Australia's temporary wetlands: what determines their suitability as feeding and breeding sites for waders?

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Australia's inland temporary wetlands provide habitat for six migrant and eight resident species of waders. The factors that determine the suitability of such wetlands as feeding and breeding sites are poorly understood. In their natural condition, the normally high productivity of these wetlands depends on cycles of flooding and drying, and the extent, timing and duration of flooding are highly unpredictable. Suitable conditions for individual wader species tend to be short-lived and they respond to changes by being highly mobile. In many species, successful breeding occurs only intermittently. River regulation for irrigated agriculture has reversed the natural timing of flooding and has reduced its frequency and extent, and so has reduced the suitability of wetlands for waders. Other anthropogenic factors such as drainage, overgrazing and increasing salinisation have also reduced the quality of wetlands for waders.

INTRODUCTION

Australian wader research has concentrated on coastal habitats and on migrant species. Yet, a characteristic feature of Australia's ecology is the great abundance and diversity of inland wetlands, which support immense numbers of waterbirds, including waders. Temporary wetlands are the most important for waders. They have arisen in several ways: along the floodplains of the major river systems, from movements of the earth's crust (Lake Eyre, for example), and from wind erosion that has formed extensive natural depressions in drier areas. These wetlands flood following rainfall, which may be seasonal or less predictable, and dry completely or partially afterwards. Fourteen wader species commonly occur on temporary wetlands, of which six are migrants that breed in the northern hemisphere, and eight are residents. Seven species are exclusively or mainly inland and seven occur at both inland and coastal habitats (Table 1). There are no reliable estimates of abundance for any of these species (Watkins 1993). The physical challenge of conducting surveys over such a vast number of wetlands ranging from a few to many thousands of hectares, usually in remote areas with limited access, is immense.

Some of the more spectacular aspects of wader biology on interior wetlands are widely known, such as the infrequent, large colonial breeding events of the Banded Stilt in South Australia and Western Australia (Minton *et al.* 1995) (for scientific names, please refer to Table 1). However, most major aspects of wader ecology on these wetlands are unknown. Most species are known to move periodically, from coastal wetlands to inland sites, or among inland sites, following some flooding events (Lane 1987, Alcorn *et al.* 1994). This, presumably, occurs in response to changes in habitat suitability, but exactly what determines the suitability of wetlands as feeding and breeding sites is poorly understood. The two are presumably interdependent as breeding clearly cannot occur unless feeding conditions are appropriate. However, an interesting aspect is the number of wetlands that now only support feeding waders, even at times when breeding is taking place elsewhere. This article discusses some of the factors that may be important in determining habitat suitability and, in particular, the nature of threats posed by human modification of wetlands. A few points are illustrated by the preliminary results of research being undertaken by the author.

CYCLES OF FLOODING AND DRYING

Temporary wetlands are characterised by cycles of flooding and drying. In the southern half of the country flooding tends to occur during winter and spring, and drying during summer when evaporation rates of 10 mm or higher per day are common. The pattern tends to be reversed in the north but in all areas there is great variability and unpredictability in the timing and amount of rainfall and hence in flooding patterns. Temporary wetlands are typically highly productive, and although the precise nature of the nutrient changes that take place during flooding cycles are not fully understood, it is nevertheless clear that productivity depends on alternating periods of flooding and drying. During the drying phase mineralisation of organic material takes place, resulting in high concentrations of nutrients, which are then available for primary producers (bacteria, algae or macrophytes) when flooding next occurs (Baldwin 1996, Mitchell & Baldwin 1998, McComb & Qui 1998). This forms the basis of dense invertebrate populations, which are prey for waders. Although productive, temporary wetlands often have a low diversity of invertebrates, and communities may be dominated by relatively small prey such as midge larvae (chironomidae), or if more saline, by brine shrimps (*Artemia* and *Paratemia*) and brine-fly larvae (*Ephydrella*).

In their natural condition these wetlands must have been highly variable and dynamic systems. At any one time, many must have been unsuitable for waders, and presumably at

Table 1. Wader species that utilise inland wetlands in Australia.

Species	Status	Habitat
Latham's Snipe *Gallinago hardwickii*	Migrant	Mostly inland, some coastal
Greenshank *Tringa nebularia*	Migrant	Mostly coastal, some inland
Marsh Sandpiper *T. stagnatilis*	Migrant	Inland and coastal
Sharp-tailed Sandpiper *Calidris acuminata*	Migrant	Inland and coastal
Red-necked Stint *C. ruficollis*	Migrant	Coastal and inland
Curlew Sandpiper *C. ferruginea*	Migrant	Mostly coastal, some inland
Painted Snipe *Rostratula benghalensis*	Resident	Inland
Black-winged Stilt *Himantopus himantopus*	Resident	Mostly inland, some coastal
Banded Stilt *Cladorhynchus leucocephalus*	Resident	Mostly inland
Red-necked Avocet *Recurvirostra novaehollandiae*	Resident	Mostly inland
Red-capped Plover *Charadrius ruficapillus*	Resident	Coastal and inland
Red-kneed Dotterel *Erythrogonys cinctus*	Resident	Mostly inland
Black-fronted Plover *Elseyornis melanops*	Resident	Mostly inland
Masked Lapwing *Vanellus miles*	Resident	Inland and coastal

times of severe drought most would have been unsuitable. However, in most years, because of the great number of wetlands spread across the continent, there must have been enough with suitable conditions for feeding that each species could at least survive in large enough numbers. The birds could have tolerated a lower frequency of conditions that were suitable for breeding so long as breeding success was high enough at such times and survival high enough in intervening periods to maintain populations. Whether this equation was delicately balanced in the natural state, and if so, how delicately, we will never know. Nevertheless, it is clear that any attempt to quantify suitable habitat conditions must be based on both local and landscape levels, and probably over a considerable time span. Human activity that causes fundamental changes in the frequencies, depths and duration of flooding could have profound effects that would be difficult to quantify. Even if population estimates were available for each species, with such an obviously variable natural system, it would take many years of data to distinguish between natural and anthropogenic changes. Prolonged and serious declines are likely to go undetected.

EFFECTS OF RIVER REGULATION

Nearly all Australian rivers are now highly regulated, mainly to provide water for irrigated agriculture. The large-scale effects of river regulation and the responses of some of the more conspicuous waterbirds, such as egrets, are well documented (Lloyd *et al.* 1994, Kingsford 2000, Kingsford & Norman 2002). Regulation reverses flow patterns so that in southern catchments, instead of flooding in winter and spring, rivers now have low flows in these seasons when water is being stored, and high flows in summer when the demand for irrigation water occurs. In the natural state, lower water levels during summer may have provided exposed substrates and shallow pools, with high densities of invertebrates and small fish, suitable for some breeding waders such as Painted Snipe and Red-kneed Dotterel and for migrant species such as Sharp-tailed Sandpipers, Marsh Sandpipers and Greenshanks. Such habitats no longer exist. Some previously temporary wetlands are now permanently inundated water storage areas, which have lost their previously high productivity and become unsuitable for waders and other wading birds (Briggs *et al.* 1994). Regulation has reduced the volume of water flowing into wetlands and so has reduced the size of the area flooded and the depth and duration of flooding. For example, the Macquarie Marshes (130,000 ha in 1990) in New South Wales have been reduced by 40–50% in the past 50 years (Kingsford & Johnson 1998). An estimated 50% of all floodplain wetlands have been lost in their entirety in the Murray–Darling Basin (Kingsford 2000).

The complete loss of so many wetlands has probably already caused a significant reduction in wader abundance, if numbers are correlated with the extent of suitable habitat, as seems likely. However, it is possible that their loss could also have a continuing effect through disruption of wetland connectivity (Haig *et al.* 1998).

Most resident waders in the south of Australia tend to breed in the spring and early summer coinciding, in general terms, with the period of natural flooding of wetlands. A few species are more flexible and may breed at any time (Lane 1987). Some wetlands such as the saline wetlands in the arid zone of southern Australia may provide suitable habitat for waders soon after flooding. For example, the breeding of Banded Stilts on Lake Ballard in Western Australia in 1995 started only 12 days after the start of the rain that produced the lake (Minton 1995). However, there is increasing evidence that many wetlands are least suitable as foraging and breeding habitat for waders when they are fully flooded and that their most suitable period occurs later, at some stage during the drying phase. There are several records of waders leaving particular wetlands following heavy rainfall (Alcorn *et al.* 1994). The interpretation of such movements has often been that the birds leave to exploit other newly flooded wetlands, but it is more likely that they leave because the existing wetlands become unsuitable for foraging following rainfall. I have recorded five separate instances involving five species on four wetlands where the birds have left within two days or less of heavy rainfall. Water levels rose by 3–6 cm on each occasion. In one case, involving Black-fronted Plovers, I was able to show that the birds' prey capture rates decreased significantly following the rise in water level. The reason was probably that the areas that had suitable water depths for foraging after the rise in levels had low densities of benthic invertebrates. The effect was to flood areas that had previously been dry and in which there were mainly aestivating stages of invertebrates. In such situations, invertebrate densities would only rise again when individuals move in from adjacent deeper areas or when the aestivating stages or newly laid eggs develop to sizes large enough

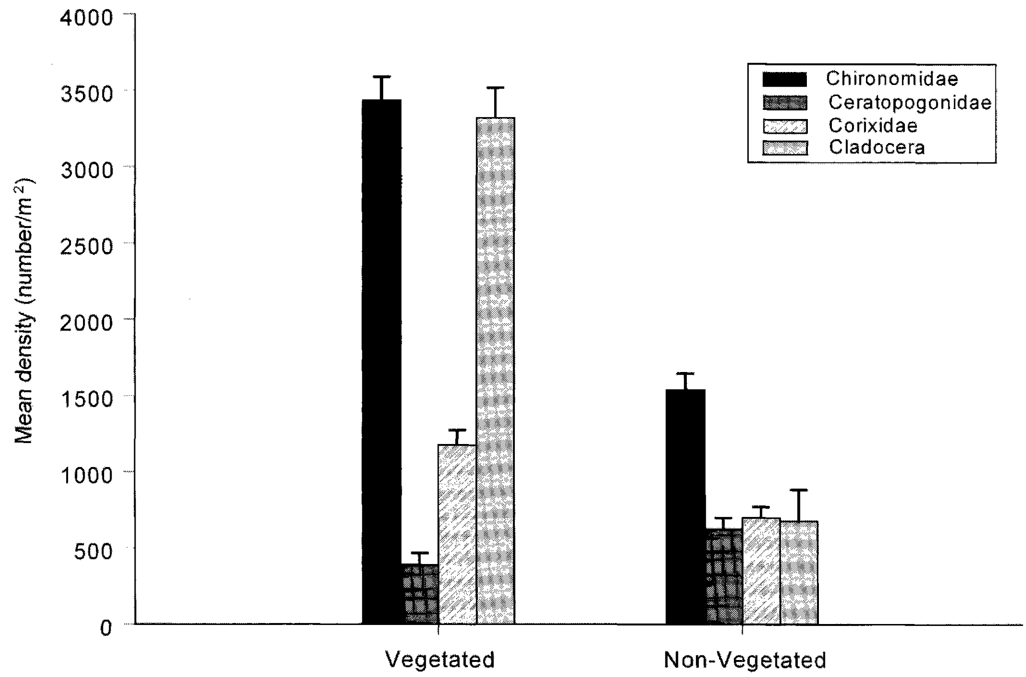

Fig. 1. Comparison of the densities ± SE of main invertebrate groups within 50 cm of vegetation and 3–5 m from vegetation at Nericon Swamp, New South Wales, December 1999. Chironomidae larvae, $P < 0.02$ (left-hand columns); Ceratopogonidae larvae, $P = 0.05$: Corixidae, $P < 0.02$; Cladocera, $P < 0.001$. Column and core samples, N = 30 in all cases.

to be wader prey. How long it takes such areas to become sufficiently profitable for waders is unknown but now under investigation. Of course, after rainfall, water levels would start to fall again at a rate depending on ambient temperatures, so re-establishing access to existing populations of invertebrates. Summer rainfall that causes sudden increases in water levels such as this is often highly localised. Birds that are forced to disperse from one wetland might find another suitable wetland relatively close by, but if wetland connectivity has been significantly reduced by the complete loss of wetlands, they might be forced to search farther, possibly with consequences for survival.

In a continuing study at Fivebough Swamp, a shallow, natural depression wetland in New South Wales, I examined the length of time for which each of six waders fed on the wetland during an average drying period. From a mean depth of around 22 cm the entire swamp of about 190 ha dried completely in 90 days. The six species formed a succession with each appearing and leaving the wetland at different stages. Each species had a distinct and different water depth preference for foraging. Peak numbers of Red-kneed Dotterel, for example, lasted only around three weeks when the maximum extent of their preferred water depths occurred. Red-capped Plovers appeared close to the end of the drying phase, and the period of maximum numbers lasted only about 4 weeks. Although preliminary, this study demonstrates that favourable conditions for individual species are probably short-lived. River regulation, by reducing the extent and depth of flooding probably reduces the length of these favourable periods. As a result, non-breeding, foraging birds are probably compelled to be more mobile, possibly with survival costs. However, for breeding birds the consequences are probably more serious. Conditions must remain suitable, at the very least, for egg formation, hatching and fledging of chicks. Also, depending on how quickly fledged young develop their foraging skills, enforced early dispersal could reduce their survival. River regulation probably reduces the frequency with which waders breed and probably also reduces the success of attempts. There may also be less time to produce replacement clutches. This could be particularly important if introduced predators such as the European fox *Vulpes vulpes* take significant numbers of first clutches.

OVERGRAZING BY DOMESTIC LIVESTOCK

The floodplains of the major river systems became centres for livestock production soon after the arrival of Europeans and many wetlands have been subject to intense grazing for the past 150 years. The large-scale negative effects on vegetation and substrate qualities have been profound (Smith & Smith 1990, Leslie 1995). Grazing has reduced the extent of vegetation around wetlands and by increasing water turbidity and nutrient levels has favoured lower diversity, algae-dominated communities (Robertson 1997). However, finer scale effects such as those on the invertebrates upon which waders feed are poorly understood.

In a study at Nericon Swamp in New South Wales, I was able to examine relationships between vegetation, invertebrate density and wader distribution. The wetland had a long history of grazing and the study was done about a year after cattle were removed from the system. A patchy growth of aquatic vegetation emerging to a height of 10–20 cm above water level and dominated by the rush *Bolboschoenus caldwelii,* had begun to recolonise about 200 m of shoreline. The aquatic invertebrate community consisted of few species, but the densities of most were significantly higher within 50 cm of the vegetation compared with samples taken in similar water depths along the shoreline 3–5 m from vegetation (Fig. 1). Sharp-tailed and Marsh Sandpipers showed

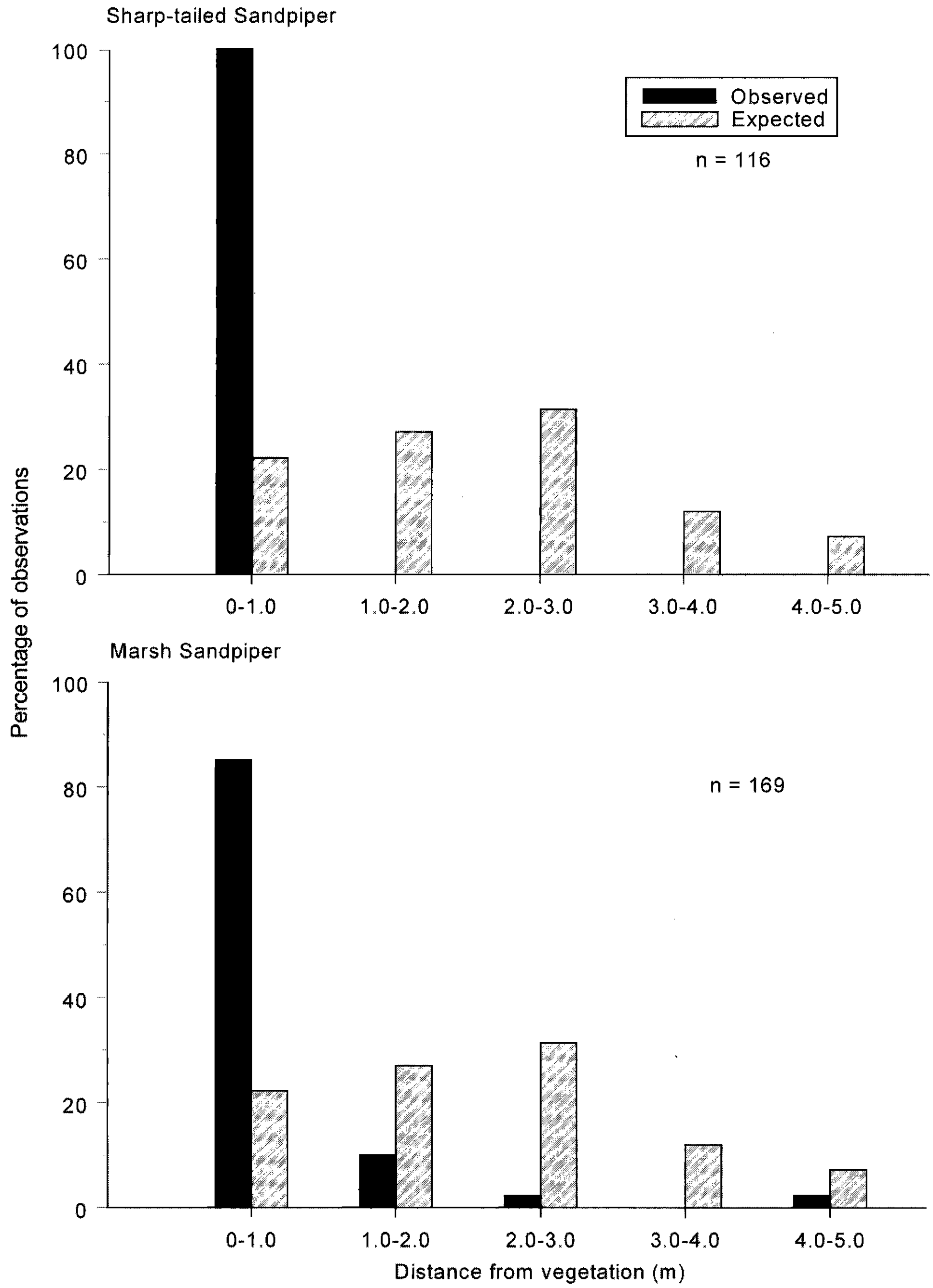

Fig. 2. Distribution of foraging Sharp-tailed and Marsh Sandpipers in relation to distance from vegetation. Observed values for percentages of birds are compared with expected values had their foraging distribution been random. Expected values calculated from 200 random point samples over the study area.

a strong tendency to feed close to the vegetation in the high prey density areas (Fig 2). This suggests that removal of vegetation may reduce the quality of habitat for waders by lowering prey density, but there is the counter-argument that grazing may open up areas of dense vegetation that otherwise would not be suitable habitat.

SALINISATION

Many Australian wetlands are naturally saline, especially those in arid areas, where high evaporation rates bring to the surface salt that had been laid down in marine deposits. Most floodplain wetlands are naturally freshwater. However, as a result of forest clearing for farming, and irrigated agriculture, water tables have risen over much of the country and salt deposited in sediments and rocks has been brought to the surface and into wetlands. Increasing salinisation of wetlands is now probably the most significant threat to all waterbirds, including waders. A three-fold increase in salinity levels of many wetlands in the Murray–Darling Basin from already greatly elevated current levels of about 500–600 EC (electrical conductivity units) is predicted within the next 100 years (MDBC 1999). It might be argued that since many waders already breed in saline wetlands there should be no great problem. However, such waders breed immediately after the wetlands have filled with rainwater, and when conditions are brackish rather than highly saline. There is increasing evidence of significant growth and developmental problems among waterbird chicks, including waders, that are reared in high salinity environments. Successful breeding cannot occur in constant hypersaline conditions (Hannam *et al.* 2003). Similar physiological problems have been demonstrated in adults of some species when deprived of freshwater (Purdue & Haines 1977, Johnston & Bildstein 1990, Barnes & Nudds 1991). It is commonly suggested that the reason why species such as the Banded Stilt respond so rapidly to the flooding of wetlands is that this enables them to complete the breeding cycle before the wetlands dry up. However, it may be that their quick response is to allow them to complete breeding before salinity levels become too high.

Increasing salinity may already have had serious effects on waders by altering the types of prey available to them. Soft-bodied invertebrates such as annelids and molluscs, and amphibians and fish are likely to be most susceptible (Metzeling *et al.* 1995.) and waders that prefer such prey may be the first to be affected. A widespread decline in Painted Snipe numbers has been reported across Australia (Lane & Rogers 2000). The species' diet in Australia is unknown, but probably includes annelids and molluscs, and it is not inconceivable that the widespread increase in salinity levels may have been the main cause of decline.

Increasing salinity will also have significant effects on aquatic vegetation (Brock & Casanova 1997), which in turn will probably also affect waders by altering prey types and densities and perhaps even cover for nesting in some species.

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