avian influenza for Australia: an ecological perspective. *Emu* 104:109-124.
- Turner, A. J.** 2004. The role of wild aquatic birds in the epidemiology of avian influenza in Australia. *Australian Veterinary Journal* 82:713-713.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes.** 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* 17:76-83.

Wetlands International. 2006. *Waterbird population estimates*. Fourth edition. Wetlands International, Wageningen, The Netherlands.

Williams, M. 2005. Dead ducks don't fly. Available online at: <http://www.drmartinwilliams.com/birdflu/birdfluintro.html>.

World Health Organization (WHO). 2008a. Areas reporting confirmed occurrence of H5N1 avian influenza in poultry and wild birds since 2003. Available online at: http://gamapserver.who.int/mapLibrary/Files/Maps/Global_SubNat_H5N1inAnimalConfirmedCUMULATIVE_200802021.png.

World Health Organization (WHO). 2008b. Areas with confirmed human cases of H5N1 avian influenza since 2003. Available online at: http://gamapserver.who.int/mapLibrary/Files/Maps/Global_H5N1inHumanCUMULATIVE_FIMS_20080205.png.

World Health Organization (WHO). 2008c. H5N1 avian influenza: timeline of major events. Available online at: http://www.who.int/csr/disease/avian_influenza/Timeline_080418.pdf.

World Organisation for Animal Health (OIE). 2006. Follow-up report No.: 1. Available online at: http://www.oie.int/wahid-prod/reports/en_fup_0000005887_20060926_130820.pdf.