

Arid Zone Networks in Time And Space: Waterbird Use of Lake Gregory in North-Western Australia

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ABSTRACT

Lake Gregory is located on the edge of the Great Sandy Desert, Western Australia. It has contained water for all but 2 or 3 years since 1969 and the estimated waterbird population in 1988, when the lake appeared to act as a drought-refuge, was 650 000 birds. During the last 20 years, 73 waterbird species have been recorded at the lake, 21 of them breeding. Despite the abundance of water and waterbirds in recent years, rainfall records suggest Lake Gregory was mostly dry between 1930 and 1968. Assessments of its conservation significance during this 'dry phase' would have been very different from the current assessment. Decisions about the importance of arid zone wetlands need to recognize that conservation values can vary enormously, depending whether wetlands are flooded or dry, and that ideal flooding conditions may occur at intervals of several decades. Factors influencing the number of waterbird species at Lake Gregory include the amount of water in the lake, the amount of water elsewhere, the extent of inundated trees and shrubs and, possibly, the taxonomic range of available food items.

Key Words: Arid zone, Australia, Conservation, Diet, Habitat use, Rainfall, Wetland, Waterbirds

INTRODUCTION

Recent surveys have shown that the larger proportion of the waterbird population of Australia, as well as most wetlands supporting very high waterbird numbers, occurs in the arid zone (Kingsford and Halse 1998). Important arid zone wetlands include Lake Eyre in South Australia (Kingsford and Porter 1993), the Macquarie Marshes and wetlands of the Paroo region in New South Wales and Queensland (Maher and Braithwaite 1992, Kingsford and Thomas 1995), Lake Woods and other Barkly lakes in the Northern Territory (R.P. Jaensch in Kingsford and Halse 1998), and Lake Gregory in northern Western Australia (Halse 1990).

Lake Gregory is a large semi-permanent lake system on the edge of the Great Sandy Desert (Figure 1). It has been within a pastoral lease and grazed by cattle since 1920 but has retained high conservation value. More than 176 species of aquatic invertebrate have

been recorded (Halse et al. 1998, this study), which is much higher than at other arid zone lakes in Australia.

The first detailed counts of waterbirds at Lake Gregory were made by Smith and Johnstone (1978), whose survey supported claims from the turn of the century that large numbers of waterbirds occurred at the lake (e.g. Carnegie 1898). Subsequent surveys, especially that of Jaensch and Vervest (1990), provided further evidence of the importance of Lake Gregory for waterbirds and, in 1988 we began documenting its conservation values more fully with additional surveys of waterbirds and surveys of aquatic invertebrates (Halse et al. 1998).

In this paper, we present data on numbers of waterbirds using Lake Gregory and relate fluctuations in numbers to rainfall patterns and lake depth. We also examine the importance of fringing trees for waterbird breeding, present data on waterbird diet and discuss factors affecting the number of waterbird species using the lake.

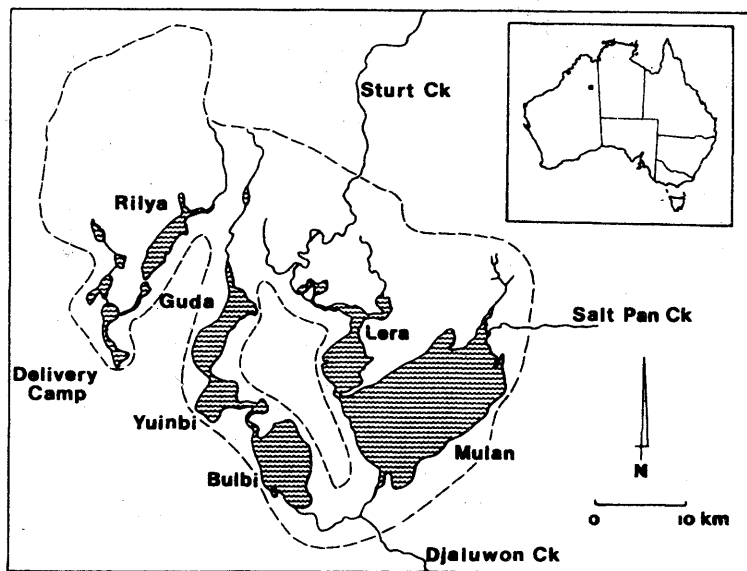


Figure 1. Lake Gregory, north-western Australia, consists of three parallel chains of waterbodies, all supplied by Sturt Creek. The dashed line indicates the extent of flooding in 1993; the area between Mulan and Guda remained above water.

STUDY SITE

Lake Gregory lies on the edge of the Great Sandy Desert, north-western Australia (Figure 1). The lake has an area of 380 km² when flooded to its normal boundary, although after major inflows it floods about 1 300 km². All significant inflow comes via Sturt Creek, which drains a catchment of 65 000 km² north-east of Lake Gregory. The catchment receives monsoonal rainfall and water levels in Lake Gregory reflect a wetter rainfall regime than is experienced at the lake itself, although the amount of rainfall in the catchment is very sensitive to the intensity of the monsoonal system (Bowler 1981).

Median annual rainfall at the nearest meteorological station, Halls Creek, c. 250 km north of the lake and just outside the catchment, is 514 mm with most rain in January and February. The wet season lasts from about November to April. Temperatures are highest early in the wet season (average daily maximum in November and December, 38°C) and lowest in the middle of the dry season (average daily maximum in July, 27°C, and minimum, 12°C), which lasts from about May to October. Annual evaporation at Lake Gregory is ca. 4000 mm.

Lake Gregory consists of three parallel chains of lakes (Figure 1). Sturt Creek breaks into a series of anastomosing channels near the lake and empties into all three chains, often by sheet flow. The eastern chain consists of Mulan, the largest and deepest waterbody, and Lera. Bulbi occurs at the southern end of the central chain and is connected to Mulan, except at low lake levels, by Djaluwon Creek. Delivery Camp and Rilya make up the western chain, which is connected to Mulan only when the system is flooded beyond the mapped boundary (Figure 1).

Between 1988 and 1995, Lake Gregory held water for all but about 12 months in 1990-91, reaching a maximum depth of about 12 m deep in 1993. Salinity in Mulan varied from 46 g L⁻¹ Total Dissolved Solids as it dried in 1989 to <1 g L⁻¹ when the lake was extensively flooded during the early 1990s (Table 1).

Table 1. Water depth (m) and salinity (g L⁻¹ TDS) at Lake Gregory during waterbird surveys, 1988-95. Salinities in Mulan are averages from several sites and representative of conditions in the centre of the waterbody (Halse et al. 1998).

Waterbody		March 1988	October 1989	June 1991	September 1991	August 1993	May 1994	October 1995
Mulan	Depth	3.5	1.5	7.8	7.4	11.7	10.8	9.3
	Salinity	6	18 ¹	0.4	0.6	0.5	-	1.2
Bulbi	Depth	-	0.1	-	-	-	-	-
	Salinity	-	82	0.2	-	0.3	-	-

¹Maximum salinity in a shallow bay was 46 g L⁻¹

The lake is currently in a wet phase (Figure 2). Prior to 1990, it dried in 1979 and, perhaps, in 1974 but otherwise held water constantly since 1969 (Figure 3). In contrast, rainfall records suggest the only major flooding event between 1927-68 was in 1959 (Figure 2).

METHODS

Waterbirds were surveyed eight times between 1988 and 1995 when Lake Gregory held water (Table 2). Surveys were undertaken from both ground and air, although in March 1993 only an aerial count was made, and in March 1988, October 1989 and May 1994

only ground counts were made. When possible, aerial counts were used to estimate overall numbers and numbers of most individual species, while ground counts provided supplementary data for species that were difficult to identify from the air, especially shorebirds. The aim of all surveys was to cover as much of the lake as possible and obtain complete waterbird counts. However, coverage from the ground in March 1988 and May 1994 was incomplete and total numbers of waterbirds present were estimated by extrapolation.

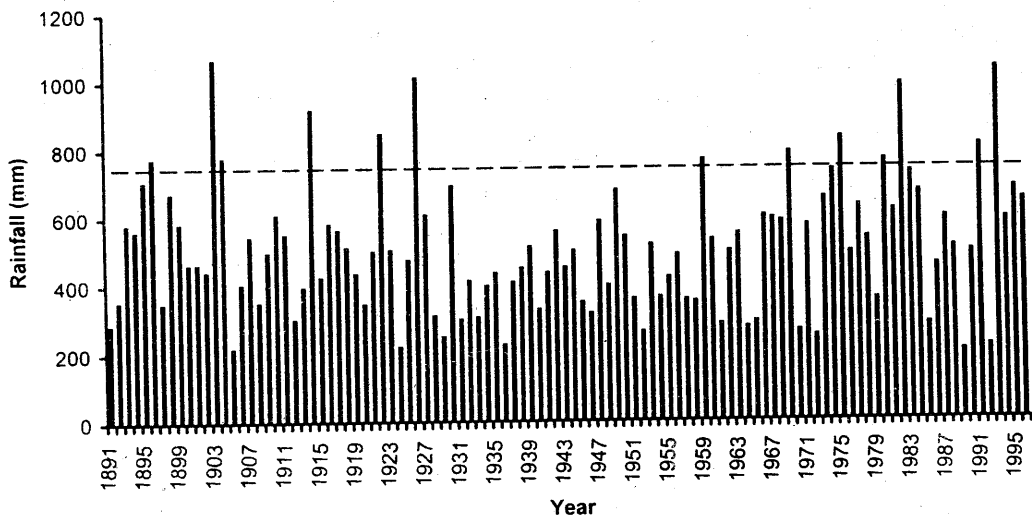


Figure 2. Annual rainfall at Halls Creek, just north of the Lake Gregory catchment, between 1891 and 1996 (data supplied by Bureau of Meteorology). The dashed line marks 760 mm; recent inflow events at Lake Gregory suggest the lake receives significant inflow when annual rainfall at Halls Creek exceeds 760 mm (Halse et al. 1998).

Ground counts were conducted over periods of 2-8 days from small boats and on foot, using binoculars and telescopes. Aerial counts lasted up to 4.5 h and were made from light aircraft (Cessna 182 or 206) flying at heights of 20-30 m and speeds of 110-180 km h⁻¹ with a front right and a rear left observer. Most waterbirds occurred near the edge of the lake in shallow water and, by flying 50-100m inside the shoreline, almost all birds could be counted in a single pass from the air. When large flocks occurred towards the centre of the lake, an orbit was made around the flock so that the inside observer could count those birds. If islands were present, detours were made to count any birds on them or in the surrounding shallow water. After completing the circuit of Lake Gregory, at least one pass was made down the centre of the major waterbodies at higher altitude to locate and count any birds on open water. In August 1993, when the system was extensively flooded (Figure 1), the area north of the lake was a mosaic of pools and islands that were unsuitable for our shoreline-based survey method, so transects were flown in this sector and results extrapolated to provide a total count. In October 1995, very mixed species composition of flocks and high waterbird density resulted in under-

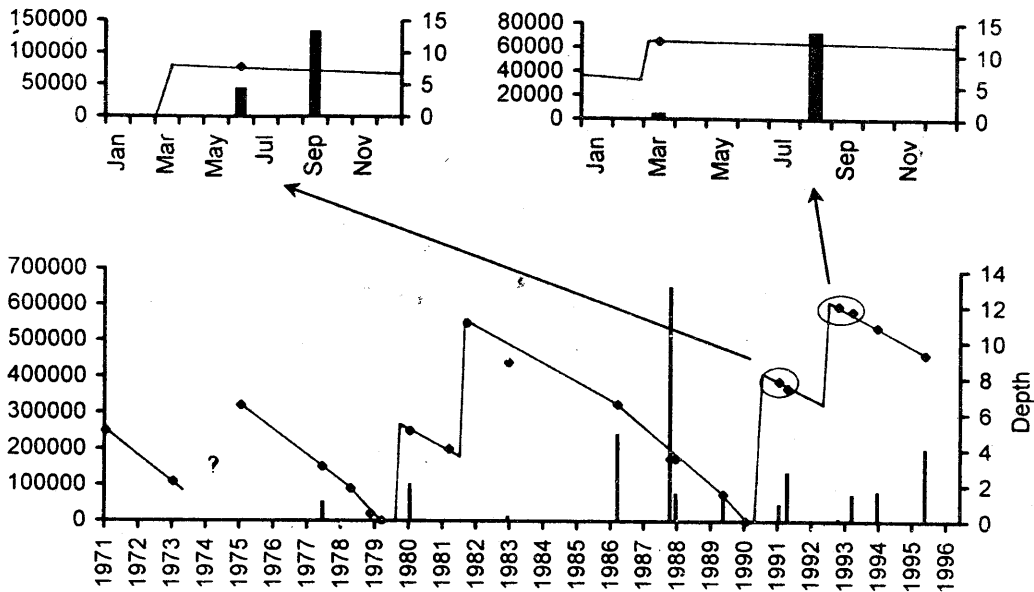


Figure 3. Number of waterfowl recorded at Lake Gregory (vertical bars) and actual or estimated water depth, 1971-95 (♦). The insets show pronounced increases in waterbird numbers during the dry season as smaller wetlands, filled by heavy rain, dry out. Data from Smith and Johnstone (1978), Start and Fuller (1983), Halse (1990), Jaensch and Vervest (1990) and this paper were used to construct the curves.

counting during the aerial survey (see Kingsford et al. 1994) and counts were partially corrected (Table 2). Based on checks of counting efficiency elsewhere (Halse et al. 1996), we regard the other aerial counts as relatively accurate.

Most nests were found during ground counts although sometimes colonies of nesting birds were located from the air. Broods of young waterbirds were recorded during both ground and aerial surveys. During some surveys, a small number of birds were shot to examine their diet. Whenever possible, they were shot while feeding actively (Briggs et al. 1985). Because of post-mortem digestion and differential digestion of various types of food in the gut (Swanson and Bartonek 1970), birds were dissected immediately and gut contents were preserved in 70 percent alcohol. All items were identified under a dissecting microscope, although only oesophageal contents were used to calculate the proportion of each item in the diet of a species using the aggregate percentage method based on dry weight (Swanson et al. 1974).

The habitats in which species occurred, and the position of all nests, were recorded during ground counts. The habitat categories used were inundated dead trees, live trees or live shrubs, trees on land, bare shoreline, shallowly flooded vegetated shoreline, and open water. Marchant and Halse (1990) used aerial photographs to estimate the reduction in area of trees between 1953 and 1988.

Waterbird names follow those of Christidis and Boles (1994); plant names follow Green (1985) and those in the Western Australian Herbarium database.

Table 2. Number of waterbirds counted or estimated to be present during surveys of Lake Gregory, 1988-95. Many of the species counts for March 1988 are estimates and some counts of duck species in October 1995 were corrected to take account of a lower counting efficiency by the rear left observer. Species first recorded at Lake Gregory during this study are marked *

Species ¹	March 1988	October 1989	June 1991	September 1991	March 1993	August 1993	May 1994	October 1995
Maggie Goose <i>Anseranas semipalmata</i>			9	601994	9	192	4	268
Plumed Whistling-Duck <i>Dendrocygna eytoni</i>	1	8000	360	6575	126	2774	80	3136
Wandering Whistling-Duck <i>Dendrocygna arcuata</i>				10	11	2108	60	1920
*Musk Duck <i>Biziura lobata</i>			2					
Freckled Duck <i>Stictonetta naevosa</i>			6	11		21		333
Black Swan <i>Cygnus atratus</i>	5000	756	137	263	941	2012	499	4183
Australian Shelduck <i>Tadorna tadornoides</i>			2			2		6
Australian Wood Duck <i>Chenonetta jubata</i>	7500	157	17	132		196	3	768
*Green Pigmy-Goose <i>Nettapus pulchellus</i>						2		10
Pacific Black Duck <i>Anas superciliosa</i>	50000	1843	43	1761	74	2249	42	6970
*Shoveler <i>Anas</i> sp.								4
Grey Teal <i>Anas gracilis</i>	150000	4770	32922	46303	1176	19943	2189	44200
Pink-eared Duck <i>Malacorhynchus membranaceus</i>	175000	1304	1023	5593	55	1486	123	8052
Hardhead <i>Aythya australis</i>	60000	1796	4098	48971	164	20618	23121	21778
Unidentified duck					6	500		22116
Australasian Grebe <i>Tachybaptus novaehollandiae</i>				5		2	9	59
Hoary-headed Grebe <i>Poliiocephalus poliocephalus</i>	2	4	11	19		3	5	28
Great Crested Grebe <i>Podiceps cristatus</i>	2			52	3	25		33
Unidentified grebe							3	
Darter <i>Anhinga melanogaster</i>	5000	83	21	111	26	564	129	723
Little Pied Cormorant <i>Phalacrocorax melanoleucos</i>			17	599	56	351	158	640
Pied Cormorant <i>Phalacrocorax varius</i>	1000	6	288	305	4	1047	160	47
Little Black Cormorant <i>Phalacrocorax sulcirostris</i>	55000	20	285	3561	6	3912	11591	4658
Great Cormorant <i>Phalacrocorax carbo</i>							1	
Unidentified cormorant								2322
Australian Pelican <i>Pelecanus conspicillatus</i>	5500	299	28	664	144	1089	204	1460
White-faced Heron <i>Egretta novaehollandiae</i>		5	11	31	61	438	31	18
Little Egret <i>Egretta garzetta</i>		1		5		1	13	1
White-necked Heron <i>Ardea pacifica</i>			17	83	63	640	5	5
Great Egret <i>Ardea alba</i>	1	44	47	373	6	310	60	1169
Intermediate Egret <i>Ardea intermedia</i>		2	9	5		4	5	2
*Cattle Egret <i>Ardea ibis</i>							11	
Unidentified egret					94	1538		
Nankeen Night Heron <i>Nycticorax caledonicus</i>			54	369	38	197	11	102
Glossy Ibis <i>Plegadis falcinellus</i>		1	34	238		553	77	1142
Australian White Ibis <i>Threskiornis molucca</i>	1	6		10	5	83	5	23
Straw-necked Ibis <i>Threskiornis spinicollis</i>	1	21	67	222	149	1030	131	676
Royal Spoonbill <i>Platalea regia</i>	1	20		108		9	4	3
Yellow-billed Spoonbill <i>Platalea flavipes</i>	1	2		1		124	3	2
Swamp Harrier <i>Circus approximans</i>				1		3	1	

Species ¹	March 1988	October 1989	June 1991	September 1991	March 1993	August 1993	May 1994	October 1995
Brolga <i>Grus rubicunda</i>	1	1929	31	1662	5	311	47	2977
*Buff-banded Rail <i>Gallirallus philippensis</i>		1						
Black-tailed Native-hen <i>Gallinula ventralis</i>	1		12	42		108	59	20
Eurasian Coot <i>Fulica atra</i>	100000	20040	2995	13777	8	3473	1331	23982
*Black-tailed Godwit <i>Limosa limosa</i>		16						1
Marsh Sandpiper <i>Tringa stagnatilis</i>		788	1					35
Common Greenshank <i>Tringa nebularia</i>		13		5			6	11
Wood Sandpiper <i>Tringa glareola</i>		41		3				45
Common Sandpiper <i>Actitis hypoleucos</i>		4		2				2
*Grey-tailed Tattler <i>Heteroscelus brevipes</i>		1						1
*Ruddy Turnstone <i>Arenaria interpres</i>		2						
Red-necked Stint <i>Calidris ruficollis</i>		833						4
Long-toed Stint <i>Calidris subminuta</i>		13						1
Sharp-tailed Sandpiper <i>Calidris acuminata</i>	12500	7674						540
Curlew Sandpiper <i>Calidris ferruginea</i>	1	433						
*Painted Snipe <i>Rostratula benghalensis</i>								1
Black-winged Stilt <i>Himantopus himantopus</i>	1	638	81	254	87	1537	63	1304
Red-necked Avocet <i>Recurvirostra novaehollandiae</i>		93	100	9	6			105
*Pacific Golden Plover <i>Pluvialis fulva</i>		1						
*Grey Plover <i>Pluvialis squatarola</i>		1						
Red-capped Plover <i>Charadrius ruficapillus</i>	1	2199	210	6		52		24
Oriental Plover <i>Charadrius veredus</i>	1	25707						901
Black-fronted Dotterel <i>Elseya melanops</i>		9	22	9		7	9	13
Red-kneed Dotterel <i>Erythronyctes alba</i>		3	38	23	1	53	303	29
*Banded Lapwing <i>Vanellus tricolor</i>		1				13	216	
Masked Lapwing <i>Vanellus miles</i>	10000	174	7	47	23	151	85	319
Australian Pratincole <i>Stiltia isabellae</i>	1	362	23		4	25	1	30
Unidentified wader					22	532		5728
Silver Gull <i>Larus novaehollandiae</i>	1	231	50	14		50	29	276
Gull-billed Tern <i>Sterna nilotica</i>	1	6	2	28	174	148	4	768
Caspian Tern <i>Sterna caspia</i>	1	802	889	735	119	399	40	216
Whiskered Tern <i>Chlidonias hybridus</i>	1	463	172	170	663	1054	147	1362
*White-winged Black Tern <i>Chlidonias leucopterus</i>					47			
Unidentified Tern								76
*Clamorous Reed-Warbler <i>Acrocephalus stentoreus</i>						1		
Unidentified waterbird								3671
Total counted	-	81618	44141	133227	4376	71940	41078	169299
No. of species	32	50	39	46	31	47	44	57
Population estimate	650000	81618	44141	133227	4376	71940	80000	200000

¹Black-necked Stork *Ephippiorhynchus asiaticus* (total of 4 birds, 2 surveys), Purple Swamphen *Porphyrio porphyrio* (2, 1 survey), Bar-tailed Godwit *Limosa lapponica* (1) and Banded Stilt *Cladorhynchus leucocephalus* (43, 2 surveys) were not recorded during this study but were seen in earlier surveys (Halse 1990)

RESULTS

Waterbird Counts

A total of 69 waterbird species were seen during our eight surveys of Lake Gregory when it contained water (Table 2). We found 14 species that had not been observed during earlier surveys but failed to record four seen previously (Table 2). Breeding activity by 21 species was observed compared with eight during earlier surveys (Table 3). Additional surveys are likely to increase both the species and breeding species lists for the lake because accumulation curves had not levelled off (Figure 4). In contrast to expectations from other studies of waterbird breeding in Western Australia (Halse and Jaensch 1989), a significant amount of breeding occurred at the end of the dry season (August - October) (Table 3).

Table 3. Numbers of breeding records for each species at Lake Gregory, 1988-95, and habitats where nests were found. Species first recorded breeding at Lake Gregory during this study are marked *.

Species	Nesting habitat	March 1988	October 1989	June 1991	September 1991	March 1993	August 1993	May 1994	October 1995
*Magpie Goose	shrubs				1		3	1	
*Wandering Whistling-Duck	ground ¹						2		
Black Swan	islands, nest mound		6	2	79	3	132	6	35
*Australian Wood Duck	tree hollows ¹							1	
*Grey Teal	tree hollows			4	1	2	2		
*Pink-eared Duck	tree hollows							4	
*Hardhead	dense ground cover ¹				3				
*Great Crested Grebe	nest mound ¹								2
Darter	trees			6	9		5	6	5
Little Pied Cormorant	trees			10	4	4	70	3	7
Pied Cormorant	trees			32	75		266	29	
Little Black Cormorant	trees			60	142		874	1865	1
*Australian Pelican	islands				26				
*Great Egret	trees						10 ²		
Nankeen Night Heron	trees						1		
*Yellow-billed Spoonbill	trees						1		
*Eurasian Coot	base of shrubs, nest mound				100				389
*Black-winged Stilt	marshy shore						2 ²		
Red-capped Plover	open shore								1
*Silver Gull	tree stumps						3		
Caspian Tern	islands				380		73		
No. of breeding species		-	1	6	11	3	14	8	7
No. of nests and broods		-	6	114	820	9	1444	1915	440

¹Only broods recorded, data on nest site from Marchant and Higgins (1990)

²Breeding records in September 1993 (Mitchell Kelly, pers. comm.)

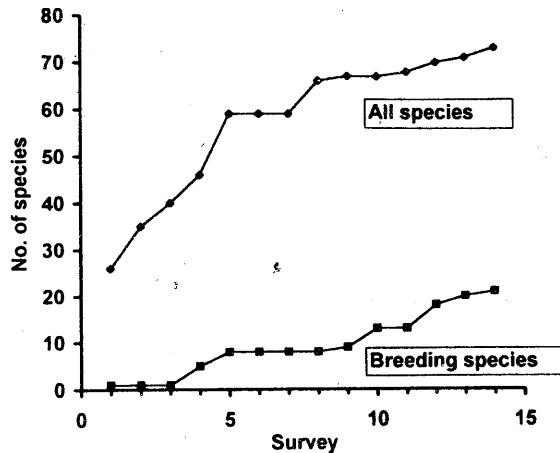


Figure 4. Cumulative number of species and breeding species recorded at Lake Gregory plotted against number of surveys. Sources of data as for Figure 3.

The highest number of waterbirds estimated to be present at Lake Gregory during our surveys was 650,000 in March 1988 and the mean annual maximum was 203,000 (Table 2). Numbers exceeded 100,000 in three of the six years, even though surveys were not always conducted when numbers were likely to be highest. Numbers appeared to decline after widespread rain and increase during the dry season. For example, in 1988 when the monsoon failed and there was no significant rainfall in northern Australia during the wet season, 650,000 waterbirds occurred at Lake Gregory in March (Table 2), after which there was widespread rain and numbers declined to 75,524 by May (Jaensch and Vervest 1990) (Figure 3). In 1991, 44,141 waterbirds were recorded in June after the dry lake had re-flooded in February but the number increased three-fold to 133,227 by September. In 1993, only 4,376 waterbirds occurred in Lake Gregory in March, following extensive rainfall and a major inflow event into the already full Lake Gregory, but 71,940 birds were counted in August.

Abundant species for which Lake Gregory was particularly important included Grey Teal, Pink-eared Ducks, Hardheads, Little Black Cormorants and Eurasian Coots (Table 2). These species were recorded during our surveys or the 1986 survey of Jaensch and Vervest (1990) in numbers that were as high as any previous records in Australia (see Halse 1990, Kingsford and Halse 1998). Large numbers of palaeartic shorebirds were also recorded some years when they were either arriving from, or departing for, the Northern Hemisphere. Lake Gregory appears to be an important staging point for migrating shorebirds: counts of Marsh Sandpipers and Sharp-tailed Sandpipers were among the highest in Australia and more than half the world's known population of Oriental Plovers occurred at the lake in 1989 (Watkins 1993).

The counts of 898 Freckled Ducks in 1986 (Jaensch and Vervest 1990) and 333 in 1995, in a small section of the lake, suggest that Lake Gregory is also the most important site in the western third of Australia for the country's rarest duck (Fullager 1988). Other rarities included a single Painted Snipe in 1995, a species that has been recorded infrequently in Western Australia, and 13 Long-toed Stints in 1989. Access to the

mudflats where Long-toed, and several hundred Red-necked, Stints were feeding was limited and heat haze was extreme. The actual number of Long-toed Stints present was probably several times the number counted, making Lake Gregory one of the more significant Australian sites for the species (Watkins 1993).

Breeding

Lake Gregory is an important site for cormorant breeding in Australia (Jaensch and Vervest 1990); cormorants have been consistently recorded breeding during surveys when the lake was fresh. Although the surveys in September 1991 and October 1995 were early in the breeding season of Eurasian Coots, so that most nests were still under construction and not recorded as breeding attempts, breeding activity by coots later in the season was probably significant at a national level. The number of breeding species and numbers of pairs breeding made Lake Gregory the most important breeding site in the western third of Australia between 1988 and 1995. Only at Lake Toolibin in south-western Australia, which has been surveyed very intensively and is in the temperate zone, have more species been recorded breeding over the past 20 years (24 vs 21) but the number of breeding pairs is much higher at Lake Gregory (see Freund et al. 1997).

Diet

Dietary analyses were based on examination of 62 birds, 48 of which had identifiable food items in the oesophagus or gizzard (Table 4). A dietary item of special interest were the unidentified larvae of the dipteran family Syrphidae in the oesophagi of two Glossy Ibis. Syrphids were not collected during extensive sampling of the lake with pondnets.

Lack of data for many species means food items in Table 4 do not necessarily reflect the most commonly consumed foods at the lake but fish *Leiopotherapon unicolor* Günther were prominent in the diet of cormorants and the Darter. Shorebirds consumed a variety of aquatic and terrestrial invertebrates and their larvae. Ibis fed on insects and, in the case of two Glossy Ibis, corms of *Cyperus bulbosus* M.Vahl. Ducks fed on seeds of *Myriophyllum verrucosum* Lindley and *Halosarcia* sp., corms and aquatic invertebrates. Overall, a great variety of food items were consumed, with seeds and corms, fish, odonates (zygopterans and anisopterans) and coleopterans being the more common items but trichopterans, terrestrial hymenopterans, ostracods and stratiomyid dipterans also being important. Items taken at Lake Gregory reflected similar feeding preferences to those recorded for the same waterbird species in other studies (e.g. Gowland 1983, Briggs et al. 1985, Dostine and Morton 1989a), although fish were more important in the diet of piscivores at Lake Gregory than at some other wetlands (e.g. Miller, 1979, Dostine and Morton 1988, 1989b).

Habitat Use

Eleven of the 21 species recorded breeding at Lake Gregory used partially inundated trees, which were sometimes dead, for nesting (Table 3). A further two species used inundated shrubs. The occurrence of trees and shrubs around the edge of Lake Gregory is vital to maintaining the present level of breeding.

Despite the ecological importance of trees, Marchant and Halse (1990) estimated there had been a ten-fold reduction in area of fringing trees between 1953 and 1988. The principal tree species, *Acacia maconochieana* Pedley, *Eucalyptus microtheca* F.Muell. and *E. camaldulensis* Dehnh., die after prolonged flooding and must regenerate from seedlings. Grazing, mostly by cattle, appears to be the main cause of seedling mortality. In addition to its impact on tree regeneration and, thus, tree-nesting waterbirds, grazing may also have the potential to affect the breeding of Hardheads and other waterbirds that require dense ground cover for nesting (Marchant and Higgins 1990).

DISCUSSION

Surveys in the 1980s and 1990s have shown Lake Gregory to be one of the most important wetlands for waterbirds in Australia. Higher numbers have been recorded only on the tropical floodplain of the Alligator Rivers (Morton et al. 1993) and among arid zone wetlands Lake Gregory is pre-eminent with its combination of high numbers, high species richness and large amount of breeding (see Kingsford and Halse 1998).

The number of waterbirds at Lake Gregory is probably influenced primarily by the amount of water elsewhere, as well as quality of habitat at the lake (Woodall 1985, Halse et al. 1993, 1995, Kingsford and Porter 1994). Thus, numbers at Lake Gregory increase during the dry season as smaller wetlands in surrounding areas dry out (Figure 3, Kingsford and Halse 1998). The congregation of 650 000 waterbirds in March 1988 may have resulted from this phenomenon occurring on a continental, rather than regional, scale as a result of droughts in eastern Australia and very low rainfall across northern Australia (Halse 1990).

Lake Gregory provides suitable waterbird habitat only if it has water. Rainfall records suggest the lake rarely contained water between 1930 and 1968 and, as a result, it presumably would have been less important for waterbirds than has been the case since 1969 or in the 35 years prior to 1930 (Figure 2). There are many wetlands in Australia that flood infrequently but have high conservation value when they contain water: Lake Torrens and many of the other large lakes where Banded Stilt breed are obvious examples (Robinson and Minton 1989) but it is also true of many small, easily overlooked wetlands such as Thunderlarra Swamp in south-western Australia (Jaensch and Lane 1993). This 135 ha wetland floods every 5-10 years and then holds water for less than a year but constitutes important breeding habitat.

The difficulty of assessing the overall conservation value of a wetland when data are available only for its dry phase has important implications for conservation strategies in the arid zone. Wetlands in arid areas are, perhaps, best viewed as networks in time as well as space, with the full value of some individual wetlands in the network being expressed at intervals of several decades. Therefore, it is critical that surveys are conducted after exceptional rainfall events as part of the process of identifying important arid zone wetlands and conserving arid zone biota.

Many species at Lake Gregory used partially inundated trees for nesting (Table 3) but this habitat does not exist when the water level is low. Absence of nesting habitat was probably the prime reason for little breeding being recorded in the low-water years of 1988 and 1989. No species was found breeding in 1988 and only Black Swans bred on

islands in 1989. Partly flooded trees, and also shrubs, appear to be critical habitat at most freshwater arid zone lakes in Australia that are important for breeding (Maher and Braithwaite 1992, Jaensch 1994). Therefore, the apparent reduction in extent of trees around Lake Gregory due to grazing is cause for concern (Halse 1990). Grazing has been identified as a threat to the conservation values of wetlands in other arid parts of the world (Denny 1991) but can be reduced by controlling access of stock to the foreshore of the lake.

The reduced breeding at Lake Gregory when the water level was low may also be partly attributable to increased salinity (see Table 1, Halse et al. 1998). Most Australian waterbirds do not breed in saline water (Goodsell 1990, Halse et al. 1993) and the Black Swan, which is tolerant of salt (Hughes 1976), was the only species recorded doing so at Lake Gregory when salinity exceeded 10 g L^{-1} . High salinity also reduced numbers of invertebrate species in the lake and plant species growing on the shoreline (Halse et al. 1988, unpubl. data) and, thus, reduced the range of food items available for waterbirds.

Abundance of Black Swans in lakes in New Zealand has been shown to depend on the amount of submerged macrophyte (McKinnon and Mitchell 1994), amount of breeding by waterfowl in eastern Australian wetlands is strongly affected by the biomass of Chironomidae larvae, especially *Chironomus tepperi* Skuse (Crome 1986) and presence of Australian Pelicans on Lake Eyre has been related to large numbers of fish (Waterman and Read 1992, Kingsford and Porter 1993). Despite a large amount of evidence that occurrences of other waterbird species are also affected by the type of food items available, few studies have examined whether a relationship exists between the taxonomic range of food items and number of waterbird species using a wetland.

Lake Gregory, which supports more species of waterbird than any other Australian arid zone wetland (Kingsford and Halse 1998), contains the highest number of invertebrate species (Halse et al. 1988). Similarly, Kingsford and Porter (1994) found 26 percent more waterbird species occurred on the freshwater Lake Numalla in eastern Australia, which contained a more diverse invertebrate assemblage, than on the adjacent saline Lake Wyara. Timms (1981) recorded four times as many waterbird species in a fresh lake compared with a saline one and seven times as many invertebrate species. Timms attributed the greater number of waterbird species in the fresh lake to differences in habitat or food items rather than salinity itself. However, the causal link between diversity of invertebrates (and macrophytes) and high numbers of waterbird species has yet to be demonstrated. In contrast to Timms (1981), Wollheim and Lovvorn (1995) suggested costs of osmoregulation were more important than low numbers of invertebrate species in reducing waterbird use of saline wetlands, partly because most waterbirds are flexible in the type of food they consume. Availability of suitable nesting and roosting habitat may be another factor that modifies any relationship that exists between the range of food items available and number of waterbird species. Further studies are needed to clarify whether a relationship exists between diversity of food items and waterbird species richness.

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