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More Than Just a Trend: Integrating Population Viability Models to Improve Conservation Management of Colonial Waterbirds

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Abstract
Waterbird populations in eastern Australia have been declining over the past 35 years primarily due to water resource development and resultant changes to natural river flows and flooding. To mitigate these impacts there is an increased allocation of water for the environment, including waterbird populations. We used population viability models to identify the frequency of breeding events required to reverse the trend and achieve long-term species' management objectives. We found that the population size of straw-necked ibis was primarily dictated by the frequency of large breeding events and to a lesser extent by adult annual survival and the frequency of small breeding events. We identified combinations of small and large breeding events over the next 10 years required for increased population growth. We also assessed the likelihood of current water management policies increasing populations and thereby reversing the decline in eastern Australia's waterbird populations.

Keywords Straw-necked ibis · Murray–Darling Basin · Colonial waders · e-water · PVA · Water management

Introduction

Waterbird populations are declining globally (Butchart et al., 2010), with estimates varying from 38% (Wetlands International, 2012) to 55% (BirdLife International, 2017) and 17.6% of all waterbird species currently Red Listed as "Vulnerable" or worse (IUCN, 2019). Declines reflect the global degradation of wetland ecosystems (IPBES, 2019; Millennium Ecosystem Assessment, 2005), driven primarily by habitat loss (Davidson, 2014), land-use changes (Higgins et al., 2002), water resource development (Kingsford and Thomas, 1995; Kreuzberg-Mukhina, 2006; Ma et al., 2009) and other anthropogenic induced changes (Žydelis et al., 2009), including climate change (Erwin et al., 2011).

Monitoring changes in biodiversity is critical for evaluating anthropogenic impacts as well as prioritising conservation actions (IPBES, 2019). Effective monitoring should detect changes in population size and demographics (Lindenmayer and Likens, 2010) which often requires long-term, multi-generational data (Field et al., 2007; Witmer, 2005) capturing stochastic population variability (Baillie, 1990), particularly where there is high unpredictability in environmental and resource variability (Yen et al., 2013). One key limiting factor is the limited data availability over long temporal periods to adequately identify trends and population viability (Field et al., 2007).

Australian waterbird populations are declining across eastern Australia with long-term declines of 72% in annual total abundances of waterbirds since 1983 (Kingsford et al., 2017). Habitat loss or alteration as a result of water resource development has been a key driver of declines in waterbird populations (Kingsford et al., 2004; Kingsford and Thomas, 2004). Declining river flows and associated flooding is the most significant impact of water resource development on waterbirds, particularly colonially breeding wading birds (including ibis, *Threskiornithidae*) (Brandis et al., 2018b; Kingsford and Johnson, 1998; Wetlands International, 2012). Many Australian species of colonially breeding wading birds, particularly ibis species, are opportunistic breeders, only breeding when habitat conditions are suitable. Suitable habitat conditions

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include seasonal timing of flooding (spring/summer), sufficient flow volumes and duration of inundation (3 months min), water depth at nesting sites (~50 cm min), sufficient food resources, and availability of nesting materials (*Duma florulenta* and *Phragmites australis*) (Arthur et al., 2012; Brandis et al., 2018a; Brandis et al., 2011; Brandis et al., 2020). Consequently, reductions in river flows have reduced flood extents and frequencies (Thomas et al., 2010), thereby reducing breeding opportunities for colonial wading birds (Arthur et al., 2012; Kingsford and Johnson, 1998; Leslie, 2001).

To mitigate these impacts the Australian government legislated an allocation of water for the environment (MDBA, 2012). This water is combined with water for the environment managed by state agencies for environmental outcomes such as fish spawning, vegetation maintenance or to support waterbird breeding (MDBA, 2014). The Basin Wide Environmental Watering Strategy (MDBA, 2014) aims to "Maintain current [waterbird] species diversity, improve breeding success and numbers". This goal includes achieving specific metrics by 2024. These include increasing waterbird abundances by 20–25%, increasing the occurrence of colonial waterbird breeding events by up to 50%, and a 30–40% increase in nests and broods for other waterbirds (MDBA, 2014).

Population viability analysis (PVA) offers a superior and effective tool over simple trends for quantification of extinction risk and assessment of conservation status (Burgman et al., 1993). PVAs allow assessment of impacts of threats and benefits of conservation actions, specific to different life stages (Fox et al., 2004). They also explicitly treat uncertainty under different exploratory or intervention scenarios (Chisholm and Wintle, 2007; Southwell et al., 2008), simulating temporal variation in patch (or population) occupancy and incorporating survival, fecundity, and dispersal variability among patches (Akçakaya and Raphael, 1998).

We used PVA to model population responses of straw-necked ibis (*Threskiornis spinicollis*) to water management policies aimed to increase waterbird abundance in the Murray–Darling Basin, the main site for the breeding of this species (Brandis, 2010). We used the model outcomes to assess the likely success of the policy and quantify changes in population to inform objectives of the Murray–Darling Basin Plan. We also examined breeding requirements for maintaining long-term population viability.

Methods

Study Species

Straw-necked ibis is colonially breeding wading birds, endemic to Australia (Marchant and Higgins, 1990). They are a charismatic species that are often identified as the target for delivering water to the environment to ensure breeding completion (MDBA, 2014). Straw-neck ibis responds quickly when there are suitable breeding conditions, completing nesting within ~42 days (Marchant and Higgins, 1990). They breed in colonies (5000–200,000 birds), which can often include smaller numbers of other breeding waterbird species (e.g., Australian white ibis *T. molucca*, glossy ibis *Plegadis falicnellus*, royal spoonbill *Platelea regia*). Consequently, straw-necked ibis is often used as a surrogate for other colonially breeding wading birds.

To estimate the annual trend in straw-necked ibis estimates in the Eastern Australia Waterbird Surveys (EAWS Kingsford et al., 2020), we fitted a linear model between the log-transformed total abundance and year of record as a continuous explanatory variable and calculated the annual trend as:

$$Annual\ change = \left(e^{(Coef.year)} - 1\right) * 100$$

Parameterising Population Models

We parametrised population models using longevity data, age demographics, frequency of breeding, and reproductive success data. We reviewed the scientific literature on straw-necked ibis life history and other related *Threskiornithidae* species. In captivity, straw-necked ibis can live to 39 years (Brouwer et al., 1994), with the longest period between sightings of banded wild birds, straw-necked ibis and an Australian white ibis (ABBBS, 2019) recorded as 29 and 26 years, respectively. For the related glossy ibis, longevity is 14–16 years (Clapp and Klimkiewicz, 1982). Survival of yearling straw-necked ibis in the wild is unknown. Annual survival estimates for yearling urban Australian white ibis (Smith et al., 2013), crested ibis (*Nipponia nippon*) (Yu and Huo, 2015), and Hadada ibis (*Bostrychia hagedash*) (Duckworth et al., 2012) were respectively 0.63, 0.6, and 0.27 compared with adults 0.82, 0.68, and 0.75.

We used this information to compile an age-structured Leslie matrix (Caswell, 2006), a discrete, age-structured model of population growth (Table 1). We assumed four life stages (fledgling to 1 year (yearlings), second year, third year, and ≥4 years), as straw-necked ibis are not sexually mature until their third or fourth year (Marchant and Higgins, 1990). We assumed a conservative annual survival probability of 0.5 for yearling straw-necked ibis and tested a range of survival estimates between $P = 0.80–0.90$ (interval 0.01) for adult birds, resulting in life expectancy ranging between 3.50 and 5.92 years, with maximum longevity of ~19–39 years, respectively (Table 2).

To parameterise breeding frequencies within the population model, we examined historic (1983–2018) breeding

Table 1 Leslie matrix of straw-necked ibis with four life stages where $X_{1\text{-}4}$, is the stage, S_x the fraction of individuals that survive from stage x to $x+1$, and F_x is the fecundity as the per capita average number of female offspring, born from a female parent of stage x under a large or small breeding event

	X1	X2	X3	X4
X1 (large event)	0	0	$F_3 = 0.50$–0.75	$F_{4+} = 0.65$–0.98
X1 (small event)	0	0	$F_3 = 0.20$–0.45	$F_{4+} = 0.26$–0.59
X2	$S_1 = 0.5$	0	0	0
X3	0	$S_2 = 0.8$–0.9	0	0
X4	0	0	$S_3 = 0.8$–0.9	$S_{4+} = 0.8$–0.9

Table 2 Relative importance of population model parameters and the examined ranges for straw-necked ibis across eastern Australia

Variable (examined range/ interval)	Relative importance (proportion)	95% CI
Prop (breeding)/large event (inexperienced, 0.5–0.75/ 0.05)	0.020	0.018–0.023
Prop (breeding)/small event (inexperienced, 0.2–0.45/ 0.05)	0.005	0.004–0.006
P (large event) (1 in 1–10 years/1 year)	0.570	0.561–0.580
P (small event) (1 in 1–10 years/1 year)	0.159	0.153–0.165
Adult survival (0.8–0.9,0.1)	0.246	0.238–0.252

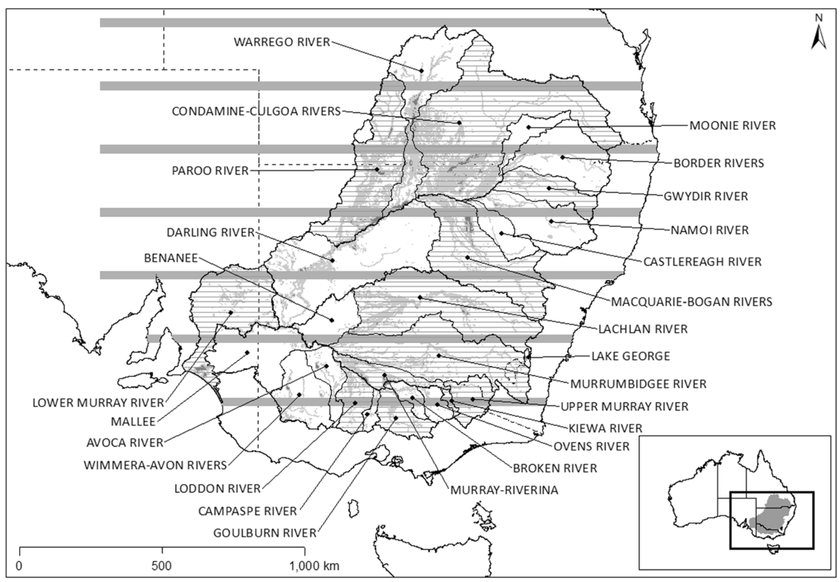

Fig. 1 River catchments with records of straw-necked ibis breeding (1983–2018) (horizontal shading), mapped wetlands (light grey shading) and Eastern Australia Waterbird Survey bands (grey) in the Murray–Darling Basin (inset)

recorded during the annual EAWS (Kingsford et al., 2020) and ad hoc historical records (1922–2008) compiled from grey literature and scientific papers (Brandis, 2010). Waterbirds were surveyed annually on wetlands along with ten aerial survey bands (30 km wide) between 1983 and 2018 (Kingsford et al., 2020) (Fig. 1).

We used estimates of clutch size (2.23 ± 0.31sd), reproductive success (fledged birds divided by total eggs laid; $P = 0.63 \pm 0.14$sd) and a number of fledglings per nest (1.45 ± 0.38sd) from ground surveys of 13 straw-necked ibis breeding colonies in the Murray–Darling Basin in 2008–2017 (Brandis, 2017; Brandis et al., 2017a; Brandis et al., 2011; Brandis et al., 2017b). Reproductive success varies with parental experience (i.e., lower for "first timers") (Limmer and Becker, 2009; Weimerskirch, 1992; Woodward and Murphy, 1999). In some cases, the reproductive success of inexperienced pairs can be as little as half that of experienced pairs (Davis, 1976). To incorporate the effect of parental experience on reproductive success, we assumed the reproductive success of experienced birds was 30% higher than inexperienced birds (third year of age).

We used EAWS data (1983–2018) which records abundance and number of nests to estimate the proportion of breeding and use as a parameter in the population model. As the total population size of straw necked ibis is unknown, we compared the proportion of breeding

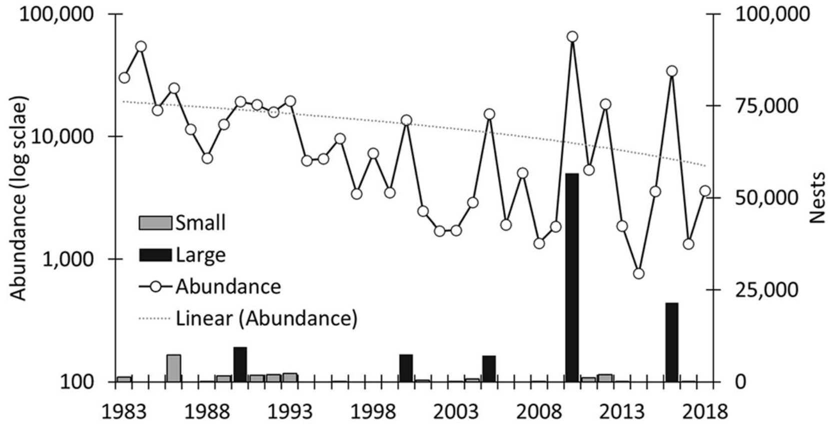

Fig. 2 Annual straw-necked ibis abundance, the linear trend (dashed line), and a number of nests surveyed during the Eastern Australian Waterbird Survey (1983–2018), (see Fig. 1). Large breeding events (black), where the proportion of breeding individuals (nests*2) exceeded a proportion of 0.65 of the total annual surveyed individuals, are depicted as black columns and small breeding events as grey columns

individuals (number of nests multiplied by two) to the total recorded abundance. Across survey bands of EAWS, in years with recorded breeding ($n = 21$), the average annual proportion was $P = 0.44 \pm 0.48$se (max $P = 1.72$ in 2010). Within the Murray–Darling Basin, the average annual proportion was $P = 0.59 \pm 0.54$se ($n = 15$, max $P = 1.76$ in 2010). We assumed the proportion of the population breeding would be higher during large (>65% of the population breeding) compared to small breeding events (<32.5% of the population breeding). Given uncertainty, we examined a range of breeding proportions respectively for inexperienced and experienced birds during large (0.50–0.75 (0.05 interval), 0.65–0.975 (0.065 interval)) and small breeding events (0.20–0.45 (0.05 interval), 0.26–0.585 (0.065 interval)) (Table 1). We examined breeding frequency ranging between annually to 1 in 10 years (1-year interval) for both large and small breeding events.

We assumed an initial population size of 1000 individuals, evenly distributed across the four life stages. The choice of initial population size was used to minimise computational time but did not compromise conclusions regarding population growth rates and annual trends. We simulated 100 replicate populations over a 30-year period at a 1-year interval, incorporating demographic stochasticity by generating multinomial random numbers for state transitions and lognormal random numbers for fertilities, using the "multiresultm" function in "popbio" package in R (R Core Team, 2018; Stubben and Milligan, 2007). For each 30-year time series, we calculated the annual trend and averaged across 100 replications for each scenario ($n =$ 39,600 scenarios). We then modelled the association between annual trend and the scaled breeding proportion under large (>65%) and small (<32.5%) breeding events, the frequency of large and small breeding events, and adult annual survival using the built-in function "lm" in R (R Core Team, 2018). We estimated the relative importance of explanatory variables to the annual trend by averaging sequential sums of squares over orderings of explanatory variables (Lindeman et al., 1980) and generated confidence intervals by bootstrapping 1000 replications using the "boot.relimp" function in "relaimpo" package (Grömping, 2006) in R (R Core Team, 2018). To identify the convergence between water regulation and straw-necked ibis breeding, we used EAWS data (Kingsford et al., 2020), supplemented with data from other surveys with comparable methods (Brandis et al., 2018b; Spencer, 2010), to determine the number, size and frequency of breeding events and total water storage capacity in each catchment of the Murray–Darling Basin (MDBA, 2020).

Results

Between 1983 and 2018, the average annual number of nests surveyed during EAWS, across all ten survey bands, was 3410 ± 10,034se (max 56,633 in 2010) and the average annual number of straw-necked ibis was 12,521 ± 14,645se (max 65,941 in 2010), (Fig. 2). Total straw-necked ibis observations during the surveys, decreased at an annual rate of ~5.5% (coefficient of year -0.055 ± 0.02se, 1983–2018) (Fig. 2) while rates of decline within the Murray–Darling Basin were higher, at ~6.8% ($-0.068 \pm$ 0.02se, 1983–2018). Straw-necked ibis breeding frequencies also varied from 1 in 1.71 years (21/36) across all survey bands, to 1 in 2.40 years (15/36) within the Murray–Darling Basin. Observed breeding frequencies of different sized events within the Murray–Darling Basin have also varied, with large events (>65% of the population breeding) occurring, on average, every 7.2 years, and small events (<32.5% of the population breeding), occurring on average, every 3.6 years.

Viability and annual trends of modelled populations of straw-necked ibis were primarily dictated by the frequency of large breeding events (relative importance 57%), followed by adult annual survival (25%) and frequency of

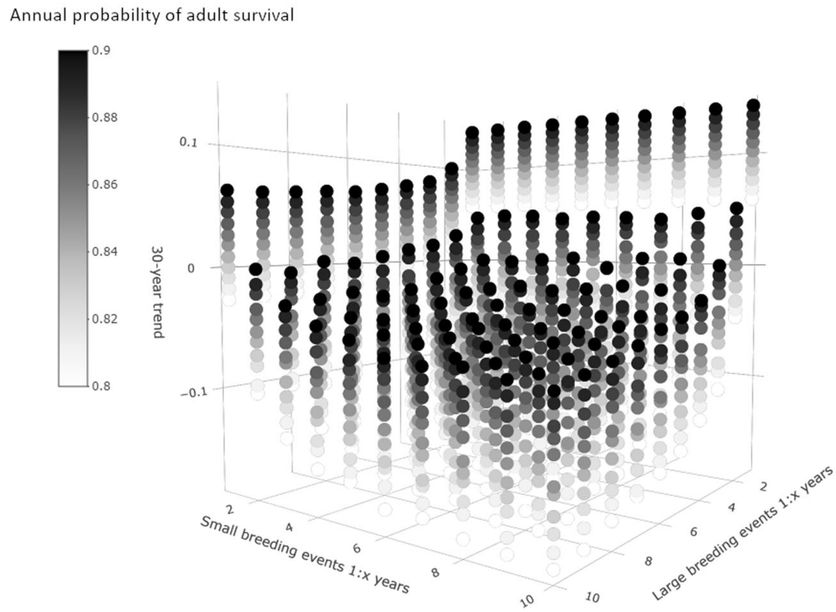

Fig. 3 Modelled 30-year trend in response to the frequency of large and small breeding events and adult survival, assuming a proportion of $P = 0.6$ and $P = 0.3$ of breeding individuals during large and small breeding events, respectively

small breeding events (16%). Positive annual trends were principally dependant on large breeding events (Fig. 3). Generally, if small breeding events occurred every year, a viable population could be maintained with infrequent large breeding events (Table S1). But as the frequency of small breeding events decreased (> 1 in 2 years), large breeding events were critical to maintaining viability (Fig. 3). For example, when adult annual survival was assumed to be $P = 0.86$ and the proportion of breeding individuals during large and small breeding events were $P = 0.85$ and $P = 0.46$, respectively, a viable population (within 95% CI) could only be maintained if large breeding events were every 1–2 years with infrequent small events (Table S1). But if large breeding events were less frequent (more than 1 in 3 years), small breeding events had to occur annually in order to sustain a positive annual trend (Table S1). To meet restoration targets of at least an annual increase of 5% (within 95% CI) in population size, small breeding events were required annually when the frequency of large breeding events exceeded one in every two years (Table S1). As the frequency of large breeding events decreased, achieving annual growth of 5% or higher required higher annual adult survival in conjunction with a higher proportion of breeding individuals during small breeding events.

Of the 26 river catchments in the Murray–Darling Basin (Geoscience Australia, 1997) straw-necked ibis breeding was recorded in 12 (Table 3); within these 12, only one catchment had no capacity for water storage (Paroo River). The Murrumbidgee River catchment had one of the most frequent straw-necked ibis breeding frequencies, once every 2 years while also having the greatest total storage capacity (3954 GL).

Discussion

We highlighted the management challenges and deficiencies for supporting waterbirds in the Murray–Darling Basin, using population models for a charismatic and colonially breeding wading bird, the straw necked ibis. We found that the combinations of large and small breeding events required to maintain stable populations are complex, representing an interaction between frequency, available habitat, proportion of the breeding population, and adult survival. With observed breeding frequencies over the past 35 years varying, large events occurring, on average, every 7.2 years, and small events occurring on average, every 3.6 years, such frequencies have been insufficient to maintain viable populations. This is evident by recorded declines in straw necked ibis numbers in key wetlands (Brandis et al., 2018b; Kingsford et al., 2004; Kingsford and Thomas, 1995) and across the Basin at an annual rate of ~6.8%. Water resource development has unequivocally reduced the frequencies of breeding events in the wetlands of the Murray Darling Basin. Historically, breeding at Narran Lakes (Condamine-Culgoa catchment), one of the key Basin breeding sites, occurred at a frequency of 1 in 2.26 years prior to water development in the 1970s compared to the recent frequency of 1 in 4.75 years (Brandis et al., 2018a). Similarly, the frequency of breeding events in the Macquarie Marshes was observed to have halved during the period 1963–1995 (Kingsford and Johnson, 1998) and has continued to decline in frequency. Observed declines in straw necked ibis abundance through EAWS surveys (Kingsford et al., 2020) and our understanding of straw-necked ibis breeding frequencies during the past 35 years, were consistent with our population models with observed historic breeding frequencies (Table S1) suggesting

Table 3 Straw-necked ibis breeding events in river catchments within the Murray–Darling Basin (1983–2018)

Catchment	Total storage capacity (GL)	No. dams	No. breeding events[a]	Mean nest count ± SD (min-max)	Breeding frequency (1983–2018)
Condamine-Culgoa Rivers	221	3	12	72,126 ± 56,451 SD (8500–200,000)	1:3
Goulburn River	3825	4	7	992 ± 713 SD (3–1919)	1:5
Gwydir	1364	1	6	48,667 ± 48,551 SD (2000–125,000)	1:6
Kiewa River	28	1	1	5	1:35
Lachlan River	1292	3	6	1400 ± 22,175 SD (22–62,508)	1:6
Loddon River	219	2	13	3072 ± 6976 SD (10–26,660)	1:3
Lower Murray River	2616	3	15	1268 ± 1600 SD (5–5334)	1:2
Macquarie-Bogan Rivers	1637	4	14	22,182 ± 23,137 SD (200–70,000)	1:3
Murray-Riverina	250	4	3	200 ± 114 SD (100–360)	1:11
Murrumbidgee River	3954	5	22	8328 ± 8130 SD (30–27,633)	1:2
Paroo River	0	0	2	613 ± 578 SD (80–1417)	1:17
Upper Murray River	3057	3	1	2	1:35

[a]Breeding data from (Brandis et al., 2018b; Kingsford et al., 2020; Spencer, 2010)

viable populations and restoration targets can only be achieved with much higher breeding frequencies of both large and small events, but also dependant on available habitat and high adult survival. Increasing breeding frequency and proportion of breeding individuals (size of the breeding event) of straw necked ibis, and likely of other colonial waterbirds, must become a priority for environmental flow management in the degraded system of the Murray–Darling Basin.

Increasing breeding frequencies could be achieved through the provision of suitable breeding conditions (flow timing, inundation duration, water depth) with environmental water allocations (Arthur et al., 2012; Brandis et al., 2011). The combination of large water storages within catchments that also support straw-necked ibis breeding provides a water management option to achieve this (Table 3). Typically, environmental flow management supports colonial breeding events through piggybacking on natural large flow events or top-up flows to maintain the inundation of colony areas. This strategy, however, may not achieve rehabilitation targets for waterbirds, and straw-necked ibis in particular, without larger environmental water allocations and more effective delivery mechanisms ensuring water, reaches targeted wetlands. Flow volumes could also be increased by changing the approach to water management and increased storage of environmental flows in dams until there are sufficient flows for a significant flood, without changing the shares of water (Kingsford and Auld, 2005).

The Basin Plan aims to mitigate the impact of water extraction on waterbirds by providing water to wetlands through the allocation of environmental flows. Specifically, by 2024 the Basin Plan aims to: (i) increase waterbird populations by 20–25%, (ii) increase opportunities for breeding by 50% through improved breeding conditions, and (iii) increase the number of birds breeding by 30–40% from the baseline. These targets were established based on predicted waterbird responses (total abundances and breeding) under the pre-Basin Plan flow availability and compared to those under the Basin Plan with assumed reduced diversions along with associated consumptive use and water-sharing arrangements (Bino and Brandis, 2017; MDBA, 2014). Providing opportunities for breeding for large colonies of straw-necked ibis, and other colonially breeding species is difficult to achieve with current water allocations due to the specific habitat and hydrological requirements for breeding of these species (Arthur et al., 2012; Brandis et al., 2018b; Chen et al., 2020). If these requirements are not met, reproductive success can be low or nests abandoned (Brandis et al., 2011). In addition, there is evidence that flows in rivers are continuing to decline with the illegal diversion of flows, including floodplain harvesting, and increased efficiencies in irrigation infrastructure leading to the capture of more river flows (Wheeler et al., 2020).

There are significant constraints to achieving large colonial waterbird breeding events, particularly because of over allocations of water entitlements, primarily for irrigation, limiting possible allocations of water for the environment (Grafton et al., 2012). Operational constraints also exist, such as dam management rules limiting the possibility of “carrying over” water entitlements for the environment to subsequent years to maximise breeding events, and necessary infrastructure to deliver water to colony sites on floodplains, as well as social constraints such as loss of property access during delivery of water (Chen et al., 2020). As a result, current allocations, management planning, and infrastructure targeting small and regular breeding events are unlikely to achieve targets set by the Basin Plan for straw-necked ibis population growth as well as for other waterbirds also highly dependent on flooding (Kingsford and Norman, 2002; Kingsford et al., 2010).

Compounding water delivery constraints is the loss of waterbird breeding habitat. The past 50 years have seen a significant loss of waterbird breeding habitat throughout the Murray–Darling Basin. Nesting habitat loss and alterations to flows have contributed to the decline in waterbird populations. There remains a limited number (<10) of suitable floodplain wetland sites throughout the Basin that support large colonial waterbird breeding colonies (Brandis 2010). Also, significant knowledge gaps still exist with regards to the total breeding population size, the proportion of breeding individuals during a breeding event as well as the longevity and life expectancy of straw-necked ibis. Continued monitoring of ibis responses across the Basin's wetlands is required to assess trends in abundances and breeding events (frequency and size) using continued aerial and ground surveys. Better estimates of population size, longevity, and movement of individuals can be derived from targeted mark-recapture approaches along with the integration of novel techniques to understand metapopulation dynamics and site fidelity (Brandis et al., 2021).

Challenges for future water management resulting in positive waterbird outcomes include the prioritisation of water allocations with competing interests such as fish and vegetation. While the delivery of water for the environment can achieve multiple outcomes that may include nesting vegetation maintenance, and supporting fish spawning events, it is difficult to achieve waterbird breeding outcomes with smaller flow volumes. The greatest challenge water managers face is reversing the 35-year decline observed in waterbirds in eastern Australia (Kingsford et al., 2017).

Data Availability

Data are available upon request from the corresponding author.

Code Availability

Code available upon request from the corresponding author.

Author Contributions KJB and GB designed and undertook the research, KJB waterbird data, GB data analytics. All authors contributed to manuscript writing.

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Compliance with Ethical Standards

Conflict of Interest The authors declare no competing interests.

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