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WATERBIRDS ON AN ADJACENT FRESHWATER LAKE AND SALT LAKE IN ARID AUSTRALIA

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Abstract

Aerial surveys of waterbirds were made on Lake Wyara (salt) and Lake Numalla (freshwater) in arid Australia, every three months, 1987–1989. These lakes were significant sites for conservation of waterbirds. Aerial counts were on average 42 000 waterbirds (2600–113 500), including at least 41 species. In March 1988, total numbers probably exceeded 280 000. More than half the population of freckled duck Stictonetta naevosa *may occur on the lakes. Although only 3 km apart and similar in size, the salt lake had about ten times more waterbirds (mainly ducks, herbivores, small wading birds) than the freshwater lake (mainly piscivores, large wading birds). Differences in waterbird communities between the lakes were attributable to food resources. There were larger numbers of planktonic invertebrates and more macrophyte vegetation in the salt lake than in the freshwater lake while the freshwater lake contained fish and shrimp populations.*

Keywords: Australia, waterbirds, arid, freshwater, salt.

INTRODUCTION

Wetlands in arid regions of the world can be fresh water but, because of high evaporation, are more often saline (Bayly & Williams, 1973; De Deckker, 1983; Seaman *et al.*, 1991). Freshwater and salt wetlands, many of which flood temporarily, are ubiquitous in arid Australia (Williams, 1981) which makes up about 70% of the continent (Stafford Smith & Morton, 1990). These wetlands had not been considered important for waterfowl (Frith, 1982) because more valuable waterbird habitats are thought to be in the tropics (Lavery, 1970; Morton *et al.*, 1990, 1993*a*, *b*) and the south of the continent (Frith, 1982; Halse *et al.*, 1990). Nevertheless there is increasing evidence that some wetlands in arid Australia support particularly large numbers of waterbirds (Braithwaite *et al.*, 1986; Halse, 1990; Kingsford *et al.*, 1990; Reid & Puckeridge, 1990; Maher & Braithwaite, 1992; Kingsford & Porter, 1993).

Despite the world-wide abundance of salt lakes (similar in volume to fresh waters), they are generally regarded as less important than freshwater wetlands (Williams, 1988). Comparative diversity of biota has reinforced this view. Fish and frogs are seldom found in salt lakes (Chessman & Williams, 1974; Hart *et al.*, 1991), and numbers of macrophyte and invertebrate species are low (De Deckker, 1983; Brock, 1985; Bolen *et al.*, 1989; Hart *et al.*, 1991; Seaman *et al.* 1991). Numbers of waterbird species may also decline with increasing salinity (Timms, 1981), but there are few studies comparing the abundance of organisms in freshwater and salt lakes.

We investigated abundance and diversity of waterbirds on two wetlands in arid Australia, Lakes Wyara and Numalla, over a three-year period. These wetlands were similar in size and were only about 3 km apart but one is a salt lake and the other freshwater. We know of nowhere else in Australia where the effect of salinity on a waterbird community can be examined without undue influence from the confounding factors of size and distance between wetlands. Our objectives were to determine the significance of these wetlands to waterbirds, and to compare the abundance and diversity of their waterbirds and propose a hypothesis to account for patterns observed.

Nomenclature for birds follows Marchant and Higgins (1990), and for vascular plants follows Harden (1990).

METHODS

Study area

Lake Numalla (2904 ha, 28°44'S, 144°18'E) is a freshwater lake and Lake Wyara (3813 ha, 28°42'S, 144°14'E) a salt lake in south western Queensland (Fig. 1). Annual rainfall measured at Boorara Station, 10 km north-east of Lake Numalla, was 431 mm, 398 mm, and 255 mm respectively during the three years of the study, 1987–1989.

Six creeks run into Lake Wyara from unnamed ranges in the west and the south and from Willies and Walters Ranges in the north (Fig. 1). *Ruppia* sp., *Chara australis* and *Lamprothamnium papulosum*, submerged macrophytes, grew extensively across the bottom of Lake Wyara, and salt-tolerant plant species, such as samphire *Halosarcia pergranulata* and creeping monkey flower *Mimulus repens*, around the edge. When full, Lake Wyara has three islands along its western shoreline (Fig. 1).

Lake Numalla receives water from Boorara Creek

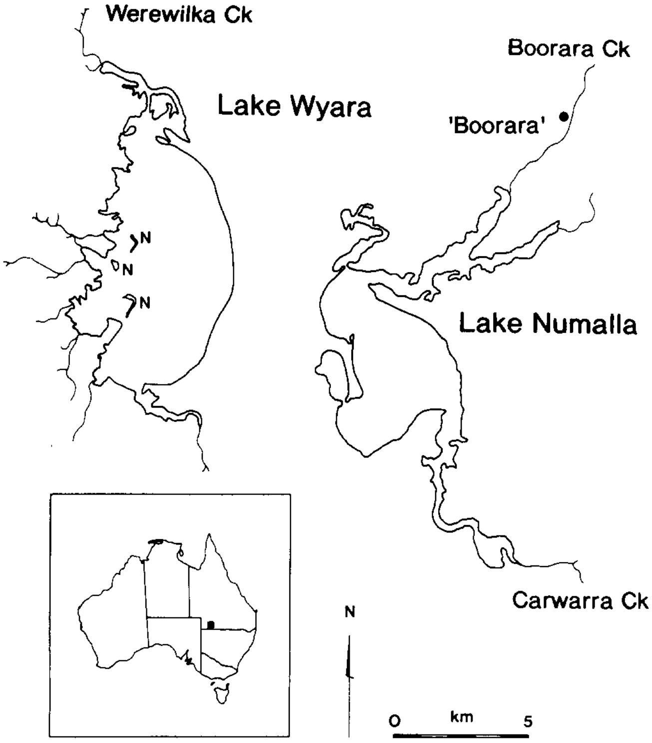

Fig. 1. Location of Lakes Numalla (freshwater) and Wyara (salt). N marks islands where there was evidence of nesting on Lake Wyara.

draining the eastern slope of Walters and Hoods Ranges, and Carwarra Creek which runs from the Paroo River (Fig. 1). It is surrounded by dead and living black box *Eucalyptus largiflorens*, coolibah *E. microtheca* and river cooba *Acacia stenophylla*. Patches of spiny sedge *Cyperus gymnocaulos* fringe the lake. In the southern and northern ends, clumps of lignum *Muehlenbeckia florulenta* occur.

Waterbird counts

Beginning in March 1987, surveys were flown over the lakes every three months until December 1989 in a Cessna 206 aircraft at a height of 30 m and a speed of 167 km h^{-1}. Two observers, one on each side of the aircraft, identified and estimated total numbers of waterbirds and recorded this information on mini cassette recorders. Most waterbirds could be identified to species, but four groups of species could not (Appendix 1, see also for scientific names). Where possible, brood sizes were also recorded. Each lake was counted four times during each three-month trip because aerial surveys of many species of waterbirds were prone to large random error (R.T. Kingsford, unpublished data). Two surveys were flown without delay and repeated within two days. The four counts were used to calculate means and standard errors for each three-month trip.

The aircraft was flown over water about 150 m from the edge of the lake, where waterbirds concentrated. To determine numbers of birds missed, distribution and abundance of waterbirds were recorded on five transects, 100 m wide, flown randomly across Lake Wyara on each of five trips. Distances of all waterbirds from the shore on Lake Numalla were estimated using marked divisions on the window of the aircraft on two trips.

Some waterbird breeding data were collected on 17 August 1989. We estimated the number of nests of a colony of Australian pelicans occupying the centre of the island (210 m × 10 m) and counted the nests of black swans and their clutch sizes. To estimate pelican nests which were uniformly spaced within the nesting area, we extrapolated a count for a 10-m length of the strip. Colonies of silver gulls and Caspian terns were independently estimated by three observers.

Invertebrate sampling

We sampled invertebrates from the two lakes 14–16 August 1989. Twenty samples of zooplankton were collected randomly from areas of high and low waterbird abundance on each lake (determined during aerial surveys). We used a 2-m perspex tube, 54 mm in diameter, which was lowered vertically through the water column until either the top end was just above the surface of the water or the bottom end came into contact with the substratum. The column of water was secured with corks and the volume measured before the water was flushed through a 75-μm sieve, designed to catch macroinvertebrates (Bottrell *et al.*, 1976). Invertebrates were fixed in a solution of 4% formalin with 60 g $litre^{-1}$ of sugar (Prepas, 1978) and identified, mostly to Order, and counted under a binocular microscope using a rafter chamber (Newell & Newell, 1973). All samples for each lake were combined; species composition and body lengths and widths of the invertebrate species recorded were determined in 10 subsamples (1 ml).

Ten wooden boards (90 mm × 200 mm) on floats were placed randomly across each lake, 5–10 cm above the water during the same 24-h period. They were covered by plastic bags coated with the sticky preparation Tanglefoot (Tanglefoot Company, Grand Rapids, USA). Plastic bags avoided Tanglefoot contact with the boards and could be easily slipped off. Sampling was repeated 24-h later after a millimetre of rain fell on the first night. After collection, invertebrates on these 'sticky-traps' were identified to Family, where possible, and counted.

Five one-litre samples of water were collected randomly from each lake and frozen. Ionic composition, total dissolved solids, total phosphorus and $CaCO_3$ in the water were determined (Franson, 1981). Conductivity and pH (PTI-52 meter, CHK Engineering, Sydney), and Secchi disk readings were collected with samples of the water column. Average depth was calculated from ten random locations along an east–west transect.

Statistical analysis

Water chemistry variables were compared between lakes using Student t- or Kruskal-Wallis tests where assumptions of the former were not met (Sokal & Rohlf, 1981). We used Wilcoxon signed ranks tests to compare numbers of waterbirds, and nests and broods of black swans between the two lakes. Each data point was the mean of four aerial estimates. Waterbirds were separated into four foraging groups: piscivores and large wading birds; ducks and little grebes; herbivores and small wading birds (see Appendix 1). Groups were based on the food that they eat (Barker & Vestjens, 1989; Marchant & Higgins, 1990) and where the birds usually forage (Kingsford, 1991).

Numbers per litre, length and width of zooplankton, and numbers of invertebrates on 'sticky-traps' were compared between lakes using two factor analyses of variance. Lake was the common factor in all analyses. Area, with two levels (high and low waterbird abundance), was the second factor in analyses of zooplankton data and Day, with two levels (rain and no rain), was used in analyses of data from 'sticky-traps'. Data for densities of zooplankton were transformed by ln $(x+1)$, as means were correlated with variance (Sokal & Rohlf, 1981). Analyses were performed using SYSTAT (Wilkinson, 1990). Standard errors were used throughout.

RESULTS

Water chemistry

Total dissolved solids were almost six times higher in Lake Wyara compared with Lake Numalla (Table 1). This was principally due to high concentrations of Na^+ and Cl^- but all anions and cations were higher in Wyara than in Numalla (Table 1). Numalla was deeper and had a lower pH than Wyara (Table 1). The water in Wyara was clear but Numalla was highly turbid (Table 1).

Waterbird abundance

An average of 42 100±10 200 waterbirds (range: 2600–113 500) was estimated during 12 trips, 1987–1989. Numbers exceeded 100 000 waterbirds during one trip (Fig. 2). Forty-one species were seen on the lakes with more on Numalla (39) than on Lake Wyara (31) (Table 2). This included large numbers of freckled duck

Table 1. Water chemistry variables (mean ± standard error) on Lakes Numalla and Wyara (14 August 1989)

Variable	Numalla	Wyara	n	Probability[a]
Anions (mg litre^{-1})				
Cl^-	745 ± 2	5 360 ± 386	5	0·008
SO_4^{2-}	34 ± 0	436 ± 51	5	0·009
Cations (mg litre^{-1})				
Na^+	600 ± 0	3 840 ± 279	5	0·005
K^+	12 ± 0	29 ± 2	5	0·005
Mg^{2+}	10 ± 0	68 ± 6	5	0·018
Ca^{2+}	23 ± 0	42 ± 5	5	0·007
$CaCO_3$ (mg litre^{-1})	436 ± 4·0	568 ± 75·8	5	0·106
pH	8·4 ± 0·02	10·8 ± 0·06	20	<0·001
Total phosphorus (μg litre^{-1})	292 ± 38·1	455 ± 55·6	5	0·016
Conductivity (μS cm^{-1})	2 239·5 ± 34·0	37 210 ± 196·0	20	<0·001
TDS (mg litre^{-1})	1 584 ± 26·9	9 400 ± 892	5	0·009
Secchi disk (cm)	12·6 ± 0·35	90 (clear)	20	<0·001
Depth (cm)	510·0 ± 40·0	90 ± 4·0	10	<0·001

[a] Results of Student t- or one-way Kruskal-Wallis tests.

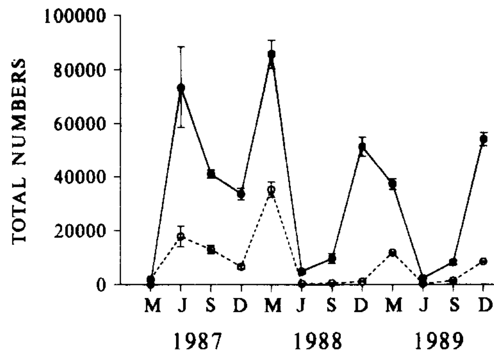

Fig. 2. Mean estimates from aerial surveys of all waterbirds on Lakes Numalla (○) and Wyara (●), 1987–1989. Standard errors calculated from four aerial counts of each wetland.

(3600±1300, n=12) (Fig. 3) which were equally likely to occur on both lakes. There was no significant difference in numbers of freckled duck (Table 2).

There were significantly fewer waterbirds on Lake Numalla compared with Lake Wyara (z=–3.06, p=0.002). On average, numbers on Wyara exceeded those on Numalla by a factor of 10.5±3.63 (range: 2.5–47.5) (Fig. 2). Three out of the four groups of waterbirds showed this pattern (Fig. 4). There were significantly fewer ducks and little grebes on Lake Numalla than on Lake Wyara (z=–3.06, p=0.002). Numbers of these waterbirds on Lake Wyara exceeded, on average, those on Lake Numalla by a factor of 23±14 (range: 1–138) (Fig. 4(a)). Similarly, there were significantly more herbivorous waterbirds on Lake Wyara than on Numalla (z=–3.06, p=0.002) with, on average 139±32 (range: 10–310) times more on the salt lake (Fig. 4(b)). Significantly more small wading birds were also estimated on Wyara compared with Numalla (z=–3.06, p=0.002) with, on average 104±37 (range: 2–406) times more small wading birds on the salt lake (Fig. 4(c)).

In contrast, there was no significant difference in the numbers of piscivores and large wading birds between Lakes Numalla and Wyara (z=0.78, p=0.94) but this did not reflect the foraging pattern of this group. Colonies of Australian pelicans were detected on islands (Fig. 1) during aerial surveys on Lake Wyara in December 1988, March 1989, September 1989 and December 1989. Adults did not feed on Lake Wyara but

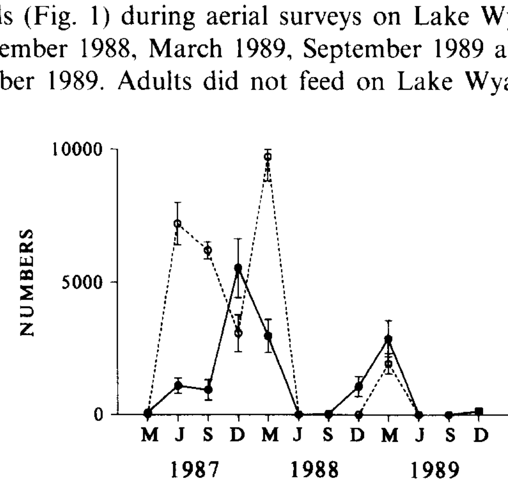

Fig. 3. Mean estimates of freckled duck on Lakes Numalla (○) and Wyara (●) 1987–1989. Standard errors calculated from four aerial counts of each lake.

Table 2. Mean estimates (± standard error) of each waterbird type on the two lakes for the 12 trips (range of mean abundances for each lake given in parentheses)

Waterbirds	Numalla	Wyara	Sig.[a]
Little grebe	0·1 ± 0·06 (0–1)	35 ± 18 (0–220)	**
Great crested grebe	0·3 ± 0·23 (0–3)	0·5 ± 0·39 (0–5)	ns
Australian pelican	440 ± 150 (86–1600)	1 300 ± 670 (0–7400)	ns
Darter	6·4 ± 2·36 (1–26)	0·03 ± 0·026 (0–1)	**
Great cormorant	16 ± 4·5 (0–43)	7·2 ± 7·21 (0–87)	*
Pied cormorant	160 ± 37 (2–420)	0·6 ± 0·38 (0–4)	**
Little black cormorant	32 ± 25 (0–310)	1·3 ± 1·14 (0–14)	**
Little pied cormorant	1·2 ± 0·65 (0–8)	0	*
Pacific heron	0·7 ± 0·19 (0–3)	0	**
Great egret	9·0 ± 3·58 (1–46)	0	**
Egret	5·2 ± 1·59 (0–17)	0	**
White-faced heron	1·4 ± 0·58 (0–5)	0·05 ± 0·052 (0–1)	0·08
Glossy ibis	1·8 ± 0·95 (0–9)	0	ns
Australian white ibis	4·0 ± 2·10 (0–25)	0	*
Straw-necked ibis	1·5 ± 0·48 (0–5)	0	**
Royal spoonbill	5·9 ± 1·75 (1–19)	0	**
Yellow-billed spoonbill	76 ± 13 (15–160)	1·0 ± 0·78 (0–10)	**
Blue-billed duck	0	2·6 ± 1·85 (0–20)	ns
Musk duck	0·02 ± 0·021 (0–1)	0·2 ± 0·09 (0–1)	ns
Freckled duck	2 400 ± 1 000 (0–9 700)	1 200 ± 500 (0–5 500)	ns
Black swan	430 ± 170 (30–1 790)	5 100 ± 1 100 (1 200–13 300)	**
Australian shelduck	0·1 ± 0·09 (0–1)	0	ns
Maned duck	31 ± 16 (0–160)	1·4 ± 0·99 (0–9)	*
Grey teal	250 ± 120 (1–1 000)	12 600 ± 16 300 (13–47 600)	**
Pacific black duck	220 ± 140 (0–1 700)	56 ± 22 (0–220)	ns
Australasian shoveler	13 ± 5 (0–52)	250 ± 120 (0–26 700)	**
Pink-eared duck	790 ± 540 (0–5 700)	13 900 ± (0–1 400)	**
Hardhead	25 00 ± 820 (7–8 100)	2 000 ± 1 600 (0–19 700)	0·06
Black-tailed native-hen	1·9 ± 1·17 (0–14)	0	*
Eurasian coot	40 ± 23 (0–270)	990 ± 440 (0–3 500)	0·09
Brolga	0·7 ± 0·23 (0–3)	0·3 ± 0·31 (0–4)	ns
Masked lapwing	0·7 ± 0·26 (0–3)	1·0 ± 0·72 (0–9)	ns
Black-winged stilt	1·9 ± 0·70 (0–8)	230 ± 84 (0–860)	**
Banded stilt	0	560 ± 390 (0–4 700)	*
Red-necked avocet	14 ± 10 (0–110)	2 200 ± 1 100 (0–12 000)	**
Small wader	3·5 ± 1·9 (0–23)	560 ± 270 (0–2 500)	**
Large wader	0·2 ± 0·21 (0–3)	0·6 ± 0·43 (0–5)	ns
Silver gull	70 ± 33 (5–420)	770 ± 290 (79–3 500)	**
Whiskered tern	26 ± 10 (1–95)	130 ± 83 (0–990)	ns
Gull-billed tern	2·0 ± 1·17 (0–13)	3·8 ± 2·76 (0–32)	ns
Caspian tern	6·7 ± 2·51 (0–32)	9·1 ± 4·38 (0–46)	ns

[a] Probabilities for Wilcoxon signed ranks tests. *, $p < 0·5$; **, $p < 0·01$; ***, $p < 0·001$; ns, $p \geq 0·10$.

flew to Lake Numalla to catch fish which were brought back to young on Wyara. Excluding these colonies, there were an average of 290±140 (4–1721) times more piscivores and large wading birds on Lake Numalla than on Lake Wyara (z=–3.06, p=0.002, Fig. 4(d)). Mean and range abundances for each waterbird are given in Table 2 with results of abundance comparisons between lakes.

Aerial estimates on Lake Wyara were more negatively biased than those of Lake Numalla because there were more waterbirds within 300 m of the shore where the aircraft flew on the latter (Fig. 5). Eleven species made up the 20% of waterbirds observed further than 300 m from the shore of Lake Wyara. On Lake Numalla, only 2.7% were further than 300 m from the shoreline; most (98%) were Australian pelicans, with black swans and pied cormorants making up the remainder.

Waterbird breeding

Australian pelicans, red-necked avocets, silver gulls, Caspian terns and black swans bred on islands of Lake Wyara. There were dead chicks of Australian pelicans and nest debris on all islands. A colony of Australian pelicans established on two of the islands in December 1988. The colony peaked in March 1989 and was confined to one island (southern, Fig. 1) by August 1989 when we estimated that there were 1 500 nests. At the same time, about 50 Caspian terns nested on the northwest corner of the island alongside a colony of about 170 silver gulls.

Most breeding of black swans was on Lake Wyara. There were significantly more nests (z=2.02, p=0.04) and more broods (z=2.03, p=0.04) here compared with Lake Numalla (Fig. 6). Where brood sizes were recorded (five trips), there were no significant differences between lakes ($F_{1,42}$=0.44, p=0.51) or among

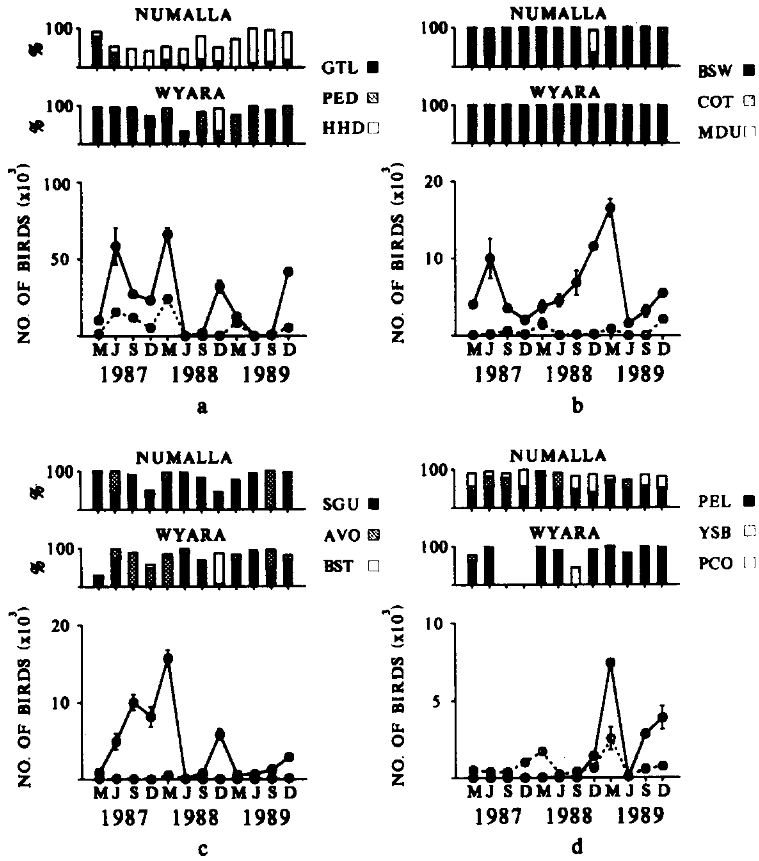

Fig. 4. Mean estimates of four groups of waterbirds (a)–(d) on Lakes Numalla (○) and Wyara (●); (a) most duck species and little grebes; (b) herbivores; (c) small wading birds; and (d) piscivores and large wading birds (pelican colonies on Lake Wyara have been omitted). See Appendix 1 for species included in each group. Errors are standard errors of four aerial counts. Histograms show the percentage composition of three common species for lakes and waterbird groups. (a) GTL, grey teal; PED, pink-eared duck; HHD, hardhead; (b) BSW, black swan; COT, Eurasian coot; MDU, maned duck; (c) SGU, silver gull; AVO, red-necked avocet; BST, banded stilt; (d) PEL, Australian pelican; YSB, yellow-billed spoonbill; PCO, pied cormorant.

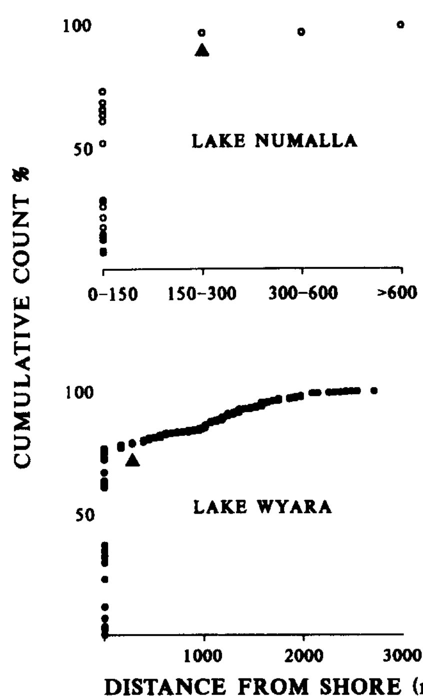

Fig. 5. Cumulative distribution of birds versus distance from shore on Lakes Numalla (a) and Wyara (b). Arrow marks where aerial surveys were conducted around each lake. Distribution of waterbirds on Lake Numalla calculated from estimates by one observer during two trips, and on Lake Wyara from 25 random transects across the lake over five trips.

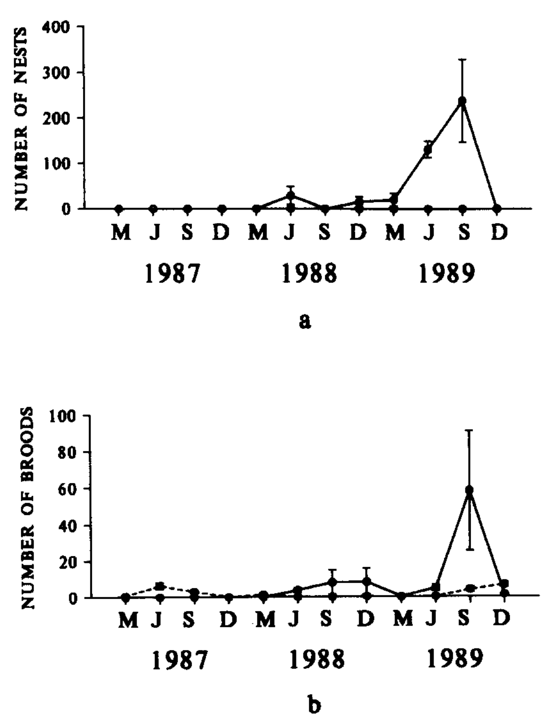

Fig. 6. Nests (a) and broods (b) of black swans estimated on Lakes Numalla (○) and Wyara (●). Standard errors calculated from four aerial counts of each lake.

Table 3. Zooplankton collected on Lakes Numalla and Wyara
Percentage (mean ± standard error) gives relative abundance of species within Orders for each lake, calculated from 10 subsamples. Body length and width (means ± standard errors) measured using *n* individuals

Lake	Order	Species	%	Length[a]	Width[a]	*n*
Numalla	Copepoda	*Boeckella triarticulata*	36 ± 2·8	9·4 ± 0·11	2·0 ± 0·02	47
		Calamoecia lucasi	45 ± 3·9	4·5 ± 0·08	1·0 ± 0·02	50
		Cyclopoid sp.	19 ± 2·6	6·3 ± 0·60	1·3 ± 0·02	39
	Cladocera	*Daphnia carinata*	11 ± 4·2	19·5 ± 0·27	5·4 ± 0·15	22
		Daphniopsis sp.	7 ± 2·2	10·0 ± 0·44	6·4 ± 0·34	19
		Ceriodaphnia sp.	2 ± 1·1	4·4 ± 0·05	2·9 ± 0·00	2
		Moina sp.[b]	5 ± 1·8	7·4 ± 0·20	4·4 ± 0·10	20
		Macrothrix sp.[c]	16 ± 3·8	3·4 ± 0·08	2·0 ± 0·05	33
		Ilyocryptus sp.	7 ± 1·6	2·8 ± 0·02	2·3 ± 0·02	19
		Pleuroxus sp.	13 ± 4·4	3·3 ± 0·06	2·8 ± 0·03	30
		Alona sp.[d]	39 ± 8·2	3·9 ± 0·06	2·6 ± 0·02	40
	Ostracoda		—	2·7 ± 0·09	1·7 ± 0·09	16
	Diptera	Chironomidae (larvae)	—	13·5 ± 0·54	1·3 ± 0·03	3
Wyara	Copepoda	*Halicyclops* sp.	—	6·3 ± 0·11	1·5 ± 0·03	50
	Cladocera	*Moina baylyi*	73 ± 5·0	6·6 ± 0·10	14·3 ± 1·09	48
		Daphniopsis sp.	27 ± 5·0	8·6 ± 0·34	5·4 ± 0·26	29
	Ostracoda		—	4·8 ± 0·14	3·1 ± 0·10	28
	Diptera	Chironomidae (larvae)[e]	—	14·3 ± 1·09	1·4 ± 0·10	18
	Coleoptera	*Necterosom*[a] sp. (larvae)	—	36·6 ± 4·12	9·5 ± 0·42	20

[a] 10^{-1} mm.
[b] Probably *Moina micrura.*
[c] Probably *Macrothrix breviseta* and *M. hirsuticornis.*
[d] *Alona macrocopa, A. rigidicaudis, A. pulchella.*
[e] *Tanytarsus* sp., *Procladius* sp.

trips ($F_{4,\,42}$=0.13, p=0.97); the interaction term was not significant. Although nests were seen in each month of 1989, there were more nests and broods in the spring and summer months (September–December). This was the pattern for the other two years. There was more breeding in 1989 compared with the other two years (Fig. 6). There were 358 nests of black swans on Lake Wyara in August 1989, with mean clutch size of 4.8±0.10 (range: 1–11).

Twenty nests of red-necked avocets were estimated on an island in Lake Wyara in September 1989. Breeding records for other waterbirds species were for Lake Numalla. Pied cormorants nested in September 1988 (1) and 1989 (30). Four Pacific heron nests were seen in September 1989. Small colonies of Australian white ibis nested in stands of lignum in September 1988 (15) and December 1989 (6). Single royal spoonbill nests were seen in December 1988 and 1989. Estimates of yellow-billed spoonbill nests numbered 1–6 and were seen in September and December 1988 and June, September and December 1989. A brood of Pacific black duck was seen on Lake Numalla in December 1989.

Invertebrates

Three copepod and at least eight cladoceran species were collected from Lake Numalla compared with one species of copepod and two of cladocera from Lake Wyara (Table 3). *Calamoecia lucasi* and *Boeckella triarticulata* accounted for most of the copepods on Numalla. The cladoceran fauna on Numalla was dominated by *Alona* sp. while *Moina baylyi* was the most abundant cladoceran on Lake Wyara (Table 3). Ostracod and chironomid species on the two lakes were not determined.

The density of zooplankton was about six times higher on Lake Wyara compared with Lake Numalla ($F_{1,75}$=59.79, p<0.001, Table 4) and significantly higher in areas low in numbers of waterbirds ($F_{1,75}$ = 5.93, p = 0.017, Table 4); the interaction term was not significant. Significantly higher densities of all invertebrate groups were found on Lake Wyara (Table 4). There were significantly more copepods in areas of low compared with areas of high waterbird numbers. Cladocerans on Lake Numalla were not as wide as those on Wyara but were similar in length (Table 3). Differences in the length of ostracods were dependent on the lake and the area of collection but ostracods were wider on Lake Wyara compared with Numalla

Table 4. Numbers of zooplankton litre^{-1} (± standard error) from areas of low and high concentrations of waterbirds on Lakes Numalla and Wyara (20 samples were taken from each lake and area combination)

Invertebrates	Numalla		Wyara	
	High	Low	High	Low
Copepoda	5·7 ± 0·6	10·2 ± 1·0	59·8 ± 14·8	101·6 ± 19·0
Cladocera	6·8 ± 2·3	9·6 ± 3·1	9·1 ± 1·3	15·9 ± 2·6
Ostracoda	1·6 ± 0·4	1·5 ± 0·6	7·2 ± 1·4	15·1 ± 2·5
Nauplii	1·9 ± 0·7	3·5 ± 0·10	47·2 ± 19·0	15·7 ± 4·9
Remainder[a]	0·9 ± 0·2	0·6 ± 0·3	15·5 ± 10·0	5·2 ± 1·0
Total	16·8 ± 2·1	25·2 ± 3·9	133·1 ± 37·7	152·4 ± 21·9

[a] Chironomidae larvae, Conchostraca, *Hydra* sp.

Table 5. Mean numbers of invertebrates (± standard error) on 10 'sticky-traps' over successive 24-h periods of rain (1 mm) and no rain on Lakes Numalla and Wyara

Invertebrates	Numalla		Wyara	
	Rain	No rain	Rain	No rain
Diptera				
Acalyptrata	1·6 ± 1·90	13·9 ± 2·09	0·90 ± 0·35	2·4 ± 0·67
Ceratopogonidae	0·2 ± 0·20	3·2 ± 0·84	0·1 ± 0·10	2·5 ± 0·54
Chironomidae	8·2 ± 1·01	93·5 ± 7·92	108·1 ± 29·1	1012·3 ± 144·1
Other[a]	1·0 ± 0·42	3·1 ± 0·55	1·8 ± 0·71	9·7 ± 1·47
Coleoptera[b]	0·2 ± 0·13	5·0 ± 0·84	0	2·7 ± 0·87
Arachnida	2·6 ± 0·75	6·4 ± 0·60	0·4 ± 0·31	18·1 ± 2·53
Remainder[c]	2·2 ± 0·94	12·4 ± 2·78	2·3 ± 0·62	2·6 ± 0·34
Total	16·0 ± 2·19	136·6 ± 9·69	113·6 ± 29·2	1050·3 ± 145·2

[a] Tipulidae, Psychodidae, Cecidomyiidae, Sciaridae, Empididae, Dolichopodidae, Phoridae, Syrphidae, Muscidae, Calliphoridae, Tachinidae.
[b] Carabidae, Hydrophilidae, Pselaphidae, Heteroceridae, Coccinellidae, Chrysomelidae.
[c] Psocoptera, Hemiptera, Thysanoptera, Neuroptera, Trichoptera, Lepidoptera, Hymenoptera, Collembola.

(Table 3). Copepods on the two lakes were similar in size (Table 3).

There were about seven times more invertebrates on 'sticky-traps' from Lake Wyara compared with Numalla ($F1,36=109.7$, $p<0.001$), chironomids being the major animal group (50–96%) (Table 5). Chironomids, other Diptera and Arachnida all showed the same pattern of abundance as total numbers but there were significantly more coleopterans on Numalla. Rain significantly affected the total numbers of invertebrates collected on 'sticky-traps' ($F1,36=176.7$, $p<0.001$, Table 5). The interaction term was not significant ($F1,36=0.9$, $p=0.36$). During the 24-h period of no rain, there were more than eight times as many invertebrates on both lakes compared with the night when it rained (Table 5).

DISCUSSION

Wetland significance to waterbirds

Lakes Wyara and Numalla are very important sites for waterbird conservation in Australia. Apart from observations by Maher (1991), there are no published accounts on waterbirds of these wetlands. Few wetlands on the continent have aerial counts exceeding 80 000 waterbirds (Fig. 2), and our aerial estimates undoubtedly underestimated actual numbers. Ground counts done at the same time as aerial counts on Lake Altibouka, a smaller inland salt lake, averaged 39 000 compared with 19 000 during aerial counts and showed evidence of density dependence (R.T. Kingsford, unpublished data). Aerial estimates on Lake Wyara, in particular, and Lake Numalla were further biased negatively by the methodology of this study (Fig. 5). Assuming a 50% underestimate, as many as 284 000 waterbirds were on the lakes in March 1988. This is a conservative estimate. Only waterbird numbers on wetlands of the Northern Territory during the dry season (Bayliss & Yeomans, 1990; Morton *et al.*, 1991), Lake Eyre North (Kingsford & Porter, 1993), Lake Galilee (Braithwaite *et al.*, 1986) and Lake Gregory (Halse, 1990) are comparable in Australia. Although most waterbirds were on Lake Wyara, Lake Numalla may be particularly important when Lake Wyara has little water—more than 100 000 waterbirds were estimated on Numalla when Wyara was almost dry in 1985 and had <300 waterbirds (M. T. Maher, pers. comm.).

There were also many waterbird species on the lakes (Table 2). As palaearctic shorebirds could not be differentiated and some species cannot be seen during aerial surveys (R. T. Kingsford, unpublished data), more waterbird species than those recorded during this study undoubtedly use these lakes.

The lakes are probably the most important dry refuge habitat on the continent for freckled duck. With a population estimated to be 19 000 (Garnett 1992), this is one of Australia's rarer species of duck, which has never been recorded in such large numbers as on these lakes (Fig. 3). Conceivably, most birds of the population collected on the lakes in March and June of 1987 (Fig. 3) but it is more likely that numbers in Australia exceed the previous estimation.

The lakes are significant breeding sites for some waterbird species, particularly Wyara where numbers of breeding black swans were considerable (Fig. 6) with broods observed in many months of the year. The lake was well known to Aborigines who collected swan's eggs (R. Robbins, pers. comm.). Most breeding of black swans probably corresponded to periods when macrophytes were abundant. The size of the 1989 colony of Australian pelicans on Lake Wyara has only been exceeded by colonies on Lakes Eyre and Cawndilla (Marchant & Higgins, 1990; Waterman & Read, 1992). Australian pelicans also bred on Lake Wyara in June 1991 and June 1992 (R. T. Kingsford, personal observations). Lake Wyara may be particularly important for this species because it supports more regular breeding than sites where particularly large breeding populations occur only sporadically.

We know of no other wetlands in arid or southern Australia which consistently support such high numbers of waterbirds. Although Lake Wyara sometimes dries out, Lake Numalla has only been dry three times this century (Maher, 1991), probably because it receives water from the Paroo River as well as from the local catchment.

Guaranteed water supply, mainly from local sources, is critical for these lakes. Both rely on water from small creeks, which originate no more than 60 km away. Although Lake Wyara is on the boundary of the large Murray–Darling catchment basin, it has no hydrological connection with these major rivers and fills almost entirely from local catchment except in exceptional floods (A. McGrath, pers. comm.). This demands a reassessment of waterfowl conservation in Australia. Waterfowl habitat is usually divided up into major catchment basins (Braithwaite, 1975; Frith, 1982) corresponding to the major rivers, and important wetlands for waterbirds such as Lake Wyara could be compromised by man-induced hydrological changes in the catchment. Wetlands in arid Australia which provide refuge for waterbirds, particularly during dry periods, need to be identified and their catchments and water supply appropriately managed to ensure the viability of these wetlands. With increasing development of arid regions of Australia for irrigated cotton, water supply must not be lost to these important waterbird habitats.

Salt vs freshwater

Amounts of major ions and total dissolved solids (Table 1) clearly defined Wyara as a salt lake and Numalla as freshwater (Williams, 1966). Salinity varies in the lakes but Total Dissolved Solids were <3000 mg litre^{-1} in Lake Numalla and 5000–30 000 mg litre^{-1} in Lake Wyara (B. V. Timms, pers. comm.), which does not compromise this distinction.

Although the lakes are similar in size, there were many more waterbirds on the salt compared with the freshwater lake (Fig. 2). There was considerable fluctuation in waterbird numbers, mainly in relation to rainfall in the preceding two months (R. T. Kingsford, unpublished data), but this difference remained consistent. Some counts on Lake Wyara were an order of magnitude higher than counts at the same time on Lake Numalla. Difference in abundance of waterbirds in favour of salt lakes relative to freshwater lakes in arid Australia is not confined to the two studied. We found much higher densities of waterbirds on Lake Eyre, a salt lake, than on freshwater lakes (Lake Blanche, Cooper Creek lakes) in central Australia (Kingsford & Porter, 1992). Lake Yamma Yamma, a large freshwater lake in southwest Queensland, also had considerably fewer waterbirds than a salt lake, Lake Galilee, in central Queensland (Kingsford *et al.*, 1990).

On Lakes Wyara and Numalla, differences in numbers of waterbirds which usually feed on invertebrates (Fig 4(a) and (c)) could be explained by the abundance of food. There were about eight times more zooplankton on Wyara compared with Numalla (Table 4), and their lengths and widths were similar or greater on Wyara for most taxonomic groups (Tables 3 and 4). There was a similar difference between the lakes in the numbers of invertebrates collected on 'sticky-traps' (Table 5).

We hypothesise that it is the salt through its physical action on the water which determines these differences in abundances of invertebrates and waterbirds. Salt in Lake Wyara caused flocculation of clay particles which then fell to the substratum allowing light to penetrate (Table 1) and submerged macrophytes to establish. More than 80% of the substratum was covered by *Chara australis* with some *Ruppia* sp. and *Lamprothamnium papulosum* during our visit in August 1989. These aquatic macrophytes provided food for herbivorous waterbirds (Fig. 4(b)) and the invertebrates. During later visits to the lakes, we usually observed extensive stands of the three species of macrophyte on Lake Wyara but only spiny sedge on freshwater, Lake Numalla. High turbidity of Numalla (Table 1) probably resulted in less primary productivity through reduced light penetration and nutrients (Buckney, 1980; Grobbelaar, 1985).

The many more piscivores and large wading waterbirds on Lake Numalla compared with Lake Wyara (Fig. 4(d)), excluding pelican colonies, were attributable to the occurrence of prey; fish and shrimps *Macrobrachium* sp. Fish occur in Lake Wyara but this may only be soon after filling. Increased salinity may result in fish kills (observed in 1992) and also clear the water making fish more vulnerable to avian predation (Bruton, 1985).

We do not know why two wetlands so close to each other are chemically so different. Both lakes lie on quaternary alluvium and lacustrine deposits. Local topography is a major determinant of whether fresh or salt waters occur (Williams, 1985) with overlying marine sediment a cause of some salt waters in arid Australia (Chivas *et al.*, 1986). As their catchments are different, further investigation of soils is needed.

Our knowledge of waterbirds on wetlands in arid Australia remains poor. Although salt lakes may be physiologically inhospitable habitats to invertebrates, frogs and fish and generally have a less diverse fauna, they can be extremely productive (McComb & Lake, 1990). We found fewer species of zooplankton on Lake Wyara than on Lake Numalla (Table 3) but abundances of invertebrates and waterbirds were far greater (Tables 2, 3 and 4). Salt lakes in other parts of the world also often have particularly high numbers of waterbirds (Vareschi, 1978; Martin & Randall, 1987; Denny, 1991; Scott, 1991*a*, *b*) with some African salt waters considered among the world's most productive systems (Melack & Kilham, 1974).

Lakes Wyara and Numalla have considerable value for waterbird conservation and it is imperative that the catchments, creeks and Paroo river on which they depend be protected from impacts which degrade water quality and quantity.

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APPENDIX 1

Common and specific names of waterbirds counted during aerial surveys of Lakes Numalla and Wyara

Waterbirds were categorised into four foraging groups: piscivores or large wading birds which usually feed on large invertebrates >5 mm (pw); most duck species and little grebes (d); herbivores (h); and small wading birds (w)

Waterbird	Specific name
Little grebe (d)[a]	
Great crested grebe (pw)	*Podiceps cristatus*
Australian pelican (pw)	*Pelecanus conspicillatus*
Darter (pw)	*Anhinga melanogaster*
Great cormorant (pw)	*Phalacrocorax carbo*
Pied cormorant (pw)	*Phalacrocorax varius*
Little black cormorant (pw)	*Phalacrocorax sulcirostris*
Little pied cormorant (pw)	*Phalacrocorax melanoleucos*
Pacific heron (pw)	*Ardea pacifica*
Great egret (pw)	*Ardea alba*
Egret (pw)[b]	
White-faced heron (pw)	*Ardea novaehollandiae*
Glossy ibis (pw)	*Plegadis falcinellus*
Australian white ibis (pw)	*Threskiornis molucca*
Straw-necked ibis (pw)	*Threskiornis spinicollis*
Royal spoonbill (pw)	*Platalea regia*
Yellow-billed spoonbill (pw)	*Platalea flavipes*
Blue-billed duck (d)	*Oxyura australis*
Musk duck (p)	*Biziura lobata*
Freckled duck (d)	*Stictonetta naevosa*
Black swan (h)	*Cygnus atratus*
Australian shelduck (h)	*Tadorna tadornoides*
Maned duck (h)	*Chenonetta jubata*
Grey teal (d)	*Anas gracilis*
Pacific black duck (d)	*Anas superciliosa*
Australasian shoveler (d)	*Anas rhynchotis*
Pink-eared duck (d)	*Malacorhynchus membranaceus*
Hardhead (d)	*Aythya australis*
Black-tailed native-hen (h)	*Gallinula ventralis*
Eurasian coot (h)	*Fulica atra*
Brolga (h)	*Grus rubicundus*
Masked lapwing (w)	*Vanellus miles*
Black-winged stilt (w)	*Himantopus himantopus*
Banded stilt (w)	*Cladorhynchus leucocephalus*
Red-necked avocet (w)	*Recurvirostris novaehollandiae*
Small wader (w)[c]	
Large wader (w)[d]	
Silver gull (w)	*Larus novaehollandiae*
Whiskered tern (pw)	*Chlidonias hybrida*
Gull-billed tern (pw)	*Gelochelidon nilotica*
Caspian tern (pw)	*Hydroprogne caspia*

[a] Australasian grebe *Tachybaptus novaehollandiae*; hoary-headed grebe *Poliocephalus poliocephalus*.
[b] Intermediate egret *Ardea intermedia*; little egret *A. garzetta*.
[c] Red-kneed dotterel *Erythrogonys cinctus*; plovers *Charadrius* sp. and *Calidris* sp.
[d] *Tringa* sp. and black-tailed godwit *Limosa limosa*.