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Decline in colonial waterbird breeding highlights loss of Ramsar wetland function

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ABSTRACT

Water resource development on rivers significantly affects life cycles of species reliant on wetlands. However, assessing ecological impacts is often difficult because they are realised over long-time periods and large spatial scales, particularly on highly variable dryland rivers. Thirty percent of all Ramsar wetlands are in drylands. We examined the effects of diversions of water upstream on colonial waterbird breeding at the Narran Lakes, supplied by a highly variable dryland river. Narran Lakes is an important Ramsar-listed wetland in Australia for its provision of habitat for wetland fauna during key life history stages, including colonially breeding waterbirds. We use historical ibis breeding data over five decades (1970–2016) to determine the flow requirements for colonial waterbird breeding and modelled the impacts of water resource management options (current and restoration) on breeding. We identified thresholds (> 154,000 ML in 90 days with a secondary threshold of > 20,000 ML in the first 10 days) of river flow volume necessary to stimulate breeding. Water resource development reduced the frequency of large flows resulting in ibis breeding by 170%, from 1 in 4.2 years to 1 in 11.4 years. Restoration efforts by government to recover water for the environment was predicted to improve colonial waterbird breeding frequency associated with large flow events to 1 in 6.71 years, representing a 59% reduction from pre-development periods. *Our framework has global application as a method for identifying long-term impacts of water resource development on key Ramsar wetland areas. This is important, as few mechanisms exist for assessing impacts and identifying restoration options on the listed criteria for many Ramsar wetlands.*

1. Introduction

Many of the world's wetlands are degrading as upstream water extraction, typically for irrigated agriculture, greatly alters historic flow regimes (Lemly et al., 2000; Coe and Foley, 2001; Kingsford et al., 2016). Riverine ecosystems and their wetlands possess important ecological assets that can be adversely affected by policy and management of water resources upstream (Snoussi et al., 2007; Bracken and Lucas, 2013; Xie and Yue, 2015). This is particularly the case for dryland river systems, where temporal patterns of wetting and drying are key determinants of wetland function. For example, river regulation and upstream water extraction in dryland rivers has been shown to alter the periodicity and extent of flooding (Maltchick and Medeiros, 2006), affecting both biota and abiotic processes dependent on historical flow and flooding regimes (Mallik and Richardson, 2009; Ruhi et al., 2016; Macnaughton et al., 2016). While many sedentary species have been shown to decline or go locally extinct in response to these changes (Angermeier, 1995), attributing changes to mobile and long-lived species, like waterbirds (Nevoux et al., 2010), has so far proven elusive. Such information is needed to inform regulation policy, proposed development evaluation, and restoration options (Arthington et al., 2006).

Waterbirds are highly dependent on wetland inundation in dryland river systems, which drives food availability and nesting resources (Wyman et al., 2014; Francesiaz et al., 2017). This makes them especially vulnerable to the effects of water resource development (Kingsford et al., 2004; Frederick et al., 2009; Reid et al., 2013; Windels et al., 2013; Kingsford et al., 2017) when inundation and flow regimes are altered (Crivelli et al., 1995; Acreman and Ferguson, 2010). Most affected are colonially breeding waterbirds as they breed in large gatherings (often in the hundreds of thousands), breed on relatively few wetlands (often < 5% of those available) (Crozier and Gawlik, 2003; Kingsford and Auld, 2005; Arthur et al., 2012; Bino et al., 2014), and can have high wetland site fidelity (Coulson, 2016). Breeding of colonial waterbirds is considered a key criterion for conservation importance under the Ramsar Convention on Wetlands of International Importance (Hails, 1996; Kleijn et al., 2014), an intergovernmental

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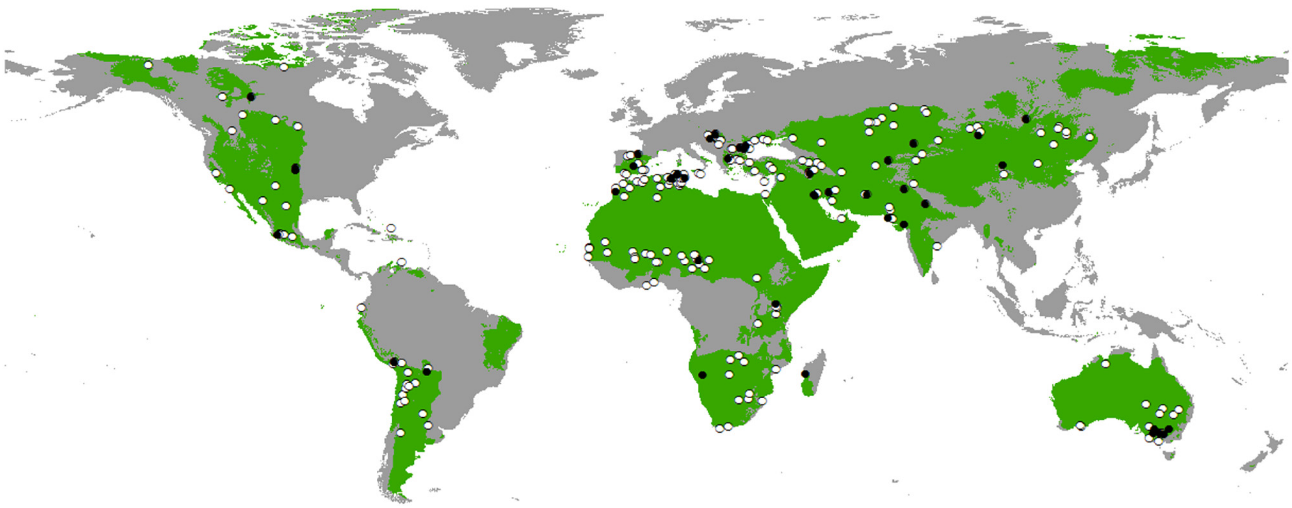

Fig. 1. Ramsar wetlands (all circles) listed for waterbird values (Criteria 5 and/or 6), in drylands (green shading) with those threatened by water extraction or dams identified by a black circle. Criterion 5 regularly support ≥20,000 waterbirds, or criterion 6 regularly supports 1% of the individuals in a population of one species or subspecies of waterbird. Data sourced from Ramsar and ESRI (2016), map created by authors. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

treaty that obligates international signatories to conserve, and use wisely, wetlands and their resources.

The Ramsar Convention lists 238 internationally significant wetlands for waterbirds within dryland river systems, fed by 68 of the world's major rivers (ESRI, 2016) (Fig. 1). Wetlands listed for waterbird values are classified by either Criterion 5 (regularly support ≥20,000 waterbirds) or 6 (regularly supports 1% of the individuals in a population of one species or subspecies of waterbird). Many of these wetlands are under threat with > 3 million ha of wetlands threatened by water resource development including extraction and/or dams (Ramsar, 2018).

Determining anthropogenic change in ecological character is the primary method of assessing compliance with the Ramsar Convention (Davis and Brock, 2008). However, meeting obligations towards colonial breeding waterbirds is challenging because of the difficulty in identifying impacts and, therefore, restoration options. Colonial waterbird breeding is highly episodic (Kingsford and Johnson, 1998; Puckridge et al., 1998), largely due to highly variable inundation frequencies and the high flow thresholds necessary to trigger breeding (Arthur et al., 2012). In addition, waterbirds are long-lived, making it more difficult to identify patterns of decline (Wheeler et al., 2003).

Understanding the nature and extent of impacts to ecological values is important for long-term conservation and protection of Ramsar wetlands and river systems. To clarify the relationship between colonial waterbird breeding and river regulation and extraction we examined the Condamine-Balonne catchment as a case study of the Murray-Darling Basin, eastern Australia. We had four key objectives: i) to identify the flow thresholds that trigger breeding of colonial waterbirds; ii) to assess the impacts of water resource development on flow regimes; iii) to assess the impact of restoration management policy to return water; and iv) to determine the long-term management implications of changes in colonial waterbird breeding on the Ramsar obligations.

2. Methods

2.1. Study site

The Condamine-Balonne catchment (143,900 km^2), is one of the largest catchments of the Murray-Darling Basin (Fig. 2). The Condamine-Balonne supplies a large deltaic floodplain of > 1.4 million ha, including the Narran Lakes ecosystem. Narran Lakes is one of Australia's more important breeding sites for colonial waterbirds and is listed under the Ramsar Convention. The Narran Lakes ecosystem (27,809 ha) consists of three lakes (Back Lake, Clear Lake, and Narran Lake), a large area of floodplain and the main channel of the Narran River. Narran Lakes supported the largest ibis breeding colony ever recorded in Australia in 1983 (400,000 pairs, Marchant and Higgins, 1990) and continues to support large concentrations of breeding ibis (> 10,000–250,000 breeding pairs) following large flood events (Beruldsen, 1985; Brooker, 1993; Ley, 1998a, 1998b; Brandis et al., 2011).

Upstream water resource development in the catchment began in the 1950s when flows from the Condamine-Balonne River were altered by small scale irrigation. In 1972, Beardmore Dam (81,700 ML) was built by the Queensland Government to supply 134km^2 of irrigated crops (ANCOLD, 2009). Further expansion of irrigation occurred downstream of St George on the Lower Balonne floodplain with the development of large private dams (> 1,500,000 ML, CSIRO, 2008) during the 1980s and 1990s (Thoms and Parsons, 2003; CSIRO, 2008). Access to upstream water resources is highly contested (CSIRO, 2008). The Australian Government recently invested > AUD $13 billion in the restoration of environmental flows to the Murray Darling Basin, including targeting the 'buy-back' of 100GL of environmental water from Condamine-Balonne catchment (Leblanc et al., 2012; Swirepik et al., 2016; MDBA, 2016). In late 2016, the Australian Government recommended a 42GL yr^{-1} reduction in the river system supplying Narran Lakes, the Condamine-Balonne (MDBA, 2016).

2.2. Colonial waterbird breeding

Narran Lakes supports breeding of 46 waterbird species. Here we focus primarily on one species of ibis, straw-necked ibis (*Threskiornis spinicollis*). Ibis are mostly represented by straw-necked ibis, with smaller numbers of glossy ibis (*Plegladis falcinellus*) and Australian white ibis (*T. molucca*). They primarily nest on lignum shrubs (*Duma florulenta*) when there is sufficient flooding and inundation (Carrick, 1962; Brandis, 2010). Colonies of straw-necked ibis, hereafter referred to as ibis, were identified from records dating from 1970 to 2016 (Beruldsen, 1985; Ley, 1998a, 1998b; Ley, 2003; Brooker, 1993, Henderson, 1999a, 1999b, 1999c; Magrath, 1991; Smith, 1993; Brandis, 2010; Appendix 1). Complete abandonment of colonies occurred in April 1997 and February 2010, with two smaller colonies occurring in 1978 and 1981 (around 260 nests and 50 nests, respectively). Successful colonies were defined as breeding without

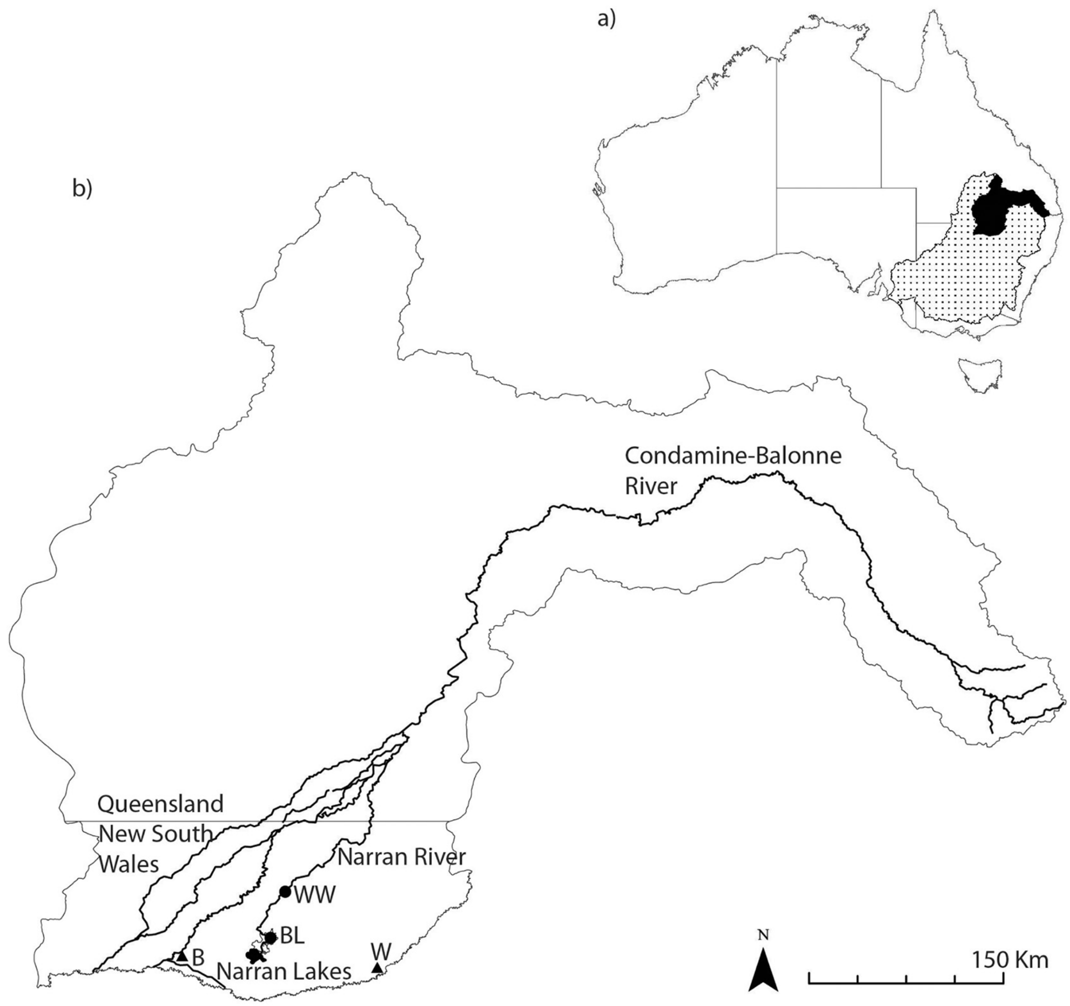

Fig. 2. Location of a) the Condamine-Balonne River catchment (shaded black) in eastern Australia in the northern Murray-Darling Basin (stippled area), showing b) the Condamine-Balonne River crossing the border between New South Wales and Queensland and flowing down the Narran River to fill Narran Lakes, with locations of the flow gauge (Wilby Wilby, 'WW') and water level gauge (Back Lake 'BL') and rainfall stations (Brewarrina 'B' and Walgett 'W').

abandonment of nests before completion.

Total daily flow volumes from the Wilby Wilby gauge on the Narran River and water level data from Back Lake gauge (Fig. 2) were used to quantify flows regimes. Like many dryland river systems, the Narran River frequently experiences long periods of zero flow, so flow events were defined as starting when flow volumes exceeded 100 ML day^{-1} at Wilby Wilby gauge, the flow volume required to reach Narran Lakes downstream of Wilby Wilby (Fig. 2) and ending when water levels at Back Lake were below 120.75 mAHD (Australian Height Datum, metres). Water level was used as a surrogate for duration of flooding rather than cessation of flow, given our objective to identify flow events related to breeding.

To identify flow and environmental thresholds that stimulated breeding, we used classification and regression tree (CART) analysis with no assumptions about distributions (Breiman et al., 1984), implemented using the 'rpart' function in the 'rpart' package (Therneau et al., 2015) in R (R Core Team, 2015). The CART analysis progressively identifies explanatory variables that best split the response variable (i.e., breeding or no breeding of straw-necked ibis in a given year) using the Gini index (Therneau et al., 2015). An overall measure of variable importance was derived by calculating the sum of the goodness of split measures for each split for which the variable was the primary variable, plus goodness for all splits in which it was a surrogate (Therneau et al., 2015).

We used six hydrological measures as explanatory variables in the CART analysis: total event duration (days), total event flow volume (ML), and four temporally graded measures of cumulative volume (ML) of flows in the first 90, 60, 30, and 10 days before ibis breeding. Event flow duration is a useful surrogate for habitat availability, given ibis require 3–5 months of inundation to establish nests and rear and fledge chicks (Leslie, 2001; Marchant and Higgins, 1990). In addition to the six hydrological measures, we included total rainfall coinciding with the flow event as large local rainfall events ($> \sim 300$ mm) can also flood the Narran Lakes ecosystem, potentially stimulating ibis breeding. We also included minimum daily temperatures coinciding with the flow event as low temperatures also reduce chick survival (McCosker, 1996; Taft et al., 2002), possibly associated with reductions in food resources (Cummins and Klug, 1979; Jenkins and Boulton, 2003). Daily rainfall and temperature were obtained from Walgett and Brewarrina, the closest available climate data to Narran Lakes.

2.3. Water resource development and restoration

We predicted the impact of water resource development on flows and opportunities for restoration using a daily time-step Integrated Quantity/Quality Model (IQQM) (Department of Water Resources, 1994), which is used for policy and management of many of the rivers of the Murray-Darling Basin (Ren and Kingsford, 2011). We used thresholds identified by our CART models to compare breeding events and frequencies for colonial waterbirds under three flow scenarios, identified by the Murray-Darling Basin Authority (MDBA) (2012): i) without development, a near natural condition scenario; ii) the developed system (as of June 2009), with historic climate; and iii) a restoration scenario increasing environmental flows (reduced diversions) by 2,800 GL yr^{-1} across the Murray-Darling Basin Authority (2011). We examined differences between the three flow scenarios based on three key hydrological metrics: cumulative flows in first 90 days, interflood interval, and duration of flow event. To compare, we used generalized linear models with flow scenario as a factor and each of the three hydrological metrics as continuous response variables. We log-transformed (ln(x)) the hydrological metrics and assumed a Gaussian probability distribution of errors. We used the 'glm' function for the generalized linear models and 'glht' function (using Tukey Contrasts) in the 'multicomp' package (Hothorn et al., 2008) in R (R Core Team, 2015). In conjunction, for each flow scenario we calculated the cumulative breeding probabilities by considering each flow event and the respective flow thresholds identified by the CART analysis and associated predicted breeding probability.

3. Results

3.1. River flow and waterbird breeding

Between 1970 and 2016 there were 34 flow events with average volumes of 197,245 ML (± 215,851 SD; 12,625–1073,279 ML) and average durations of 162 days (± 106 SD; 21–604 days) (Fig. 3).

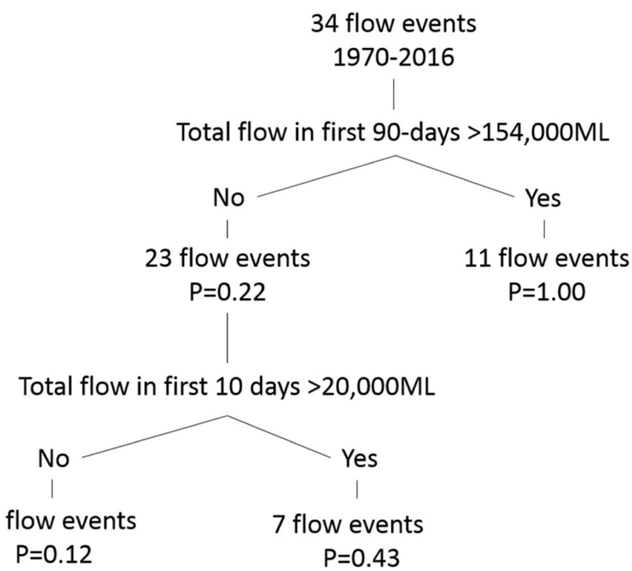

Fig. 4. Results of CART analysis identifying the variables predicting probability (P) of successful breeding based on different flow thresholds.

During this time, 22 ibis colonies were recorded of which 18 were successful (Appendix 2). Successful colonies were associated with 15 flow events, with three flow events resulting in two colonies (1983–85, 1988, 1990). No breeding occurred during periods of low or no flow. Breeding was generally concentrated (70%) between October and March (1970–2016), occurring in all months of the year apart from August and September Breeding coincided with periods of high flows, with 77.5% of flows also occurring between October and March.

The most accurate classification tree was achieved with flow volumes in the first 90 days and flow volumes in the first 10 days. The

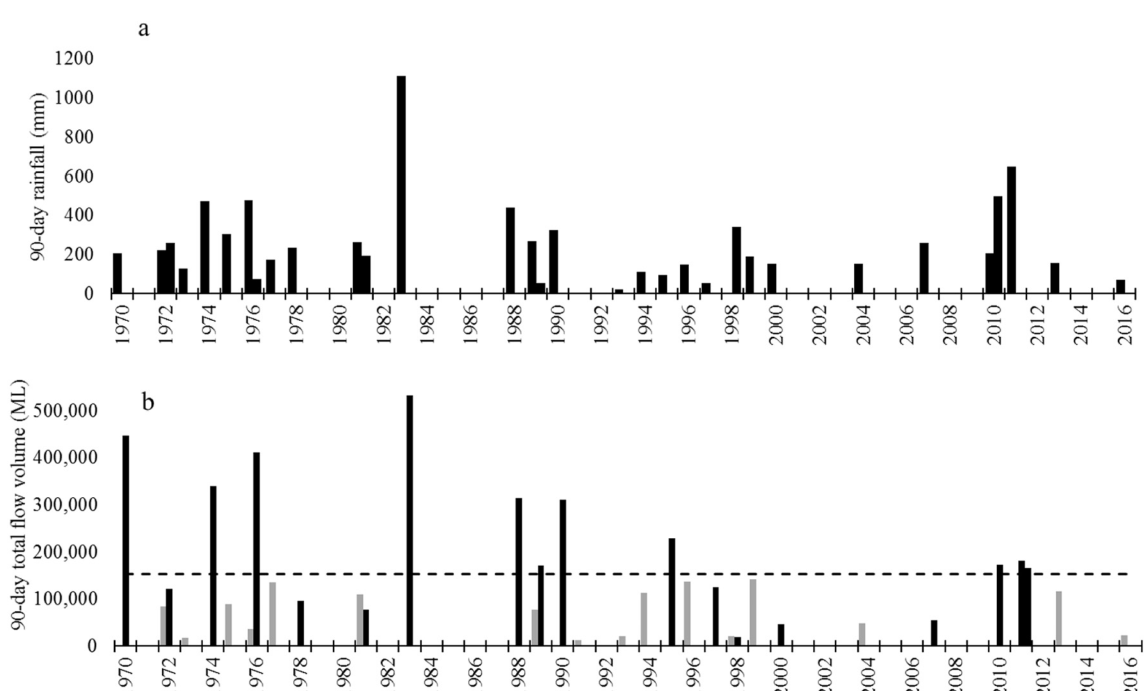

Fig. 3. (a) Total rainfall at Walgett in the first 90-days of flow events and (b) all flow events with breeding (black bars) and non-breeding (grey bars) occurrences (1970–2016) and the identified threshold of a 154,000 ML (dashed line).

Table 1
Predicted mean (± SE) 90-day flow volume, inter-flood periods and flow event duration for the three water resource management scenarios (water resource development, no water resource development and restoration) for flow events potentially triggering the breeding of colonial waterbirds in the Narran Lakes, Australia.

Modelled time period	Variable	Development N = 75 (1900–2014) N = 25 (1970–2014)	Restoration N = 98 (1900–2014) N = 34 (1970–2014)	No development N = 123 (1900–2014) N = 43 (1970–2014)	Historic N = 33 (1970–2014)
1900–2014	90-Day flow volume (ML)	83,580 ± 9651	96,400 ± 9040	105,965 ± 9516	
	Inter-flood period (days)	412.1 ± 47.9	290.3 ± 27.5	190.7 ± 17.1	
	Flow duration (days)	133.6 ± 15.4	138.4 ± 14.0	144.5 ± 13.0	
1970–2014	90-Day flow volume (ML)	107,307 ± 2,1461	109.146 ± 18,765	114,740 ± 17,498	139,142 ± 23,178
	Inter-flood period (days)	514.8 ± 103.0	345.3 ± 55.6	219.1 ± 33.4	327.4 ± 64.5
	Flow duration (days)	139.0 ± 27.8	134.9 ± 17.3	160 ± 24.4	152.9 ± 17.9

classification tree indicated that successful breeding was always triggered when total cumulative flows on the Narran River exceeded 154,000 ML in the first 90 days of the flow event (Fig. 4). If cumulative flows in the first 90 days were lower than 154,000 ML, breeding probability was low ($p = 0.22$). For such flow events, cumulative river flow volumes above 20,000 ML in the first 10 days, increased the probability of breeding to $p = 0.43$, rather than $p = 0.12$ if this threshold was not reached (< 20,000 ML in first 10 days).

Eleven colonies established above the 90-day flow volume threshold, while seven colonies established below the 90-day flow volume threshold of 154,000 ML: three were unsuccessful (1978, 1981, and 1997) while four were successful (1972, 1998, 2000, and 2007). The unsuccessful 1978 and 1981 events met the 10-day volume and flow duration thresholds while the unsuccessful 1997 event did not. One colony (2010) met the 90-day volume threshold but not the 10-day volume or flow duration threshold and was unsuccessful (Appendix 2).

3.2. Impacts of water resource development and environmental flow restoration

For all defined flow events on the Narran River, simulation of IQQM models showed that water resource development reduced total volume of flows in the first 90 days by around 20% compared to the no water resource development model ($z = 1.99$, $p = 0.06$, Table 1, Fig. 5). Environmental restoration marginally improved flows over the water resource development model ($z = 0.775$, $p = 0.47$) and the frequency of ibis breeding. Water resource development also more than doubled inter-flood intervals compared to the no development model ($z = -4.76$, $p < 0.001$), while inter-flood intervals improved under the restoration model over the water resource development model ($z = -1.95$, $p = 0.067$) (Table 1, Fig. 5). Contrastingly, flow duration did not significantly differ among scenarios. Using the three identified thresholds to predict ibis breeding events, water resource development reduced the overall frequency of ibis breeding by 110%, from 1 in 2.26 years to 1 in 4.75 years, while restoration efforts reduced the impact water resource development to a reduction of 35.4% with ibis breeding frequency of 1 in 3.06 years. Critically, the frequency of breeding events associated with large flow events decreased by 170% under water resource development and by 59% under the restoration scenario. Noticeably, the impact to the frequency of breeding events associated with medium flows under the restoration scenario was not as severe, decreasing breeding frequency by 11.7%, from 1 in 6.98 years under the no development scenario to 1 in 7.8 years (Table 2).Water resource development had the greatest impact on the number of large flow events (> 154 GL/90 days) that had a predicted breeding probability of $p = 1.0$, with a 63% reduction (27 vs 10 breeding events; Table 2). Number of breeding events associated with medium flows (> 20 GL/10 days & < 154 GL/90 days) were reduced by 47.4%, while number breeding events associated with small flows (< 20 GL/10 days) were reduced by 23.7%. Under the restoration scenario model, the number breeding events associated with large flow events were predicted to decrease by 37%, medium flows by 10.5% and small flows by 20.3% (Table 2).

4. Discussion

Analysis of historical records of breeding with modelled flow alterations showed that nearly five decades of water resource development in the wetland's supply river system have significantly reduced flow volumes (47% of median flows; CSIRO, 2008) and frequencies. By simulating flows using the Australian Governments IQQM scenarios, ibis were predicted to breed 1 in 2.26 years without development, decreasing in frequency to 1 in 4.75 years with development. This impact was likely to be conservative because the IQQM development scenario does not adequately capture the full impacts of river regulation on the Narran Lakes system as it does not include effects of small dams, levee banks, or unlicensed water extracted or diverted from the river system upstream (CSIRO, 2008) and has been reported to underestimate hydrological impacts on large floodplain ecosystems (e.g. Macquarie Marshes, Ren and Kingsford, 2011). Nevertheless, modelled water resource development was predicted to significantly reduce opportunities for ibis breeding in the Narran Lakes system by disrupting the frequency of large flow events that always resulted in breeding (> 154 GL over 90 days) by 170%.

Reduced opportunities for breeding are likely to result in significant reductions in ibis productivity in the long term. Narran has previously resulted in an average of 66,478 ibis nests during 18 past successful colonies (Appendix 2). The modelled loss of 26 breeding events due to water resource development (Table 2) would result hypothetically, in a loss of 1,756,348 ibis nests. Given a reported fledgling success of 1.35 birds per nest (Brandis et al., 2011), this would result in > 2.3 million less juvenile ibis being contributed to the Australian population. This demonstrates that water resource development negatively impacts on ibis populations through decreased productivity.

Narran Lakes is one of 16 Ramsar-listed sites in the Murray-Darling Basin, Australia's most developed river basin (Kingsford, 2000; Leblanc et al., 2012). It is also one of Australia's more important sites for breeding ibis (Brandis et al., 2011), meriting its listing under the Ramsar Convention criterion as a site for providing habitat during a critical stage in their life cycle i.e. breeding (Criterion 4). Despite evidence of regular high abundances of waterbirds (> 20,000 waterbirds; Beruldsen, 1985; Brooker, 1993; Ley, 1998a, 1998b; Brandis et al., 2011), Narran Lakes was not listed under Criterion 5. Our findings suggest this oversight should be rectified. Straw-necked ibis are known

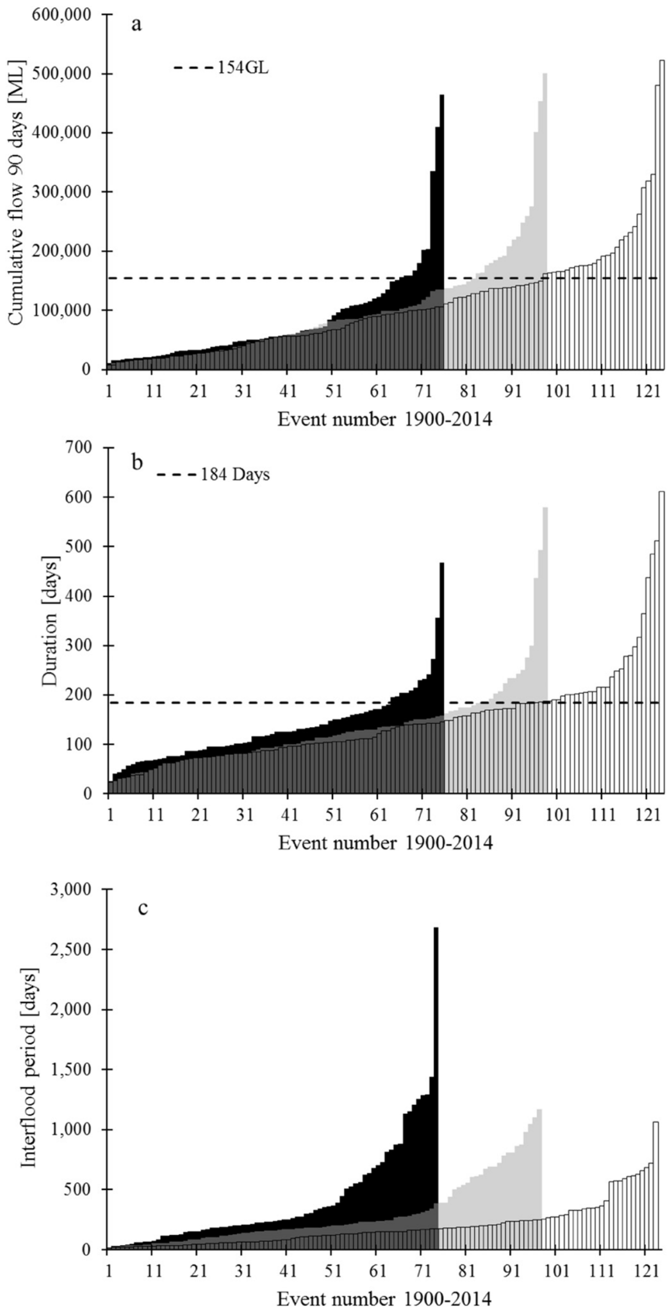

Fig. 5. Results of modelled scenarios of no development (white bars), water resource development (black bars) and restoration (grey bars) (1900–2014), showing (a) the number of events with cumulative flows over 90 days; (b) duration of flow events (ibis breeding threshold of 165 days shown as dashed line); and (c) number of events and inter-flood periods.

to breed on only a few sites throughout Australia (Carrick, 1962; Arthur et al., 2012), with most breeding on < 5% of these sites when opportunities present themselves (Brandis, 2010). Long-term impacts on breeding of colonial waterbirds at Narran Lakes, combined with similar degradation at other major breeding sites in the Murray-Darling Basin (e.g. Macquarie Marshes, Lowbidgee wetlands (Kingsford and Thomas, 1995; Kingsford et al., 2004; Kingsford and Johnson, 1998)), are increasingly affecting the long-term productivity of this waterbird species.

Like the Narran River, dryland rivers around the world are increasingly under stress from direct and indirect human influences, with long-term declines of dependent biota (Micklin, 2007; Onuoha, 2008; Poff and Zimmerman, 2010). The building of dams and development of water resources is continuing at pace, with 13,000 new large dams predicted by 2030 (Zarfl et al., 2015). This is particularly disruptive as large river systems discharge water either via important estuaries or are endorheic basins ending in large wetlands (e.g. Aral Sea, Micklin, 2007). Understanding of the nature of this disruption usually relies on hydrological indicators of change (e.g. Vörösmarty and Sahagian, 2000) as biotic information is limited over long temporal scales and lacks relevance at watershed scales. However, breeding of colonial waterbirds is an effective indicator of wetland function changes due to regulation because water resource development impacts usually occur over considerable temporal and spatial scales (Vörösmarty and Sahagian, 2000). By analysing historical records of breeding and flows, we overcame these difficulties for one of Australia's prime dryland rivers, which is among the world's more variable river systems (Peel et al., 2001; McMahon et al., 2007).

Using breeding of waterbirds as an indicator of degradation has global applicability to many Ramsar and important wetland sites recognised for their waterbird populations at risk from decreasing river flows. Waterbirds are useful indicators of wetland health (Amat and Green, 2009; Ogden et al., 2014; Kalinkat et al., 2017) and environmental change (Kushlan, 1993; Samraoui et al., 2011), given their high position in the trophic web. This allows tracking of environmental change across entire ecosystems (Kingsford et al., 2017), particularly at key stages in their life history (e.g., breeding) when they are most vulnerable to change (Ogden et al., 2014). Colonially breeding species are useful flagship or umbrella species for other species of waterbirds (Brandis and Bino, 2016) and other biota at watershed scales. Waterbirds populations are in decline at many Ramsar wetlands, including Doñana, south-west Spain (Rendon et al., 2008) the Macquarie Marshes, Australia (Kingsford and Johnson, 1998), Kerkini Reservoir, northern Greece (Crivelli et al., 1995), and Rio Cruces Wetland, Chile (Lagos et al., 2008). Given the protection that many Ramsar wetlands are afforded, such impacts may be more severe on less protected wetlands (Kleijn et al., 2014).

Furthermore, as climate shifts to a warmer world, dryland river systems are likely to be adversely impacted (IPCC, 2014). In the case of the Narran Lakes river system, current policy and management of the Murray-Darling Basin does not adequately manage for climate change risks (Grafton et al., 2013; Pittock, 2013), primarily because there has been no allowance of decreasing water resource availability (Chiew et al., 2010). By 2050, reduced flows are expected to reduce benefits to waterbirds from currently negotiated environmental flows in the Murray-Darling Basin from 18% to only 1–4% (Kingsford et al., 2017). Based on hydrological modelling (CSIRO, 2008) and our analyses for breeding of colonial waterbirds, the predicted decline in ecological character of this site is likely as bad or worse than other sites for which the Australian Government has officially admitted a likelihood of a change in ecological character (e.g. Gwydir wetlands and the Macquarie Marshes; CSIRO, 2008).

Although our approach has highlighted how decline in opportunities for breeding of colonial waterbirds is indicative of loss of wetland function from water resource development, our approach also highlights opportunities to investigate restoration options sufficient to trigger breeding using environmental flows. For example, Australian Governments are attempting to restore environmental flows for Narran

Table 2
Modelled number of flow and breeding events (1900–2014) meeting each of the three breeding thresholds predicted by the CART model under each water management scenario.

Metric	Development	Restoration	No development
No. small flow events: < 20 GL/10 days	45	47	59
No. of breeding events (Prob = 0.12)	5.4	5.64	7.08
No. of medium flow events: > 20 GL/10 days & < 154 GL/90 days	20	34	38
No. breeding events (Prob = 0.43)	8.6	14.62	16.34
No. of large flow events: > 154 GL/90 days	10	17	27
No. breeding events (Prob = 1.00)	10	17	27
Sum breeding events	24.00	37.26	50.42
No. of flow events (1900–2014)	75	98	124
Total breeding frequency (1 in X years)	4.75	3.06	2.26
Large breeding frequency (1 in X years)	11.40	6.71	4.22
Medium breeding frequency (1 in X years)	13.26	7.80	6.98
Small breeding frequency (1 in X years)	21.11	20.21	16.10

Lakes. Our modelling clearly showed an increase in opportunities for breeding under the restoration scenario, which is current government policy. However, these policy initiatives are under long-term pressure from irrigation agriculture and are unlikely to deliver the extent of benefits originally envisaged, particularly as environmental flows continue to be renegotiated and climate change alters overall flows. We strongly advocate for similar analyses in dryland river systems, where data are available, to provide a reliable and comparable tool for protecting Ramsar wetlands from resource development around the world.

Acknowledgements

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Appendix 1. Details of breeding observations at Narran Nature Reserve 1970–2016

Year of breeding	Reference	Data source	Data collection method	Number of nests
1971	Smith, 1993	Observed by Mr. C.H. Young	Ground based estimate	10,000
1972	Smith, 1993	Royal Australian Ornithological Union record	Ground based estimate	No information given
1974	Smith, 1993	Observed by Mr. B. Lane	Ground based estimate	No information given
1976	Smith, 1993	Observed by Mr. B. Lane	Ground based estimate	No information given
1978	Brooker, 1993	Surveyed by M. Brooker	Aerial Survey and ground counts	No information given
1983	Smith, 1993	Observed by National Parks and Wildlife Staff	Ground based estimate	200,000
1988	Smith, 1993	Observation by Smith, J	Aerial Survey	71,000
1989	Magrath, 1991	Observation by Magrath, P.	Canoe survey	8500
1990	Smith, 1993	Observation by Smith, J.	Aerial Survey	50,000
1996	Ley, 1998a	Observation by Ley, A.	Canoe survey	102,000
1997	Ley, 1998b	Observation by Ley, A.	Repeated canoe survey	No information given
1998	Henderson, 1999a	Observation by Henderson, A.	Canoe transects and aerial survey	50,000
2001	Ley, 2003	Observation by Ley, A.	Canoe survey	No information given
2008	Brandis et al., 2011	Observation by Brandis, K.	Repeated canoe surveys, aerial photography	74,000
2010	Spencer et al., 2015	Spencer, J.	Aerial photography and ground observations	13,303
2011	Spencer et al., 2015	Spencer, J.	Aerial photography and ground observations	21,018
2012	Spencer et al., 2015	Spencer, J.	Aerial photography and ground observations	131,442

Appendix 2. Details of straw-necked ibis breeding and associated flow events at Narran Lakes

Flow event	Flow duration (days)	Number of nests	Event volume (ML)	90-Day volume (ML)	10-Day volume (ML)
18/12/1970–22/6/1971	187	10,000	489,738	446,713	27,938
6/1/1972–10/4/1972	96	Unknown	121,804	121,804	28,389
2/1/1974–13/8/1974	224	Unknown	356,034	339,787	27,136
3/1/1976–15/8/1976	226	Unknown	457,498	411,725	21,963
19/07/1978–2/01/1979[a]	168	Unknown	103,149	96,043	20,074
19/02/1981–30/09/1981[a]	224	Unknown	134,260	77,860	20,744
14/5/1983–6/1/1985[b]	604	200,000	1073,279	532,612	29,101
26/2/1988–8/11/1988[b]	257	71,000	414,866	314,812	15,139
13/4/1989–6/10/1989	177	8500	177,331	170,892	23,690
9/4/1990–4/10/1990[b]	179	50,000	317,668	311,495	43,500
5/12/1995–22/4/1996	140	102,000	229,107	229,065	17,017
13/02/1997–7/06/1997[a]	115	Unknown	124,614	124,614	13,834
17/5/1998–10/12/1998	208	50,000	190,185	20,093	11,964
14/11/2000–12/1/2001	60	Unknown	46,565	46,565	32,078
21/12/2007–20/4/2008	122	74,000	55,159	55,159	23,026
16/2/2010–17/07/2010[a]	152	13,303	172,847	172,642	15,074
9/10/2010–6/9/2011	333	21,018	625,134	166,331	3879
21/11/2011–13/9/2012	298	131,442	323,653	181,384	1230
Averages	209	66,478	300,716	211,208	20,876

[a] Unsuccessful colonies.
[b] Low event that resulted in two colonies.

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