

Studies of ibises in Victoria, III: Sexual dimorphism, sex ratio, breeding season, reproductive success, mating patterns, site fidelity, movements and survival of Australian White Ibis at three locations in southern Victoria

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Abstract. Wild, free-ranging Australian White Ibises *Threskiornis molucca* were studied between 1978 and 1984 at three breeding sites in southern Victoria: Rhyll Swamp and Coolart Lagoon (where the Ibises fed in 'natural' sites including wetlands, pastures and intertidal mudflats) and at Healesville Sanctuary (where they fed predominantly on food provided to captive animals and in urban fringe areas). Clutch size, breeding success, mating patterns and site fidelity of individually recognisable birds were studied over three breeding seasons at Healesville. There was frequent change of mates, and breeding pairs that stayed together over the three breeding seasons were more successful than those that changed mates. Adults had high site fidelity at all sites. Recoveries of birds banded as nestlings showed variation in dispersal and philopatry between the sites and provided rates of recruitment into the breeding population. The data presented add substantially to knowledge of breeding at natural sites. Comparisons of population-level data with previous studies show that the breeding season was later and shorter, breeding success was lower, and there was more juvenile dispersal at natural than at 'urban' sites. Sexual size dimorphism is documented in bill length, which showed no overlap between males and females, and therefore allows reliable identification of sex. The novel combination of detailed study of breeding by individuals and at a population level over multiple seasons provides deeper insights into the species' ecology than have previously been possible.

Introduction

Numbers of the Australian White Ibis *Threskiornis molucca* (hereafter referred to as Ibis) in Victoria have dropped dramatically over the past 40 years (Kingsford & Porter 2009; Lowe 2025). In the same period, this species has begun nesting in 22 urban areas across Victoria, such as at Coburg Lake and Jells Park in Melbourne (Lowe 2025), as well as at numerous sites around Sydney, New South Wales, the Gold Coast and Moreton Bay, Queensland, and Adelaide, South Australia (Murray & Shaw 2006; Corben & Munro 2008; Martin *et al.* 2011; Smith *et al.* 2013a; Paton 2016; Willis *et al.* 2024). In these locations, the species is considered by some to be a nuisance native species despite the birds apparently being refugees from the diminished inland 'wild' populations (Martin *et al.* 2010; Davis *et al.* 2021). Although the northern urban populations are well studied, there is little information available on breeding in more natural settings, with the exception of a preliminary study at Millewa Forest in southern New South Wales (McGinness & Brandis 2016) and at Winter Swamp in rural Victoria (Kentish 1999). Our knowledge of Ibis ecology in Victoria remains patchy and includes documenting changes in breeding events across the state over two time periods (Cowling & Lowe 1981; Lowe 2025) and factors affecting the breeding success, such as body size, age and dominance status, at a site with a predominantly artificial food supply (Beilharz 1988).

Literature reviews, such as McGinness & Brandis (2016), have documented the significant knowledge gaps that exist for this and related colonially nesting waterbirds, which affect our ability to manage and predict waterbird populations and diversity at appropriate scales. These gaps in knowledge include survival and mortality rates of different age groups, sex ratios, movements during and

between breeding events, site fidelity, impact of quality and productivity on breeding event size and success and how these interact. Despite the intervening decade since the McGinness & Brandis (2016) review, these knowledge gaps continue particularly for the Australian White Ibis.

This study aims to fill many of these gaps by intensive study of three breeding populations in southern Victoria. Comparisons are made between two sites that can be described as natural (where birds utilise mainly natural habitats and food supplies) and a third site (where birds predominantly capitalise on artificial foods provided to captive animals and at rubbish tips). Unique observations of a large population of individually identifiable birds allowed novel insights into sexual dimorphism, mating patterns, breeding season and success of individual birds that are usually documented only at a whole-of-population level. Banding of nestlings over several years provided data on philopatry and recruitment to the breeding population.

Methods

Study sites

This study was conducted between 1978 and 1984 on wild, free-ranging Ibises breeding at three sites in southern Victoria: Rhyll Swamp, Coolart Lagoon and Healesville Sanctuary (Figure 1), which are some of 79 breeding sites known across the state (Lowe 2025).

Rhyll Swamp (hereafter referred to as Rhyll; Figure 2) (38.46°S, 145.28°E) is a natural shallow freshwater marsh filled by local runoff and is located at Phillip Island, ~80 km south-east of the Melbourne Central Business District. The area of water in the marsh was ~41 ha and

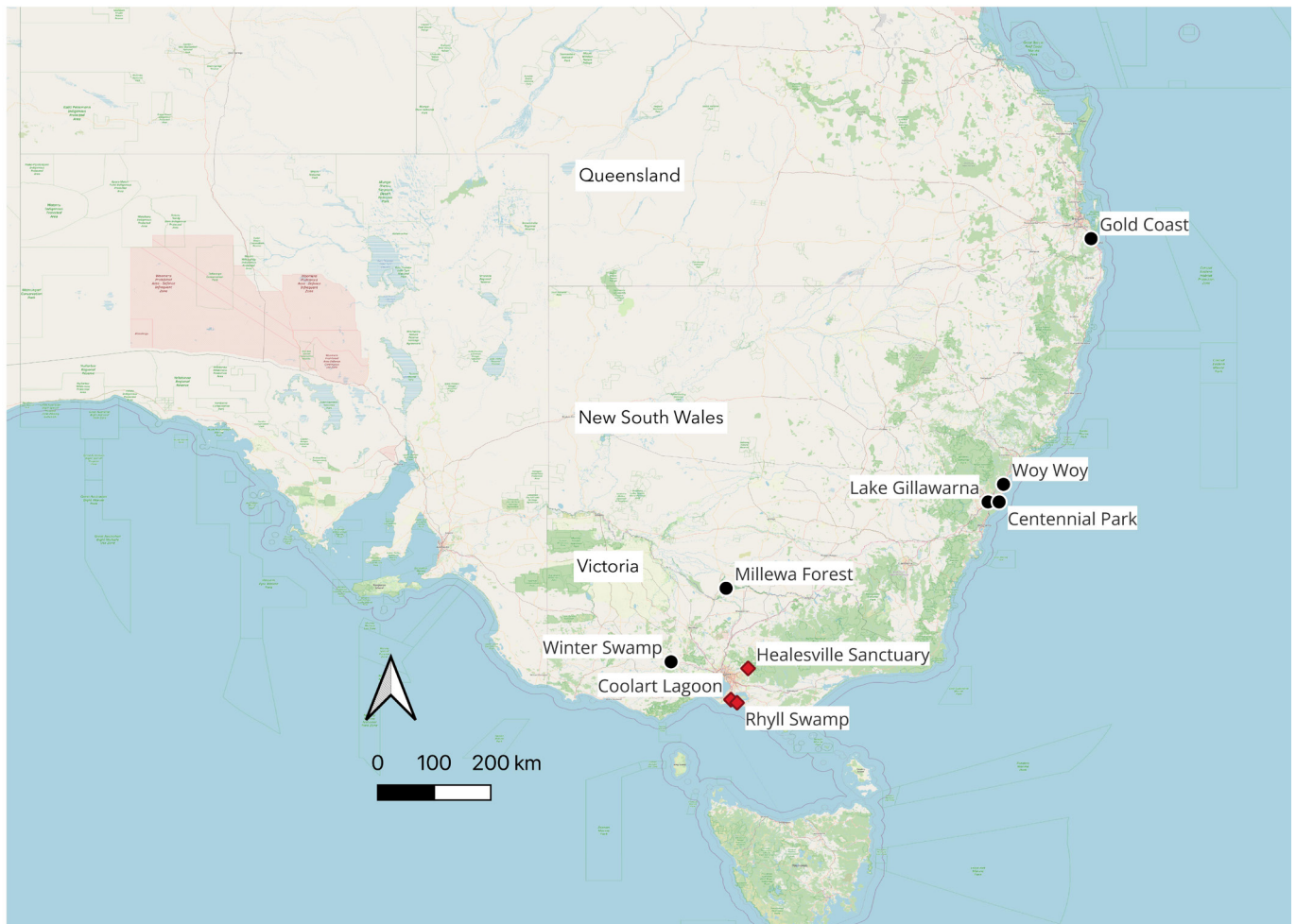


Figure 1. Study sites – red diamonds this study, black spots other studies.

dried out only once between 1961 and 1984. Phillip Island forms the southern extent of Western Port, which is a shallow marine embayment with intertidal mudflats (Lowe 1981). The Ibis breeding site is dominated by Swamp Paperbark *Melaleuca ericifolia* and contains islands surrounded by water at least 1 m deep during most breeding seasons. The islands may be covered with reeds *Phragmites* sp. or are bare earth. Breeding occurred throughout the swamp at the bases of the paperbarks and on the islands on reeds or bare ground. All nests were surrounded by water. The surrounding area includes land used for grazing and intertidal mudflats (Lowe 1981). The first record of Ibis breeding at Rhyll was in 1960 (Cowling & Lowe 1981).

Coolart Lagoon (hereafter Coolart: Figure 3) (38.39°S, 145.14°E) is a 4-ha natural shallow freshwater marsh filled by local runoff and is located ~65 km south-east of the Melbourne Central Business District and is 15 km from Rhyll. The vegetation, physical structure and water depth were similar to Rhyll. It is on a peninsula of the mainland that separates Western Port and Port Phillip Bay, and this peninsula forms the western extent of Western Port. Ibis breeding occurred throughout the marsh at the bases of the paperbarks and on the islands on reeds or bare ground. All nests were surrounded by water. Like Rhyll, the surrounding area includes land used for grazing and intertidal mudflats (Lowe 1981). The first report of Ibis breeding at Coolart was in 1961 (Cowling & Lowe 1981).

Healesville Sanctuary (hereafter Healesville) (37.68°S, 145.53°E) is a government-run wildlife park on the edge of the semi-rural township of Healesville and is located ~60 km east of the Melbourne Central Business District. It covers ~20 ha encompassing animal enclosures, many of which are walk-through and some are open-air (Figure 4). Food is provided to captive animals in the Sanctuary and is accessible to the free-ranging Ibises. Vegetation is variable and includes natural riparian habitat along Badger Creek and remnant Manna Gums *Eucalyptus viminalis* with clearings for enclosures, walkways, picnic tables and open cultivated lawn. Water is diverted through artificial ponds that have been revegetated with willows *Salix* sp., paperbarks *Melaleuca* sp. and wattles *Acacia* sp. Ibis breeding occurred around the ponds in these trees and on islands within the ponds. The predominant land use outside the breeding site is a mixture of agriculture, predominantly grazing on improved pastures, and urban areas. The first record of Ibis breeding at Healesville was in 1963 (Cowling & Lowe 1981).

Rhyll and Coolart were classified as natural sites and Healesville as a man-made and urban fringe site. The climate at the study sites is characterised by warm-hot summers and cold winters with moderate-high rainfall (Table 1). Records of Ibis breeding events for all three sites between 1955 and 2024 are listed in Cowling & Lowe (1981) and Lowe (2025).



Figure 2. Aerial view of Rhyll Swamp. Australian White Ibis nests were placed at the bases of the paperbark trees and on islands. Note the grazing pastures adjacent to the wetland reserve. Photo: Kim Lowe



Figure 3. Aerial view of Coolart Lagoon. Australian White Ibis nests were placed at bases of paperbarks and adults perched on adjacent branches. Photo: Kim Lowe



Figure 4. Elevated view of part of the Australian White Ibis breeding site at the Pelican Ponds, Healesville, with nests in willows, paperbarks and wattles and on islands. Note close proximity of administration buildings and public pathway under the nest trees. Photo: Kim Lowe



Figure 5. Colour-banded adult Australian White Ibis at Healesville taking food provided by visitors to the sanctuary. Photo: Kim Lowe

Sex determination

Fifty-four Ibises were collected by shooting near Rhyll between June 1978 and November 1981 for studies of food, breeding activity, plumage development and sexual dimorphism (Lowe 1984). They were measured and dissected, and sex was determined from internal anatomy.

Individual identification of Ibises

To assess breeding activity, success, mating pattern, survival and site fidelity, adult Ibises at Healesville were

trapped, measured, notes made on plumage, and each bird was banded with a numbered metal band and colour-banded with unique band combinations (Figure 5). They were caught in a permanent wire cage trap (~4 m wide × 3 m high × 6 m long) made with wooden poles and chicken wire.

Site fidelity was also assessed through transport of 40 adults from Healesville to Dowd Morass near Sale in November 1984 as part of population control at Healesville. Birds were individually colour- and metal-banded, and observers near the release site conducted regular searches for the birds for 4 weeks post release.

Table 1. Climate averages at meteorological stations near the study sites. Source: Bureau of Meteorology climate statistics for Australian locations (accessed 9 June 2025).

Site	Nearest weather station (and distance, km)	Mean daily maximum and minimum temperature (°C)				Annual rainfall (mm)	No. annual raindays
		January		July			
		Max.	Min.	Max.	Min.		
Rhyll	Rhyll (0)	24.1	15.9	13.4	8.2	696	106
Coolart	Stony Point (3)	23.5	15.2	12.9	7.1	761	117
Healesville	Coldstream (7)	28.1	12.1	13.4	4.0	757	102

To assess site fidelity in the Rhyll area, adults were captured between May 1979 and January 1981 using a canon-net set on freshwater dams in the pastures within 10 km of the breeding site at Rhyll. Each captured bird was banded with a numbered metal band and a unique combination of coloured plastic leg-bands, and was measured. Searches were made for birds carrying colour bands in feeding areas on mudflats, dams and in pastures in the vicinity of Rhyll by me and other observers from 1979 to 1984.

Censuses of Ibises at Healesville

A continuous census, in 3-month periods, of all colour-banded adults was initiated in December 1981 and maintained until June 1984. Records of all birds seen in each census period were made, and towards the end of each quarter particular attention was directed towards searches for birds not yet sighted in that quarter.

Banding and observations of nestlings

Between 1978 and 1980, 942 nestlings were banded (metal band combined with one colour band identifying the year and location of banding) at Rhyll and Coolart. Searches were made for birds carrying colour bands at the three breeding sites during the breeding season by me and other observers from 1979 to 1984.

Banding records

All band recoveries and sightings of colour-banded birds reported by the public of Ibises banded and released at Healesville, Rhyll and Coolart and held in the Australian Bird and Bat Banding Schemes database (ABBBS 2025) up to 31 December 2024 were obtained. Records were mapped and checked for accuracy. Recoveries of bands without birds (i.e. band-only records) were excluded from the analysis. Distance between banding and recovery location and time elapsed as calculated by the ABBBS were used. Records of sightings of colour-banded birds were included.

Feeding activity

Searches for colour-banded Ibises in feeding habitat outside the breeding sites and within 10 km were made at Rhyll and Healesville. These were *ad hoc* at Rhyll between 1978 and 1983 (on 97 occasions) and systematically and fortnightly at Healesville between 1980 and 1983. Searches were made irregularly at rubbish tips and the abattoir at Healesville.

Breeding activity at Healesville

At Healesville, breeding activity was observed from August 1980 to March 1984 at least fortnightly from vantage points throughout the park, including a water tower, ladders placed against trees within 20 m of nests, and from the

ground. Regular and methodical sightings of breeding Ibises were recorded. The identity of the birds at each nest, nest locations, dates of laying, clutch size, hatching, fledging and interactions with neighbouring nesting birds were recorded. Most nests were inaccessible, and contents of nests were inspected with a mirror on a pole.

Individual identification of Ibises at Healesville allowed tracking of mating patterns and related breeding success. To simplify the various patterns, a classification was applied to individual birds and not pairs to allow discrimination of the outcomes for each individual. Three categories of mating pattern were established and terminology is adapted from Beilharz (1988):

1. Single – single attempt (and therefore single mate),
2. Shared – multiple attempts with one or more mates and the mate is shared with others,
3. Sole – multiple attempts with the same mate with sole access to that mate.

Individual birds were assigned a mating pattern and so a breeding attempt may be between birds with different patterns (e.g. one bird had the Single pattern and the other had the Shared pattern). Mating patterns were applied for breeding within a single year (Annual pattern) and for all pairings across the three breeding seasons studied (1981–1982, 1982–1983 and 1983–1984) (Total pattern) (i.e. individual birds were assigned a mating pattern for each year and for the 3-year period). For simplicity, each breeding season is identified by the year it started (e.g. the breeding season of 1980–1981 is called 1980). Approximately half the breeding birds at Healesville were unbanded so the pairing arrangements for many birds were unclear.

Breeding activity at Rhyll and Coolart

At Rhyll, breeding activity was observed from August 1978 to January 1981, with at least fortnightly visits during the breeding season. Nests were inspected directly from a boat paddled through the wetland.

At Coolart, breeding activity was observed weekly from August to December 1979 from the shoreline and by wading in. In subsequent years until 2025, observations were by the Warden of the reserve. Nests were tagged for identification, and nest location, dates of laying, clutch size, hatching and fledging were recorded. Eggs were generally not handled, with the exception of a sample of eggs that were measured (these clutches were excluded from the analysis of clutch size and breeding success).

Clutch size was defined as the maximum number of eggs seen in a nest at least 2 days apart, as laying occurs at 2-day intervals (Lowe 1984). If eggs were known to have disappeared soon after laying, these nests were excluded from the analysis of clutch size but were included in nest success. A nesting attempt was defined as the laying of one or more eggs that were attended by a pair of birds; hatching success as the proportion of eggs that hatched; egg success as the proportion of eggs that produced fledged young; and fledging success as the number of young fledged from a nest. With weekly or fortnightly visits, hatching and breeding success could not be

Table 2. Body measurements of 54 Australian White Ibises that were collected at Rhyll and dissected. F = female, M = male; SD = standard deviation, *n* = number.

Measurement	Sex	Mean	Range	SD	<i>n</i>	<i>t</i> -test
Body weight (kg)	F	1.72	1.45–2.00	0.14	35	<i>P</i> < 0.0001
	M	2.19	1.95–2.40	0.13	18	
Bill length (mm)	F	151.0	131–164	8.2	35	<i>P</i> < 0.0001
	M	190.1	180–198	4.5	18	
Tarsus (mm)	F	84.9	71–91	4.1	35	<i>P</i> < 0.0001
	M	99.1	88–107	5.9	18	
Wing (mm)	F	35.5	33.5–38.0	0.2	35	<i>P</i> < 0.0001
	M	38.1	35.5–40.0	0.3	18	

measured precisely. For nests observed weekly, nestlings were considered to have fledged if they were last seen alive when they were >4 weeks old. For nests observed fortnightly, nestlings were considered to have fledged if they were last seen alive when they were >3 weeks old.

Causes of egg and nestling loss were sought by examination of nests and their surroundings for remains and by direct observation of losses. Visits to nests were for <10 minutes and were timed to avoid extremes of weather.

Results

Observations in non-breeding season

After breeding had ceased at Rhyll and Coolart in December each year, few Ibises were seen throughout the day or night at these breeding sites. Birds were seen roosting in mangroves around the shores of Western Port often in groups of ~100 birds at a single site (Lowe 1981). Outside the breeding season, Ibises fed on nearby intertidal mudflats around Western Port and in pastures (Lowe 1981). By April each year, several hundred birds were roosting at each of the breeding sites each night and departing in the morning. By early July, hundreds were present at the sites throughout the day. Ibises fed in the marsh and adjacent pastures during the breeding season and were regularly seen flying in flocks to pastures up to 30 km away, returning during the day and in the evening to the breeding sites.

At Healesville, Ibises were present throughout the year during the day and night. Breeding had ceased in either December or January and the birds roosted at the site throughout the year. Most fed throughout the year within the Sanctuary on food stolen from captive animals. Some were fed by visitors to the site. Ibises also fed outside the park (within 5 km of the breeding site) in pastoral lands, river floodplains, suburban gardens, a municipal rubbish tip and a poultry abattoir.

Measurements of adults and determination of sex

Sex was determined from the reproductive anatomy of collected birds, including presence of testes, or egg in oviducts or ovaries. All were identified as adults based on bare neck and head skin. Thirty-five were identified as

females, 18 as males, and the sex of one could not be determined. Measurements of bill, tarsus, flattened wing length, and body weight showed that means for males were significantly larger than for females, and all but bill length overlapped (Table 2). There was no overlap in bill length (measured as the chord from the soft skin above the culmen to the tip, to the nearest 1 mm): all females had a shorter bill (131–164 mm) and all males a longer bill (180–198 mm).

To further clarify bill dimorphism, the distribution of bill length of 225 birds trapped at Healesville was plotted (Figure 6) and showed a gap in the range with 172–173 mm being used as the dividing point. This was used to allocate sex to each bird, with males having bill length >173 mm and females <172 mm. The allocated sex was tested continually by observing Ibises breeding at Healesville, noting copulation position and identity of mate. All observations of the 225 recognisable birds agreed with the sex assignment from the bill measurement. This indicates a sex-ratio near parity.

As an indicator of body condition, the mean weight of the 35 females collected near Rhyll between June and December (pooled over years) was compared with a randomly selected sample of 35 females trapped at Healesville during the same months. The mean weight of females at Rhyll (1.73 kg) was significantly larger than those at Healesville (1.63 kg) ($t = 2.81$, $P = 0.003$).

Site fidelity of adults

Site fidelity was defined as the degree to which a bird returns to a specific site, in this case to the site where it was banded, in line with the definition used by Martin *et al.* (2012). Ibises banded as adults had similar site fidelity at Healesville and Rhyll – adults were highly sedentary. Over the three breeding seasons of this study, 208 of 225 (92%) colour-banded Ibises (banded as adults) from Healesville were resighted by me and other researchers within 5 km of Healesville and none were resighted further away. The recovery of 23 birds banded as adults at Healesville between 1980 and 1990 was reported through the ABBBS: all recoveries were at the banding site and were spread over time from 1 year 4 months to 15 years 9 months after banding. Over the five breeding seasons in the period 1979–1984, 38 of 45 (84%) adult colour-banded birds near Rhyll were resighted by me and other researchers within 5 km of Rhyll; none were resighted further away. There

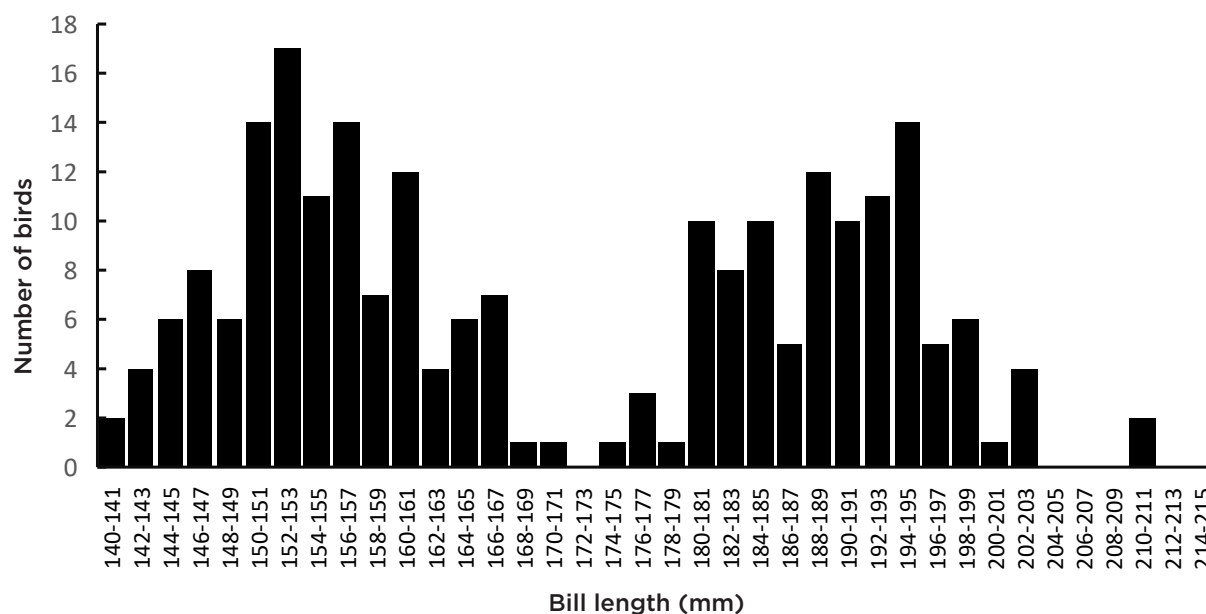


Figure 6. Distribution of bill length (2-mm intervals) of Australian White Ibises trapped as adults at Healesville.

were no sightings or recoveries of birds banded as adults at Rhyll reported through the ABBBS.

Another measure of site fidelity came from the 40 Ibises that were captured at Healesville, transported to and released at Sale, Victoria (155 km away), on the same day. Nine returned to Healesville – seven between 14 and 34 days after release and two were found dead or dying at Healesville between 4 and 13 years after release. None were observed or recovered elsewhere, including at the release site.

Feeding activity at Healesville

Forty-nine of the 208 colour-banded adults were observed outside the breeding site and 22 of these were known to be breeding at the same time as observed. Ibises were

observed moving back and forth between their nests and the outside feeding site multiple times throughout daylight hours. Nesting birds were frequently seen taking food provided to captive animals and from the public.

Recovery of Ibises banded as nestlings

Eighty-four Ibises banded as nestlings at Healesville and Rhyll were recovered through the ABBBS up to 26 years after banding at various distances up to 3273 km away (Table 3). Recovery distances of those recovered >3 months after banding (time for the nestlings to become independent) differed between the sites: 50% of those banded at Healesville were recovered at or near the banding site compared with 16% of those banded at Rhyll. Both presumed immature birds (<36 months old) and

Table 3. Australian White Ibises banded as nestlings at Healesville and Rhyll that were recovered >3 months after banding, excluding colour-band sightings (see text). Data from ABBBS.

Site	No. recovered (and %)	Time after banding (months)	Distance from banding site (km)	Mean distance	No.(immature vs mature) recovered (and mean distance from banding site)	
					Immature (4–35 months)	Mature (36+ months)
Healesville						
At site	13 (50)	4–158	0	$t = 1.1344$ $P = 0.2831$	4	9
Away from site	13 (50)	4–180	55–1934		6 (468 km)	6 (131 km)
Rhyll						
At site	9 (16)	6–198	0	$t = 0.7871$ $P = 0.4362$	2	5
Away from site	49 (84)	4–312	5–3273		21 (161 km)	18 (299 km)

Table 4. Laying periods (black shading) of the Australian White Ibis at the study sites over multiple years.

Site	Year	Month of laying						
		Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Rhyll	1979–1980							
	1980–1981							
	1981–1982							
Coolart	1979–1980							
	1980–1981							
	1981–1982							
Healesville	1980–1981							
	1981–1982							
	1982–1983							

mature birds (at least 36 months old) were recovered at and away from banding sites. Of birds recovered away from the banding site, the proportion of birds <36 months old and those at least 36 months old was close to equal at both sites. The mean distance from the banding site was the same for birds <36 months old and those at least 36 months old for birds banded at both sites.

Sightings of Ibises colour-banded as nestlings

Birds colour-banded as nestlings with different sites and year combinations were observed on 39 occasions between 1981 and 1984 by me and the public. Twelve were sighted at Coolart: eight of these were banded at Coolart and four at Rhyll. Two were sighted at Healesville: both banded at Coolart. Of the remaining 25, eight were sighted >50 km from the banding site.

Age of first breeding and recruitment to breeding population

There were three sightings of Ibises colour-banded as nestlings with known natal site and age, one each in 1981–1982, 1982–1983 and 1983–1984 seasons. Their ages were 3.0, 2.9 and 3.0 years, respectively (mean = 3.0 years). All were sighted at Coolart, two were females hatched at Coolart and the other a male hatched at Rhyll.

Using these observations, the proportion of nestlings that were first recruited as breeding adults was estimated using the number of birds banded 3 years before for each age/site cohort of birds. The female that bred at Coolart in 1981–1982 was part of a cohort of 67 nestlings banded at Coolart in 1978–1979. The male that bred at Coolart in 1982–1983 was part of a cohort of 189 nestlings banded at Rhyll in 1979–1980. The female that bred at Coolart in 1983–1984 was part of a cohort of 182 nestlings banded at Coolart in 1980–1981. This was 1.5%, 0.5% and 0.5% (respectively) of birds banded that were later seen nesting at age 3 years. Birds with the same colour-banding cohort were seen at the breeding site and none were seen breeding up to April 1984.

Breeding season

Ibises bred at all sites in all years of the study and the timing and length of the breeding season was similar each year at Rhyll and Coolart and varied between years at Healesville (Table 4). At Healesville, breeding started at least 1 month earlier and continued for 1 month longer than at Rhyll and Coolart in two of 3 years. Egg-laying was spread throughout the breeding season, with birds nesting in small groups (usually 1–15 nests per group) which were out of phase with each other but highly synchronised, to a laying period within 1–2 days, within each group.

Clutch size

Incidental observations showed that Ibises laid one to six (commonly two to four) eggs per clutch ($n = 624$). The clutch size in sample nests varied from one to four eggs (Figure 7). At all sites and in all years, modal clutch size was three and the next most common clutch size was two. The mean clutch size varied between years and sites (Table 5). In 1980–1981, mean clutch was significantly smaller at Rhyll than in the other years (ANOVA, $P < 0.001$). At Healesville, it was significantly larger in 1981–1982 than in 1982–1983 (t -test, $P < 0.002$). In 1981–1982, the mean clutch size at Healesville was larger than at Rhyll (t -test, $P < 0.05$).

Within-season variation in clutch size

Mean clutch size varied within season at Rhyll and Coolart but not at Healesville. At Coolart, it was lower in August whereas at Rhyll the month of the lowest clutch size varied between years. At Healesville, clutch size did not vary within season (1981–1982 ANOVA, $P = 0.09$; 1982–1983 ANOVA, $P > 0.25$).

Breeding success

All measures of breeding success, including hatching success, fledging success and egg success, were higher at Healesville than at the other two sites (Table 5). Fledging

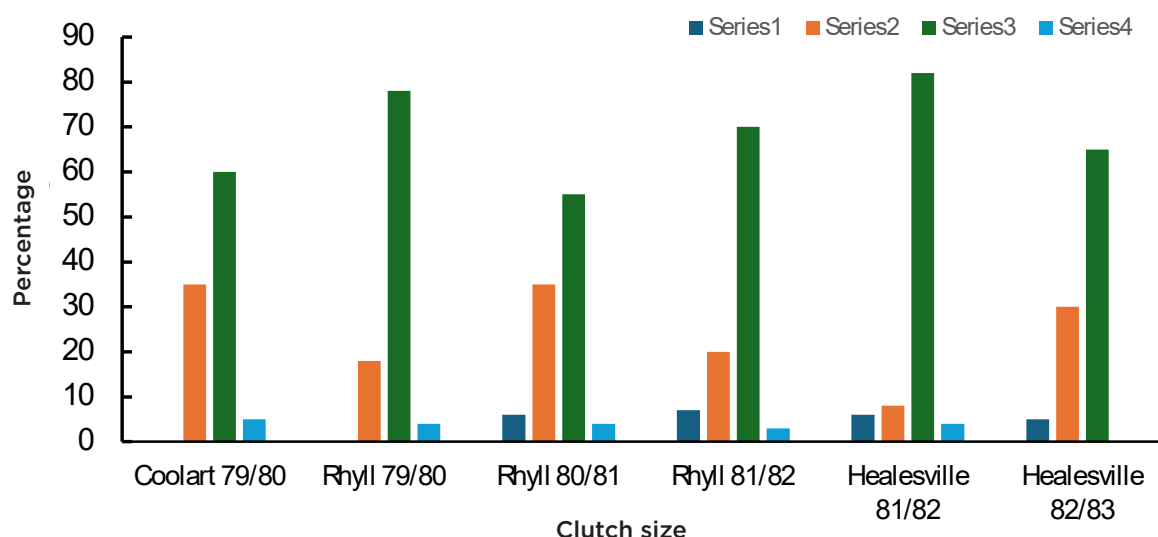


Figure 7. Clutch size of Australian White Ibises: percentage of clutches of sizes shown at sites (Coolart, Rhyll and Healesville) and years indicated.

success varied within a season only at Rhyll in 1979–1980 (ANOVA $P < 0.01$). The proportion of nests failing at Healesville (30–33%) was much lower than at Rhyll and Coolart (51–72%) (Table 6). Furthermore, more than one young fledged at 48% of nests at Healesville but at only 5–17% of nests at Rhyll and Coolart.

Causes of egg and nestling mortality

Overall, one-third to half of the eggs did not hatch; nevertheless, it was uncommon to find unattended or damaged eggs in or near nests. Ravens *Corvus* sp. were frequently seen scavenging in the breeding colonies and

Table 5. Breeding parameters of the Australian White Ibis from this and other studies (in Victoria unless specified). NA = data not available.

Location	Year	Mean clutch size	Mean hatching success per egg	Mean fledging success per nest (nest success)	Mean fledging success per egg (egg success)	Source
Natural						
Coolart	1979–1980	2.67 (58)	0.55	0.59	0.22	This study
Rhyll	1979–1980	2.82 (90)	0.58	0.67	0.24	This study
	1980–1981	2.56 (135)	NA	0.59	0.23	This study
	1981–1982	2.72 (182)	NA	0.34	0.13	This study
Winter Swamp	1990–1997	2.25 (8)	NA	NA	NA	Kentish (1999)
Millewa	2015–2016	2.3 (98)	0.3	0.62	0.27	McGinness & Brandis (2016)
Urban						
Healesville	1981–1982	2.88 (92)	0.68	1.29	0.46	This study
	1982–1983	2.60 (67)	NA	1.23	0.47	This study
	1983–1984	2.76 (178)	NA	0.97	NA	Beilharz (1983)
	1984–1985	2.62 (333)	NA	0.83	NA	Beilharz (1988)
	1985–1986	2.73 (352)	NA	0.74	NA	Beilharz (1988)
	1986–1987	2.78 (141)	NA	0.91	NA	Beilharz (1988)
Gold Coast, Qld	2002–2003	2.46 (124)	0.48	0.60	0.29	Murray & Shaw (2006)
Centennial Park, Sydney, NSW	2003–2004	2.7 (27)	NA	2.64	NA	Corben & Munro (2006)
Woy Woy, NSW	2005–2006	2.53 (851)	0.38	0.63	0.65	Smith <i>et al.</i> (2013a)
Lake Gillawarna, NSW	2005–2006	2.52 (337)	0.51	1.02	0.79	Smith <i>et al.</i> (2013a)
	2005–2006	NA	0.67	0.69	0.67	Martin <i>et al.</i> (2007)

Table 6. Number of young Australian White Ibises fledged per nest: percentages of nests with the number of fledglings shown; n = number of nests.

Location	Year	Number of fledglings				n
		0	1	2	3	
Coolart	1979–1980	60	23	13	4	58
Rhyll	1979–1980	52	32	13	3	90
	1980–1981	51	37	9	3	77
	1981–1982	72	23	4	1	50
Healesville	1981–1982	33	19	33	15	87
	1982–1983	30	22	43	5	81

might have removed eggs when the observer was not present. They were never seen to come within reach of a sitting adult nor being aggressive towards the Ibises. However, on some occasions they were seen pecking at and eating eggs and chicks <3 weeks old when adult Ibises were flushed from nests by humans. Accordingly, nest contents were only inspected twice a fortnight at a sub-sample of nests in 1979–1980 at Rhyll and in 1981–1982 at Healesville to observe their immediate fate. After inspection, the nests were observed from a distance, and the incubating birds returned to their nests within a few minutes and no eggs were lost to predation during these inspections. Tiger Snakes *Notechis scutatus* were occasionally found at nest sites at Rhyll and Coolart but there was no evidence that they preyed on Ibis eggs or chicks. Red Foxes *Vulpes vulpes* are known to feed on eggs at other colonies (Lowe 1983) but nests at the study sites were never accessible to foxes.

Adult Ibises might have attacked each other's eggs and chicks but this was rarely observed. On one occasion, eggs and chicks were pushed out of nests during bouts of fighting between adults at nest sites. The birds were not identifiable and those that remained did not retrieve the eggs or chicks. Overall, eggs and chicks disappeared between observation sessions and the causes could not be determined.

Number of nesting attempts at Healesville

Over the study period (1981–1984), 408 nesting attempts by identifiable birds at Healesville were documented,

Table 7. Number of nesting attempts by Australian White Ibises per year, over the period 1981–1984, at Healesville. Percentages are shown separately for females (F) and males (M); n = number of nests.

Sex	No. attempts					n
	0	1	2	3	4, 5, 6	
1981–1982						
F	30	37	26	7	0	46
M	24	30	24	14	8	37
1982–1983						
F	38	45	14	2	1	95
M	29	41	23	6	1	90
1983–1984						
F	22	21	30	15	12	76
M	16	11	20	34	19	64

comprising 217 by females and 191 by males. The number of nesting attempts by individuals in a breeding season varied from zero to four for females and from zero to six for males (Table 7). In any given year, 16–38% of sexually mature birds did not breed (16–29% of males, 22–38% of females). Most females (51–63%) made one or two attempts per year. In two of the years, most males (54–64%) made one or two attempts per year; in the other year, most males (53%) made more than two attempts. There was positive correlation between the number of attempts made by individuals between successive years – 1981–1982 compared with 1982–1983 (Spearman: males, $P < 0.02$; females, $P < 0.05$) although most birds made fewer attempts in 1982–1983 than in 1981–1982. The number of attempts made by individuals was also correlated between the 1982–1983 and 1983–1984 seasons (Spearman: males, $P < 0.001$; females, $P < 0.005$).

Effects of multiple nesting

At Healesville, many females laid more than one clutch per season (Figure 7). The time interval between when one brood fledged and the commencement of the female's next clutch that season (breeding lag) was significantly related to the size of the female's last fledged brood ($F = 11.7$, $P = 0.002$, $n = 32$) (Figure 8). The breeding lag varied by a mean of c. 40 days depending on brood size.

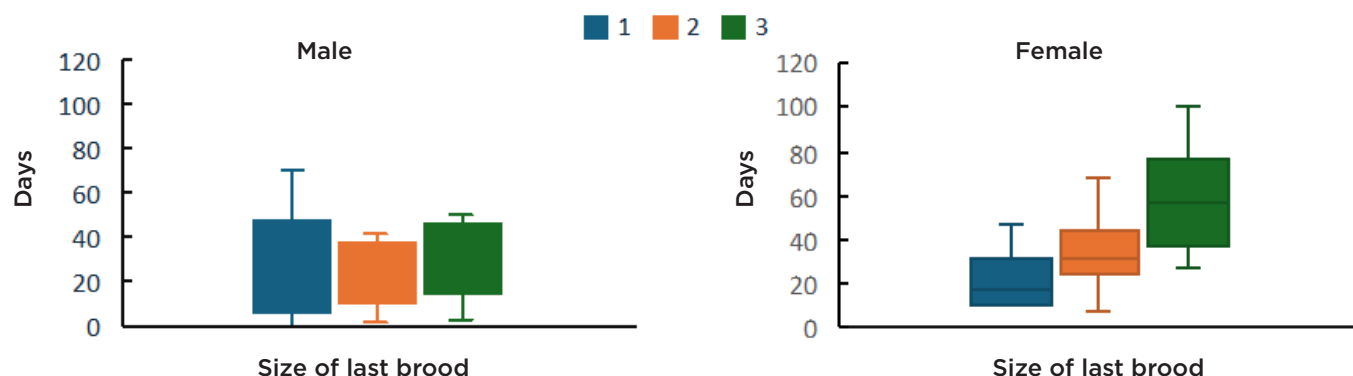
**Figure 8.** Breeding lag (days) and size of the last fledged brood for Australian White Ibis males and females at Healesville. Breeding lag for females was significantly related to the size of her last fledged brood ($Y = 19.5X - 1.3$, $F = 11.7$, $P = 0.002$, $n = 32$) but was not for males ($Y = 1.1X - 29.4$, $F = 0.06$, $P > 0.25$, $n = 24$).

Table 8. Number of Australian White Ibis young fledged per year, over the period 1981–1984, at Healesville. Percentages are shown separately for females (F) and males (M); n = number of nests. SD = standard deviation.

Sex	No. of young fledged								n	Mean	SD (%)
	0	1	2	3	4	5	6	7, 8, 9			
1981–1982											
F	8	8	40	32	4	8	0	0	25	2.4	1.2
M	8	16	32	12	16	0	0	16	25	3.0	2.4
1982–1983											
F	17	22	46	9	4	2	0	0	46	1.9	1.4
M	14	21	36	14	11	2	2	0	56	2.0	1.8
1983–1984											
F	20	5	32	27	12	0	3	0	59	2.2	1.5
M	6	12	24	12	24	16	8	0	51	3.1	1.7

For females that successfully fledged young, the time period between starting consecutive clutches included 23 days for incubation and 35 days for the nestling period, and varied from 78 to 118 days.

Breeding lag for males showed no relationship to the size of the male's last fledged brood ($F = 0.06$, $P > 0.25$, $n = 24$). Nearly all females that bred were still alive the following year (97% of 32 females) irrespective of brood size (X^2 , $P = 0.99$).

Annual fledging success versus sex

The annual fledging success of individuals varied from zero to six for females and from zero to nine for males (Table 8). Annual fledging success did not vary between years: the modal number of young fledged in all years by both males and females was two. Annual fledging success between years was correlated for males (Spearman: 1981–1982 and 1982–1983, $P < 0.05$; 1982–1983 and 1983–1984, $P < 0.02$) but not for females (Spearman: 1981–1982 and 1982–1983, $P > 0.2$; 1982–1983 and 1983–1984, $P > 0.1$). There was a significant correlation between the number of nesting attempts made and annual fledging success for each sex (Spearman: 1981–1982, males $P < 0.001$; females $P < 0.001$; 1982–1983, males $P < 0.00$, females $P < 0.001$; 1983–1984, males $P < 0.001$, females $P < 0.001$).

Observations of individually marked Ibises at Healesville

All breeding birds shared nest building, incubation, brooding, feeding of nestlings and nest defence. Ibises bred as monogamous pairs (i.e. one male and one female). There were no observations of multiple males attending one female (polyandry) and no cases of uniparental care of young.

Monogamous mating patterns across nesting attempts took several forms. Some birds nested only once per season and stayed with a mate between seasons. Some changed mate between seasons. Some had multiple attempts in a season and stayed with the same mate, other birds changed mates. Three categories of mating pattern were observed:

Table 9. Mating patterns of Australian White Ibises within a breeding season, over the period 1981–1984, at Healesville. Percentages of birds with specified mating patterns are shown separately for females (F) and males (M); n = number of nests. See text for details of mating patterns.

Mating pattern	1981–1982		1982–1983		1983–1984	
	M	F	M	F	M	F
Single	39	46	29	53	0	15
Shared	43	39	48	28	75	66
Sole	18	15	23	19	25	19
n	23	26	31	36	36	47
Chi-square	$P > 0.05$		$P < 0.05$		$P < 0.05$	

1. Single – single attempt (and therefore single mate),
2. Shared – multiple attempts with one mate but the mate is shared with others,
3. Sole – multiple attempts with the same mate with sole access to that mate.

Individual birds were assigned a mating pattern for each year and for the 3-year period.

Mating patterns within a breeding season

The mating pattern of individual birds within a breeding season varied between males and females and between years (Table 9). Single pattern was more common for females than males. More males showed Shared pattern than other patterns. A higher proportion of males than females showed Sole pattern.

Annual fledging success and mating pattern

Annual fledging success (number of young that fledged) varied between males and females and between years. Individuals that had a single attempt were usually least successful for the season (Table 10). For females, the most successful pattern was Shared and Sole in 1981–1982 and Sole in 1982–1983. Males that had more than one attempt in a season were equally successful regardless of their patterns of mate choice.

Table 10. Mean annual fledging success of males and females and mating pattern in Australian White Ibis, over the period 1981–1984, at Healesville. Number of birds is shown in parentheses. * indicates significantly higher mean. See text for details of mating patterns.

Mating pattern	Males			Females		
	1981–1982	1982–1983	1983–1984	1981–1982	1982–1983	1983–1984
Single	2.1 (8)	1.4 (9)	– (0)	1.6 (12)	1.6 (19)	1.3 (6)
Shared	4.0 (10)	2.7* (15)	3.4 (27)	3.4* (9)	1.4 (10)	2.4 (30)
Sole	4.3 (4)	3.5* (7)	2.7 (9)	4.3* (4)	3.4* (7)	2.7 (9)
ANOVA	$P > 0.5$	$P = 0.05$	$P > 0.25$	$P = 0.005$	$P = 0.0025$	$P > 0.25$

Table 11. Mean total fledging success of Australian White Ibises, pooled over the three breeding seasons studied (1981–1982, 1982–1983 and 1983–1984), at Healesville for each sex and mating pattern. Number of birds is shown in parentheses. * indicates significantly higher mean. See text for details of mating patterns.

Mating pattern	Males	Females
Single	5.6 (5)	5.2 (6)
Shared	9.1* (10)	7.1* (7)
Sole	10.3* (7)	8.8* (7)
ANOVA	$P < 0.025$	$P < 0.01$

Table 12. Change of mate vs no change of mate in relation to size of last fledged brood within the same breeding season for Australian White Ibis individuals at Healesville. Figures in the first two rows show the total number of young fledged by each bird over the period 1981–1984 (three breeding seasons) and then averaged for each combination of mating pattern and sex. See text for further details.

	Size of last fledged brood				Total
	0	1	2	3	
Change of mate	14	4	19	6	43
No change of mate	15	3	3	0	24
Total no. broods	29	7	22	6	67
% change	48	57	86	100	
Binomial probability (P)	0.7	0.5	<0.001	<0.02	<0.001

Total fledging success and mating pattern

The total fledging success of 42 adults was tracked over the three breeding seasons studied (1981–1982, 1982–1983 and 1983–1984) (Table 11). Total fledging success was defined as the pooled number of young fledged over this period. Males fledged more young than females for each mating pattern. Males and females following the Sole pattern fledged more young but this was not significantly different from those following the Shared pattern. Males and females that had more than one attempt per season fledged more young than individuals that had only one attempt.

Possible factors affecting breeding success and mating pattern

Clutch size, feeding location, food type and mating pattern were investigated as factors affecting breeding success and mating pattern.

1. Clutch size and mating pattern – Clutch size at Healesville did not vary between years nor between individuals (Lowe 1984) and so had no influence on mating pattern.

2. Feeding location, food type and mating pattern – Food available to nesting birds at Healesville was of two main types: artificial food (as supplied to captive animals at the park and human food wastes or ‘natural foods’ from pastures, wetlands, and riparian zones away from the park. The proportion of banded birds observed feeding outside the park was the same for both males and females (X^2 : $n = 34$, $P > 0.25$). Birds with different mating patterns were as likely to be seen feeding outside the park (Fisher’s Exact Probability Test: males $P > 0.05$, $n = 19$; females $P > 0.05$, $n = 15$).

3. Factors affecting change of mates – The chance of changing or not changing mates was equal when broods failed (i.e. size of fledged brood was zero), and the chance of changing increased as size of the fledged brood increased (Table 12). The mean length of breeding lag (period from fledging of a brood to laying of next clutch) for females was longer if either bird of the pair changed mate (mean = 26.0 days vs 56.6 days, U -test: $P < 0.05$, $n = 14$). There was no significant difference in fledging success before (mean = 1.3 fledged) and after (mean = 1.1 fledged) a change of mate (Wilcoxon Matched Pairs Signed Ranks test: $n = 23$, $z = 0.198$, $P > 0.05$).

A small sample suggested that when males changed mate, post-fledging care of young was affected: three males stopped feeding young when they formed a new pair; four males continued feeding young for 4 weeks and did not start a new pair. Their female mates all fed their young for 4–5 weeks after they left the nest.

Discussion

This study provides novel insights into the breeding ecology of the Australian White Ibis firstly by documenting the reproductive parameters of individually recognisable birds rather than with population-level averages that are typically reported and, secondly, by documenting breeding at natural sites for which few data have been published.

Individually recognisable Ibises at Healesville

Most novel is the description of the variation in mating patterns and breeding parameters of individuals that were followed over three breeding seasons at Healesville, providing deeper insights into the breeding ecology of this species. The species is monogamous: both male and female shared all aspects of nesting and care of young, and the sex ratio was close to parity. There was considerable variation in a range of breeding parameters between individual birds. A significant part of the mature population (16–38% of birds) did not breed in any given year and the number of nesting attempts (including failures) made by individual breeding birds varied from zero to six per year and was larger for males. The number of nesting attempts was correlated between years for individuals, suggesting that this may be related to intrinsic and consistent attributes of the individuals. Beilharz (1988) showed that these individual attributes included dominance status, body weight and age.

The interval between nesting attempts for females, but not males, was correlated with size of the last brood, suggesting that the number of young raised to fledging by a pair is related to the reproductive effort of a female, and that larger broods have a greater impact on the female. Female survival between years was high (97%) and was not affected by brood size so the impact of breeding on the female can be overcome.

Although clutch size was consistent, annual fledging success of individuals varied from zero to nine, modal size was two, and did not vary between years, and was larger for males. Beilharz (1988) suggested that in broods of three the low survival rate of the third chick from starvation provides a clue to the reason for the small number of clutches larger than three eggs. Annual fledging success was correlated between years for males but not for females. 'Younger' adults had significantly lower fledging success than the rest of the Healesville breeding population, indicating that experience has benefits (Beilharz 1988).

Adults had high site fidelity and annual survival which would allow for intimate knowledge of their habitat, weather conditions and possibly attributes of mates.

Banding of nestlings showed that between 16 and 50% of nestlings remain near the Healesville natal site but others travel long distances. Mature-age birds (3+ years) were equally likely to be found near their natal site as away from it (mean distance varied from 131 to 468 km from natal site). Such a mixed strategy of dispersal or philopatry indicates plasticity in the species consistent with that seen in the closely related Straw-necked Ibis *Threskiornis spinicollis* (McGinness *et al.* 2024).

A prominent feature of the mating system of the Australian White Ibis was the frequent change of mates and complexity of the mating patterns. The Single pattern (only a single attempt in a year) was more common for females than males. The Shared pattern (multiple attempts and multiple mates in a year) was the most common pattern for males. The Sole pattern (multiple attempts with the same mate) was more common for males than females (Table 9). The chance of changing or not changing mates was equal when broods failed but the chance of changing increased as brood size increased (Table 12). Length of breeding lag (period from fledging of a brood to laying of

the next clutch) for females was longer if her mate changed mate, and increased with fledging success; this was not seen for males, reflecting the likely greater cost on females than males. There was no significant difference in fledging success before and after a change of mate, indicating that change did not incur a penalty to reproductive output.

Annual fledging success was most affected by the number of attempts made by an Ibis. Individuals with a single attempt in a year were least successful. Those that made more than one attempt in a year were equally successful regardless of their patterns of mate choice except for females in one year. However, in these long-lived birds, 1-year outcomes may not be representative of lifetime success, which would be the ultimate measure. Stochastic events might have occurred in one particular year that could 'average out' over a long time period.

When nesting attempts were pooled for each individual over the three breeding seasons studied, their total fledging success varied with sex and mating pattern (Table 11). Males were more successful than females. Both males and females achieved highest total fledging success by nesting more than once and only with the same mate (Sole nesting pattern).

These patterns are consistent with pair formation being more likely controlled by males than females (Beilharz 1988). Beilharz (1988) found pairs that had previously bred together nested earlier in the season and so their opportunity for multiple broods was increased. There may be other effects that have not been studied, such as competition between females for a favoured male. A key driver of these patterns may be explained by males trading-off maximising the number of breeding attempts in a year versus the possible benefits of pair stability.

Mating system patterns of the Australian White Ibis have not been published before. Historically, studies of the mating system of birds have focused on polygamous, co-operative breeding and lekking species based on the long-held assumption that there is little variation between individuals of monogamous species (Krebs & Davies 1981). More recent studies (Reichard & Boesch 2003; Kvarnemo 2018) have shown that mating systems involving one female and one male can lead to considerable variation in breeding success when the individuals separate after a breeding attempt and recommence breeding with other individuals (so-called 'serial monogamy': Wittenberger 1979). This can occur within the annual breeding season or between years, as was observed in the present study.

Beilharz's (1988) research, undertaken after the current study, documented the structure of a dominance hierarchy among male Ibises at Healesville and its influence on breeding success. Body weight was the major trait contributing to a male's dominance status, and high-status males achieved a higher seasonal reproductive success than did low-status males in two seasons when resources were apparently at low levels. Reproductive success over five consecutive years was largely dependent on survival, but no significant relationships between individual traits and survival were found, possibly because of the short time frame of Beilharz's (1988) study compared with the life-span of this species.

Comparison of Ibis breeding between 'unnatural' and 'natural' sites in this study

At a population level, the ecology of the Australian White Ibis at Healesville was different from that at the two natural sites. At Healesville, Ibises remained present all year but at the other two sites (Coolart and Rhyll) they were absent for periods outside the breeding season. Repeated sightings of individually marked adults near Rhyll, however, indicated that they remained in the general vicinity (if not at the breeding site) over a 5-year period, suggesting that adults had high site fidelity at all sites.

The breeding season at Healesville was earlier and longer than at the other sites. Mean clutch size was larger at Healesville, as also were mean hatching success and fledging success. Fewer nests failed at Healesville. At Healesville, Ibises mainly took high-quality food provided to captive animals supplemented with a relatively small amount of food from human visitors and from the local landfill. Only a minority (~25%) were seen feeding outside the breeding site, indicating the relative importance of the food sources. This may be reflected in their long breeding season, high breeding success, site fidelity and survival at Healesville, which might be anticipated when Ibises breed in human-dominated environments with plentiful food supply. This is consistent with observations at other unnatural breeding sites where the human-dominated environment apparently provides consistent and abundant foraging and habitat resources for ibises (McKinney 2002; Martin *et al.* 2012). To test this assumption, one possible indicator of differences in food supply between the Healesville and Rhyll populations, body weight, was compared. Contrary to expectation based on assumed food supply, female weight during the breeding season at Healesville was lower than at Rhyll. Food quality in urban areas has been shown to be poorer than in rural wetlands (Chard *et al.* 2017, 2018; Coogan *et al.* 2017) but this is not likely at Healesville where the food was specially prepared for highly valued captive animals. Another possibility is that larger clutches and broods and the longer breeding season were placing a toll on the females.

Other differences were found between the sites that may be related to population size: the breeding population at Healesville was increasing (Beilharz 1988), whereas that at Coolart was relatively stable (Lowe 2025). Band recoveries showed that nestlings were more likely to remain near their natal site at Healesville than they were at Coolart.

Delayed breeding age was similar at Healesville and Coolart. Mean age of first breeding at Coolart (for three birds) was 3.0 years. Beilharz (1988) found that the age of first breeding for seven females and seven males at Healesville was either 2 or 3 years old (mean = 3.3 years) and was not significantly different between males and females. There was no evidence of birds first breeding when older.

The rate of recruitment of young birds into the breeding population at Coolart was ~1% in their first breeding year. In contrast, Beilharz (1988) found a rate of recruitment of young birds into the breeding population at Healesville of ~14%.

High rates of dispersal of nestlings, delayed breeding age and low rates of philopatry are consistent with the

population saturation hypothesis (Kokko & Lundberg 2001), suggesting that habitat may be saturated at Coolart but not at Healesville.

Novel data from natural populations in this study

There are only two other published studies of Australian White Ibis breeding in natural situations (Kentish 1999; McGinness & Brandis 2016). Data on length of breeding season in the current study are similar to these other studies of natural populations, indicating that there is only time for one successful breeding event per year. Hatching success at Millewa (McGinness & Brandis 2016) was about half that at Coolart and Rhyll. Fledging success was similar at all sites except for at Rhyll in 1 year, when low success might have been associated with a drought in Victoria (Lowe 1984).

McGinness & Brandis (2016) documented high rates of nest predation whereas in the present study few predation events were observed at Coolart and Rhyll – the major cause of mortality there appears to be low availability of food.

Comparison of urban sites

Data from Healesville can be compared with several other studies of Ibis breeding in urban situations (Murray & Shaw 2006; Corben & Munro 2008; Martin *et al.* 2011; Smith *et al.* 2013a; Willis *et al.* 2024). Timing of breeding varied greatly between the various studies, presumably reflecting differences in food supply in each location. The relatively long breeding season at these other urban sites suggests that birds may be breeding multiple times per year, as they do at Healesville.

Mean clutch size was similar at all urban sites and is consistent with the low variation seen in this parameter at all sites that have been studied. Hatching and fledging success varied widely. Six consecutive years of data were available at Healesville and show that fledging success varied by a factor of two between years. Similar variation may be expected at the other sites, and caution should be used when interpreting the values observed in one season. This variation in fledging success could be affected by a variety of factors, including the characteristics of individuals, such as body condition, dominance status, age and familiarity with the habitat. For example, Beilharz (1988) found that high-status, heavy and old males were particularly successful. Variation in fledging success may also be related to conditions at the breeding site, such as predation, food availability and extreme weather.

Conclusions

Population modelling by Smith *et al.* (2013b) concluded that a fledging rate of 0.5 fledgling per nest annually would result in a stable population of the Australian White Ibis. This rate was achieved at all sites in this study in all years except one. A much higher fledging success rate was observed in Sydney (Corben & Munro 2006; Martin *et al.* 2007; Smith *et al.* 2013a) and at Healesville (this study).

Combined with long breeding seasons, where multiple nesting attempts are possible, Ibis populations in urban areas are likely to continue growing.

In overview, the combined knowledge from the various studies describes a species that is highly successful, has high reproductive output, is long-lived and dispersive. The species' ability to utilise a wide variety of habitat types and food sources supports its breeding expansion into novel locations whilst the overall national population has declined because of the impacts of water use and climate change.

Although aspects of the ecology of the Ibis are documented in the literature, including food availability and quality, disease transmission, movements, genetics and population demography, breeding ecology has been documented at only a few sites and over a few years. Even fewer of these data are for populations in natural settings, where more work is needed to provide greater clarity about the future for the species in these areas. A significant focus of public interest has been channelled towards the perceived pest status of the Ibis in some urban areas (Martin *et al.* 2007; Smith *et al.* 2013a). Understanding by the public of the species' status across its range and, in particular, declines away from the urban population centres remains patchy (McKiernan & Instone 2016; Allatson & Connor 2018). Recognition amongst the community that urban populations are likely refugees from their historical breeding sites and that seemingly isolated populations may continue to be in contact (Smith *et al.* 2013a; Davis *et al.* 2021) seems to be growing. There remains a continuing need to monitor samples of the variety of populations if only to be confident that the perception that this is a pest species that continues to expand its range and population size is evidenced.

The Ibis is amongst the most well-studied native birds in Australia but the knowledge base is much less robust than that for many species in the Northern Hemisphere. The advent of new and less expensive technologies such as electronic trackers and genetic analyses provides new opportunities to enhance our knowledge. Combined with the large potential of volunteer bird observers, citizen science and data capture through hand-held digital devices, improved conservation outcomes for the species could be achievable. One area that needs more attention is development of purpose-driven campaigns focusing on this species to harness this potential and there are good prospects in this regard through community-driven organisations.

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