The wetting and drying regime of a terminal flood plain–wetland system: implications for waterbird habitat

SCOTT C. RAYBURG & MARTIN THOMS
Riverine Landscapes Research Laboratory, University of Canberra, Australian Capital Territory 2601, Australia
martin.thoms@canberra.edu.au

Abstract Suitable habitat is essential for successful colonial waterbird breeding in ephemeral wetlands located throughout inland Australia. Two important habitat requirements for waterbirds are an inundated area of sufficient depth and of suitable duration for breeding, and a sufficient inundated area of shallow water from which they can feed. We investigated the influence of a variable wetting and drying regime on these habitat requirements, and related them to known waterbird breeding events in the Narran Lakes, Australia. The complexity of the Narran lakes ecosystem, with its different wetland components, makes it an ideal site for the provision of these habitat conditions. As a collective, they provide the essential breeding and feeding habitats for sufficient durations to enable breeding to occur. This spatial complementarity of habitat is fundamental to the importance of the Narran flood plain–wetland complex as a waterbird refuge. Habitat complexity within this system is capitalised on by waterbirds and must be recognised in water management plans.

Key words Narran lakes ecosystem; aquatic habitat; waterbird breeding; habitat complexity; spatial complementarity; dryland wetlands

INTRODUCTION

Wetlands in semi-arid or arid environments are hotspots of biological diversity and productivity. Approximately 70% of Australia is classified (climatically) as dryland, so dryland wetlands are of particular importance. Indeed, the largest recorded waterbird breeding events in Australia occur within dryland wetlands (Kingsford *et al.*, 1999). These wetlands fill as a result of highly unpredictable, spatially and temporally variable rainfall and streamflow conditions. Therefore, these areas typically face extended wet/dry periods (Stafford Smith & Morton, 1990). An important consideration in the suitability of dryland wetlands for waterbird breeding is the availability of suitable feeding and breeding habitat for sufficient duration to allow breeding to occur and chicks to be fully fledged. Habitat suitability is a function of both the quantity of the habitat, and its quality and diversity (e.g. shallow water and deep water areas, vegetated and open water areas) (Taft *et al.*, 2002). Placing habitat in a patch context, it is evident that the diversity of wetlands is maximised where there is an optimal mix of patch (or core) and edge habitats (Naiman *et al.*, 1988). In this state, exchanges of organic material, energy and organisms between patches is enhanced and biodiversity is not reduced through excessive fragmentation or by the homogenisation of habitat that accompanies high connectivity (Ward *et al.*, 1999).

A number of aspects of wetland habitat have been shown to be critical to waterbird richness and abundance. Among these are wetland size (Brown & Dinsmore, 1986; Suter, 1994) and trophic status and/or shallowness (Hoyer & Canfield, 1994; Colwell & Taft, 2000). In arid or semi-arid environments, dryland wetlands are driven by a boom–bust cycle where inundation can trigger large population increases in waterbirds, but during dry periods, wetlands may be devoid of bird life (Kingsford & Norman, 2002). However, the suitability of these wetlands for waterbird breeding is governed by the same principals as those in humid areas. Waterbirds have two habitat requirements: an inundated area of sufficient depth (typically greater than 50 cm) and suitable duration (typically at least 3 months) to offer protection from ground based predators, and shallow water areas with high productivity that facilitate feeding. Diverse feeding and breeding habitats (during the infrequent inundation events) is the key to supporting a diverse and vibrant waterbird population. For example, Taft *et al.* (2002) have shown that there is a wide range of potential feeding habitat depths for different waterbird classes (e.g. >25 cm for diving waterbirds, 5–25 cm for dabbling ducks and <15 cm for waders). Thus, wetlands that provide a wide range of water depths are likely to host the most diverse bird communities.

Despite considerable knowledge about waterbird habitat requirements and the character of wetlands, it is still largely unclear why particular dryland wetlands are favoured over others as feeding and breeding sites. It is also unclear how inundation patterns drive habitat variability in semi-arid wetlands and how water resource development could impact on the long-term viability of dryland wetlands as breeding sites. This study investigates the links between successful waterbird breeding events and the provision of breeding and feeding habitat in a semi-arid wetland, the Narran lakes ecosystem, in eastern Australia. The Narran lakes ecosystem is a complex flood plain–wetland system, characterised by two principal lakes (each with a distinct morphology and vegetation) and extensive flood plains. This study shows how this complex morphology interacts with spatially and temporally variable inundation patterns to yield a highly diverse set of habitats, which are favourable to waterbird breeding.

MATERIALS AND METHODS

Site description

The Narran lakes ecosystem is a terminal flood plain–lake–wetland complex at the end of the Narran River in north-central New South Wales, Australia (Fig. 1). The system comprises two principal lake complexes: the Northern Lake complex in the northeastern part of the system and the Narran Lake complex at the southern end of the system. The Northern Lake is considerably smaller in surface area (~3000 ha) and volume (~17 500 ML). It is also more morphologically complex than Narran Lake, with several deep areas and a large network of interconnecting channels and flood plains. Narran Lake consists of a single large lake (~12 000 ha and 122 500 ML) with several overflow areas.

The climate of the Narran lakes ecosystem is hot and dry; summer maximum temperatures reach nearly 50°C and winter maximum temperatures are around 20°C. Average annual precipitation is 480 mm year^{-1}, in contrast to the average annual evaporation of 2000 mm year^{-1}.

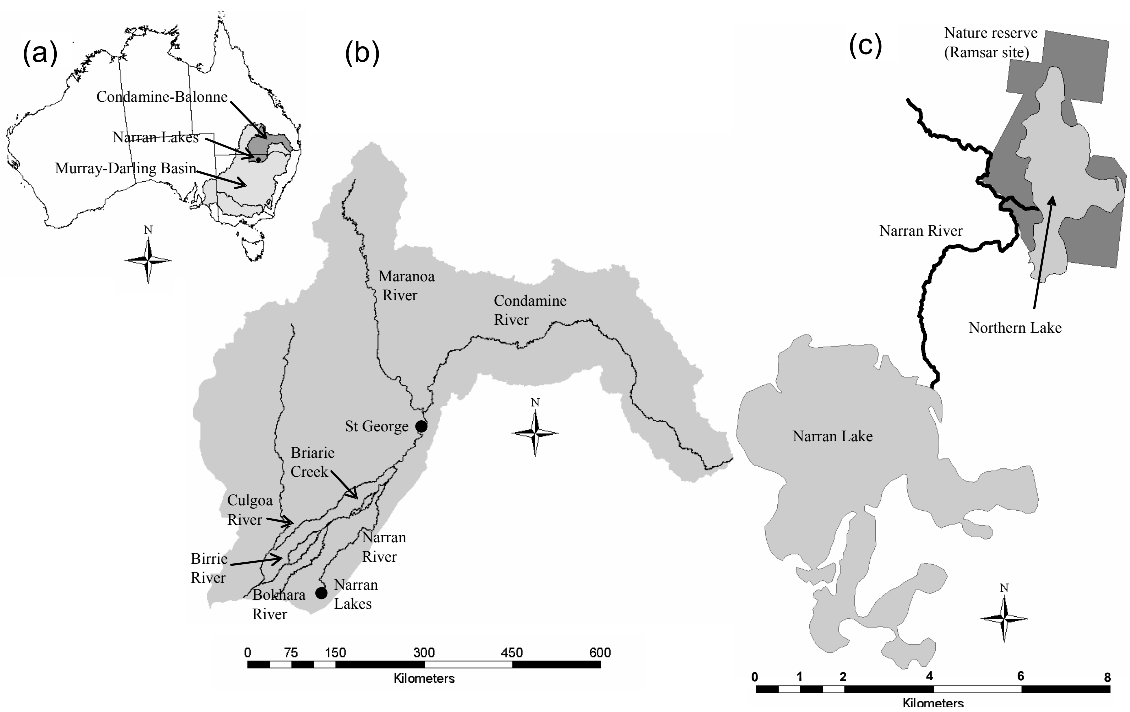

Fig. 1 Site map for the Narran lakes ecosystem: (a) within Australia; (b) within the Condamine-Balonne catchment; (c) illustrating the location of the two principal lakes, the nature reserve and the Narran River.

Rainfall is highly variable from year to year and secular wet and dry periods are a feature of the region (Thoms & Parsons, 2003). The local catchment area of the Narran flood plain–wetland system is relatively small (~46 km^2). Consequently, this terminal system does not fill as a result of local precipitation, but from flows in the Narran River that are generated in the upper catchment of the Condamine–Balonne river system. Periods of no flow in the Narran River occur approximately 60% of the time and mean annual flow is about 141 000 ML (sd > 150 000 ML), with the maximum annual flow recorded as 567 100 ML in 1983. The high interannual variability of flows in the Narran River ensures that the Narran lakes ecosystem experiences complex flood inundation patterns with periodic wet/dry cycles (Thoms, 2003).

A large portion (5500 ha) of the northern section of the Narran lakes ecosystem was designated as a Ramsar site in June 1999, and has also been managed as a nature reserve by the New South Wales National Parks and Wildlife Service since 1988. The Ramsar site, in particular, is characterised by large areas of the flood-tolerant shrub *Muehlenbeckia florulenta* (tangled lignum), which provides an important breeding habitat for many species of colonially breeding waterbirds. Land use in the surrounding region is predominantly sheep and cattle grazing, and mineral exploration. Further upstream, land use is dominated increasingly by intensive crop irrigation associated with expanding water resource developments in recent years.

METHODS

The bathymetry for the Narran and Northern Lakes was derived from a light detection and ranging (LiDAR) survey flown in October 2004 (Fig. 2). This survey included over 6.5×10^8 data points (or one point per m^2), with an internal accuracy of ±1 cm (Rayburg *et al.*, 2009).

These data illustrate the different geomorphic character of the two lakes — the shallow but morphologically complex Northern Lake (Fig. 2(a)) and the deeper but morphologically simple Narran Lake (Fig. 2(b)). The bathymetric data were used to generate a series of habitat-specific (breeding and feeding) water-depth maps at increasing water surface elevations, ranging from the lowest to highest lake water surface elevation levels. Breeding habitat was defined as areas with depths greater than 50 cm (sufficiently deep to inhibit ground-based predators from reaching nesting sites) and feeding habitat was defined as areas with depths less than 25 cm (sufficiently shallow to allow light penetration to the lake bed). These maps were then used to create a series of hypsometric curves, illustrating the changes in breeding and feeding habitat with increasing water depth.

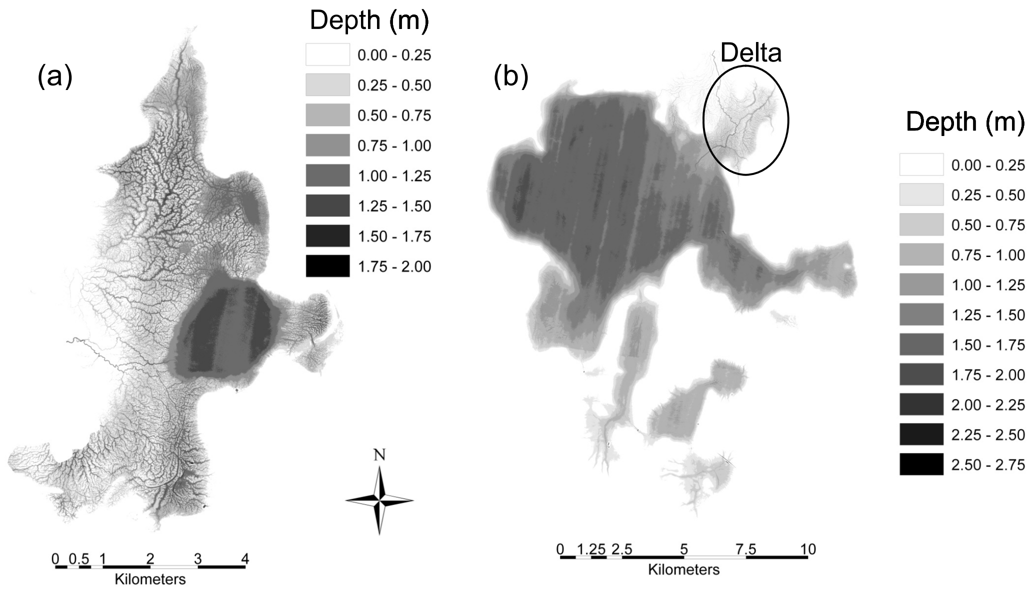

Fig. 2 The bathymetry of Northern Lake (a) and Narran Lake (b).

There were 16 recorded waterbird breeding events in the Narran lakes Ecosystem between 1971 and 2004. To investigate the habitat dynamics of these events, it was necessary to recreate the inundation levels that existed in the lakes at the time of the breeding events. Rayburg & Thoms (2009) built a hydrological model capable of accurately recreating the flow conditions within the Narran lakes ecosystem over the period for which waterbird breeding data are available. The model and the hyposmetric curves of habitat availability were used to generate breeding and feeding habitat abundance and duration curves for each waterbird breeding event between 1971 and 2004. For each breeding event, data were extracted to indicate the average (i.e. the mean habitat available over the duration of the event) and maximum abundance of breeding and feeding habitat in each lake.

The number of days above 20, 150, and 300 ha (for both lakes combined) of breeding habitat was also noted. These levels were chosen to represent the lowest level of habitat needed to initiate breeding (20 ha), an intermediate value (150 ha) and an upper value (300 ha) near the maximum breeding habitat abundance (366 ha).

Ratios of the relative abundance of feeding, breeding and total habitat in the Narran and Northern Lakes were also computed. Time series plots were generated for breeding and feeding habitat availability in the Northern and Narran lakes, with respect to breeding event occurrence. Comparative plots of the breeding and feeding habitat availability, relative to breeding event duration, were produced. Breeding events were segregated into large events (>20 000 nests) and small events (<20 000 nests), and summary statistics for habitat availability were produced for each category. Finally, time series plots of each breeding event were calculated with respect to event size, to determine if there are clear associations between the quantity and duration of habitat availability, and the number of waterbirds breeding during an event.

RESULTS

Table 1 summarises the breeding and feeding habitats in the Narran and Northern lakes for each of the 16 waterbird breeding events recorded in the Narran lakes ecosystem between 1971 and 2004. These data show that Narran Lake has only a marginal role in providing breeding habitat (maximum 34 ha compared to over 300 ha in Northern Lake, and typically about 5–10% of that available within Northern Lake). However, Narran Lake provides a disproportionately large feeding habitat (maximum 3449 ha compared to only 819 ha in Northern Lake, and typically 2–3 times that available in the Northern Lake).

The importance of Northern Lake as a breeding habitat is further confirmed by the time series plots of habitat availability against the occurrence of waterbird breeding events (Fig. 3(a),(b)). In every case, breeding events are correlated to high abundance and long duration of breeding habitat in Northern Lake. Many of these events occur when there is no breeding habitat available in Narran Lake. In both lakes, every breeding event correlates with abundant feeding habitat availability, which is maintained for the duration of the event (Fig. 3(c),(d)).

With respect to breeding event duration, a consideration of breeding habitat availability (Fig. 4(a)) shows that for all but one event (in 1978), Northern Lake breeding habitat attained a maximum level for at least part of the event. Furthermore, habitat area tends to increase rapidly to trigger an event and decrease somewhat more slowly. An event ends when habitat area falls below approximately 20 ha. In comparison, Narran Lake breeding habitat is only a minor component of overall breeding habitat availability, and tends to both rise and fall more slowly than in Northern Lake.

When feeding habitat is considered (Fig. 4(b)), both lakes seem to attain an equilibrium feeding habitat quantity (roughly 1200 ha in Narran Lake and 650 ha in Northern Lake). However, the feeding habitat in Narran Lake, in addition to being larger in quantity, also tends to be available (at the equilibrium level) before the onset of breeding and maintained after the breeding event is completed. Feeding habitat in Northern Lake tends to peak early in the event and decline as the event progresses. There are also several large peaks in feeding habitat availability in Narran

Lake that occur early in the onset of breeding. These are not matched by similar increases in Northern Lake.

If the breeding events are grouped into large (>20 000 nests) and small (<20 000 nests) events, clear differences in the abundance and duration of feeding and breeding habitat availability are revealed (Table 2). For feeding habitat, neither Narran Lake nor Northern Lake showed meaningful differences in habitat availability for large and small events.

Breeding habitat, on the other hand, is considerably different for both lakes: the average breeding habitat available for large events is 30% greater than that for small events in Northern Lake, and 300% greater in Narran Lake (although this is only a minor difference, given the small amount of overall breeding habitat available in Narran Lake). Similarly, the duration of breeding habitat availability is approximately 1.2, 2.0 and 2.5 times greater for the >20 ha, >150 ha and >300 ha breeding habitat durations, respectively, for large compared to small breeding events. Time series plots of habitat availability for large *vs* small events (Fig. 4(c),(d)) support these

Table 1 Summary of 16 breeding events recorded in the Narran lakes ecosystem between 1971 and 2003.

		Narran Lake				Northern Lake			
Year	Nests (no.)	Max breeding habitat (ha)	Average breeding habitat (ha)	Max feeding habitat (ha)	Average feeding habitat (ha)	Max breeding habitat (ha)	Average breeding habitat (ha)	Max feeding habitat (ha)	Average feeding habitat (ha)
1971	20 000	34	20	3448	1343	332	219	819	669
1972	NC	7	6	1462	1174	332	170	819	675
1974	NC	31	19	3448	1323	332	222	819	680
1976	150 000	34	23	1582	1254	332	222	819	667
1977	40	9	7	1409	1248	332	149	819	601
1978	520	0	0	2179	1309	168	79	794	544
1981	350	0	0	3442	2115	219	122	819	661
1983	400 000	34	15	3428	1400	332	202	819	648
1984	NC	34	26	1362	1239	332	259	819	717
1988	49 500	20	10	3449	1561	332	229	819	693
1989	18 000	17	10	1412	1288	332	193	819	641
1990	100 000	34	16	1469	1266	332	146	819	594
1996	204 000	13	6	3448	1381	332	212	819	701
1997	2 500	6	6	1519	1256	332	170	819	656
1998	100 000	6	5	3005	1517	332	144	819	624
1999	81	6	6	1519	1232	332	176	819	661
		Narran Lake ecosystem				Narran : Northern ratio			
	Nests (no.)	Days breeding habitat >20 ha	Days breeding habitat >150 ha	Days breeding habitat >20 ha		Breeding habitat	Feeding habitat	Total habitat	
1971	20 000	225	159	225		0.09	2.01	1.53	
1972	NC	189	108	189		0.04	1.74	1.40	
1974	NC	221	162	221		0.09	1.95	1.49	
1976	150 000	218	155	218		0.10	1.88	1.44	
1977	40	292	122	292		0.05	2.08	1.67	
1978	520	81	8	81		0.00	2.41	2.10	
1981	350	176	50	176		0.00	3.20	2.70	
1983	400 000	152	97	152		0.08	2.16	1.66	
1984	NC	365	320	365		0.10	1.73	1.30	
1988	49 500	231	176	231		0.04	2.25	1.70	
1989	18 000	142	81	142		0.05	2.01	1.56	
1990	100 000	300	116	300		0.11	2.13	1.73	
1996	204 000	273	204	273		0.03	1.97	1.52	
1997	2 500	169	94	169		0.04	1.91	1.53	
1998	100 000	108	47	108		0.04	2.43	1.98	
1999	81	194	108	194		0.03	1.86	1.48	

ha: hectares; max: maximum; NC: no counts taken.

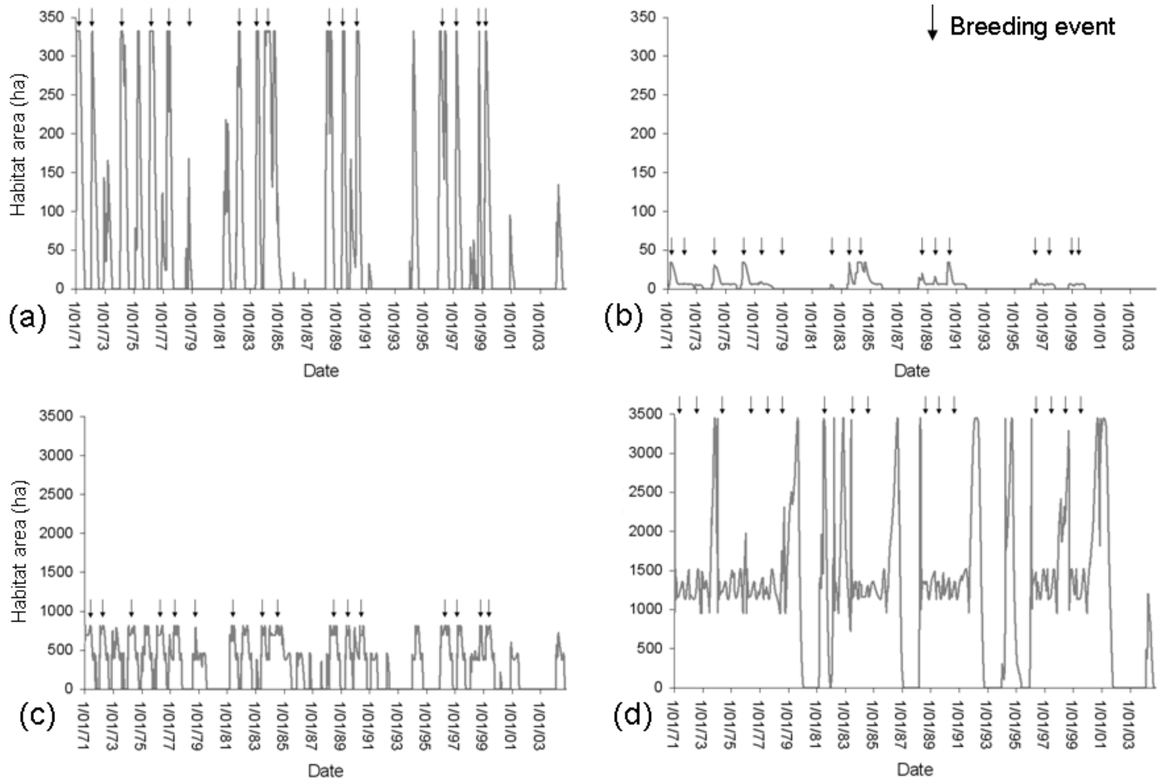

Fig. 3 Habitat areas and the timing of recorded breeding events for: (a) breeding habitat in Northern Lake; (b) breeding habitat in Narran Lake; (c) feeding habitat in Northern Lake; (d) feeding habitat in Narran Lake.

Table 2 Habitat characteristics of large (>20 000 nests) and small (<20 000 nests) waterbird breeding events in the Narran lakes ecosystem (1971–2003).

	Large	Small
Narran Lake breeding habitat (ha)	13	5
Narran Lake feeding habitat (ha)	1389	1408
Northern Lake breeding habitat (ha)	196	148
Northern Lake feeding habitat (ha)	656	627
Days breeding habitat (>20 ha)	215	176
Days breeding habitat (>150 ha)	136	77
Days breeding habitat (>300 ha)	76	30

findings and illustrate that breeding habitat peaks tend to be higher and more sustained in larger breeding events, but there is no clear difference in feeding habitat availability for large and small events.

DISCUSSION

Between 1971 and 2004, there were 16 recorded waterbird breeding events (an average of one every 2 years) and at least seven of these were large events (with more than 20 000 nests present). For a waterbird breeding event to be successful, two principal types of habitat must be present in sufficient quantity and duration, to enable waterbirds to fledge their young: breeding habitat and feeding habitat. In the Narran lakes ecosystem, one of the most important types of breeding habitat is lignum, a dense tangled shrub that provides a suitable location for nesting. Lignum is particularly favoured by various species of ibis (e.g. glossy, straw-necked, white). In the Narran

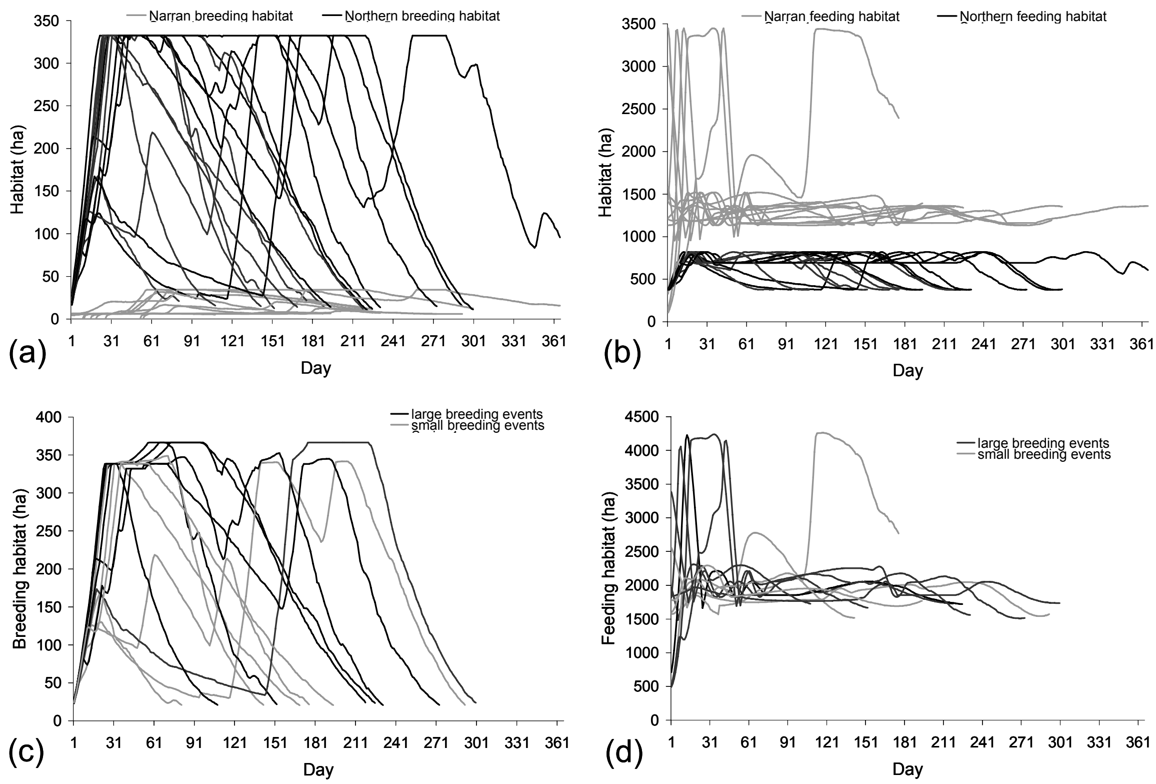

Fig. 4 Availability of habitat during breeding events. (a) Breeding habitat; (b) feeding habitat; (c) comparison of breeding habitat for large and small breeding events; (d) comparison of feeding habitat for large and small breeding events. Note: those events of indeterminate size are not included in these plots.

lakes ecosystem, lignum is prevalent in many locations, including on flood plains and in shallow lake areas. However, only within Northern Lake (and a small delta region that feeds Narran Lake), is lignum of sufficient size and density to provide adequate breeding habitat.

For these waterbirds, water must remain at least 50 cm deep under the lignum (at least in medium to large-sized floods) for at least 3 months (the minimum time required for ibis young to be fully fledged). Shallower waters or shorter durations of inundation either inhibit the commencement of breeding or encourage the birds to abandon their nests. Consequently, Northern Lake is the dominant location for waterbird breeding in the Narran lakes ecosystem, as it provides the most abundant high-quality nesting habitat (Table 1 and Fig. 3). Narran Lake (especially the delta) provides supplementary breeding habitat during large floods. It is highly unlikely that any major waterbird breeding would occur in the Narran lakes ecosystem if the Northern Lake habitat was unavailable – there simply would not be sufficient nesting sites. This conclusion is supported by Fig. 3. For the time period studied, every successful breeding event in the Narran lakes ecosystem occurred when a large quantity of breeding habitat was available in Northern Lake – during several of these events, minimal or no breeding habitat was available in Narran Lake.

Narran Lake provides a sustained high level of feeding habitat, compared with Northern Lake, with its much smaller feeding habitat that lasts for a comparatively short time. Feeding habitat in Narran Lake tends to become available early in a flood event (before breeding habitats are fully inundated), which means that waterbirds can gain condition onsite prior to breeding. Narran Lake also maintains a high abundance of feeding habitat after the breeding habitat becomes suboptimal or disappears altogether (Fig. 3), and thus provides an opportunity for young and adult birds to remain in the area and build condition following a successful breeding season.

The availability of feeding habitat in Narran Lake can extend long enough to lead into the next flood – there have been several periods in which waterbirds have bred in the Narran lakes ecosystem for several years in a row (Table 1 and Fig. 3). Feeding habitat in Northern Lake, however, is considerably less abundant than in Narran Lake and tends to be present for much shorter durations (Table 1 and Fig. 3) – for the duration of the breeding event and for a short time before and after the event. This feeding habitat is advantageous to the waterbirds as it is close to the nests, so the birds do not have to travel far to feed. However, without the feeding habitat provided by Narran Lake, the Narran lakes ecosystem would probably be a less-rich waterbird breeding site – as it is, birds can gain condition onsite, before and/or after a breeding event and, with the sustained availability of feeding habitat between breeding events, birds are less likely to abandon a site post-breeding and successive breeding events are more likely to occur.

Each breeding event in the Narran lakes ecosystem differs in terms of the duration of feeding and breeding habitat (Fig. 4(a),(b)), although breeding events tend to be similar in terms of habitat abundance. In all but one breeding event recorded, breeding habitat availability reached a maximum in Northern Lake; this only occurred on 5/16 occasions at Narran Lake. However, there are marked differences in the duration of breeding habitat availability – during the shortest events, breeding habitat was available for fewer than 81 days; during the longest events, breeding habitat was available for more than 1 year. Thus, a key trigger of waterbird breeding in the Narran lakes ecosystem may be sufficient flooding to inundate all of Northern Lake to provide at least some breeding habitat for a minimum of 3 months.

Nearly every breeding event of those recorded followed a similar pattern in terms of feeding habitat, with an equilibrium feeding habitat of approximately 2000 ha maintained for nearly the entire duration of the event (of which 1500 ha was available in Narran Lake and 500 ha in Northern Lake). In addition, for each breeding event, feeding habitat declined in Northern Lake over the course of the event, but was maintained in Narran Lake. Four events also showed large initial spikes in feeding habitat availability in Narran Lake, although these were not ubiquitous and did not seem to be a prerequisite for breeding. Every breeding event involved a long sustained period of abundant feeding habitat in Narran Lake; therefore, this condition may be a key waterbird breeding trigger and prerequisite for breeding success in the Narran lakes ecosystem.

Of the 16 breeding events recorded in the Narran lakes ecosystem from 1971 to 2004, seven were classed as large (>20 000 nests), three were of unknown size (no specific nest counts were made for these events) and six were small (<20 000 nests) (Table 1). To examine whether the abundance and duration of habitat availability (or both) is a key determinant of breeding event size, the habitat availability in both lakes was considered in light of these event size classes. There were clear differences between the abundance and duration of habitat for large and small breeding events. These differences were largely associated with the availability of breeding habitat; Northern and Narran lakes had considerably more breeding habitat for large events than for small events (Table 2). Similarly, the duration of breeding habitat availability for the whole ecosystem was longer for large breeding events than for small breeding events. This difference was magnified when durations above large size thresholds (>150 days and >300 ha) were considered. Thus, a defining characteristic of a large breeding event is abundant breeding habitat that persists for a long duration (2–7 months). Small breeding events may be characterised by moderately abundant breeding habitat that persists for shorter durations (1–6 months) (Table 2).

It is important to note that there must be other factors involved in the size of the breeding event – a few small breeding events had breeding habitat characteristics similar to those of large events and *vice versa* (Fig. 4(c)). Thus, it is also important to consider factors such as time since last breeding event, concurrent breeding in other wetlands and magnitude of other recent breeding events, in determining whether or not a particular breeding event will be large or small.

The results of this study show that there is a tendency for large breeding events to be closely associated with abundance and duration of breeding habitat availability, but abundance and duration of feeding habitat is similar for large and small breeding events. If large and small events are plotted on the same graph (Fig. 4(d)), there is no obvious separation between the two types of events in terms of either magnitude or pattern of habitat availability. Thus, although feeding habitat may be an important factor controlling the initiation of breeding, it is not a contributing factor to the overall size of the breeding event.

The outcomes of this study can be used to inform water resource management decisions in the Narran lakes ecosystem. For example, waterbird breeding is only successful when both principal lakes are inundated, despite the fact that breeding mostly occurs in Northern Lake where breeding habitat is plentiful. This is largely a result of the important contribution Narran Lake makes in the provision of an abundant and persistent feeding habitat. Narran Lake provides feeding habitat during, before and after breeding events, enabling adult and young birds to build condition onsite before and after breeding.

Water management decisions must recognise that protection and water delivery to the Ramsar-listed portion of the Narran lakes ecosystem alone is unlikely to yield desired ecological outcomes. The site must be managed as a whole ecosystem, with both lakes maintained and protected. Magnitude and duration of flooding is a critical control on the size of waterbird breeding events. Although small flooding events are important, it is the largest flooding events that need to be maintained if large-scale waterbird breeding is to continue in the Narran lakes ecosystem. Many large flooding events are harvested extensively for irrigation upstream. The reduction of these inflows as a consequence of water harvesting will have a direct and negative impact on the size (and likelihood of success) of waterbird breeding in the Narran lakes ecosystem.

The Narran lakes ecosystem is a complex system of flood plains, wetlands and lakes that serves as a critical habitat for colonially breeding waterbirds in Australia. The success of the Narran lakes ecosystem as a waterbird breeding site is founded on a diverse array of feeding and breeding habitats – these are the result of a complex physical structure and a highly variable wetting and drying regime. Healthy functioning wetlands, like the Narran lakes Ecosystem, dispersed through out the dry interior of Australia are critical for successful waterbird migration across the continent and their role as key refugia depends on providing a variety of habitat features.

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