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THE BREEDING BIOLOGY OF THE INTERMEDIATE EGRET
PART 2: PARENTAL BEHAVIOUR AND NESTING INVESTMENT BY THE MALE AND FEMALE

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Data are from four nests observed prior to incubation and a different two from incubation through chick independence. The breeding male Intermediate Egret is estimated to spend 22 per cent more time at the nest than the female, due to him spending twice as long there during pre-incubation, on average. The sexes made the same number of feeding visits, but the two males regurgitated 15.2 and 8.0 per cent more food boluses than their females. The male's high level of pre-incubation nest attendance, while sometimes less than 100 per cent, is seen as a necessary defence against cuckoldry and nest stick theft. The single chick was brooded and guarded longer than the brood of two. At both nests feeding sessions became significantly shorter after the chicks converted fully to direct feeding.

INTRODUCTION

Biparental care of the young is normal practice among ardeids (see species reviews in Hancock and Kushlan 1984), but there is little information on the investment of time and energy by the sexes in their brood. Gladstone's (1979) prediction of nearly equal parental investment by male and female monogamous, colonially nesting birds is supported for ardeids by Werschkul (1982) in his study of the Little Blue Heron *Egretta caerulea* and Van Vessem and Draulans (1986) in their study of the Gray Heron *Ardea cinerea*. Werschkul did not, however, measure investment beyond incubation, and neither study compared the amount of food brought to the nest by the sexes.

This study of the Australasian subspecies of the Intermediate Egret *Egretta intermedia plumifera* followed nesting events from nest building to independence of chicks. The use of marked parents of known sex and marked young allowed a comparison of the parental behaviour of the sexes and their individual contributions to rearing the brood and to feeding each chick. The development, behaviour and food intake of the chicks are described in Part 1 (McKilligan 1990a).

METHODS

Two Intermediate Egret nests (Nest 1 and Nest 2) were observed from the completion of their clutches until the fledged young left the heronry, spanning 19 November 1987 to 23 February 1988. At a different heronry, in 1988, three nests (3, 4 and 5), were observed from about 0600–1800 h on each of 11 and 13 November and one (Nest 6) on 13 November only, to gather data on pre-incubation behaviour. The adults at Nests 1, 2, 3 and 4 were uniquely marked by propelling a missile soaked in acrylic paint on to their plumage using a blowpipe from a hide. This procedure only distracted them momentarily. The adults at Nests 5 and 6 were identified by colour differences and loral marks. Other aspects of the methods are described in Part 1.

Three adults attended Nest 1 initially. They were sexed as a male and two females, the male being identified by his longer scapular plumes and stick-collecting behaviour (Blaker 1969a). This possible bygyny is described by McKilligan and McConnell (1989). Only the male and the primary female incubated and remained past incubation. Nests 2, 3, 4, 5 and 6 each had a male and female who were sexed from their positions in copulation.

Nest 1 hatched all four of its eggs, with the fourth chick dying at about two days and the third disappearing between 12 and 14 days. Nest 2 hatched two out of three eggs, but Chick 1 disappeared aged four to nine days. By the end of observation of Nests 3, 4, 5 and 6, only Nest 4 had an egg, laid on the second day. Subsequently each of these four nests hatched a chick(s).

RESULTS

Breeding plumage and skin colours

All adults had well developed scapular and pectoral plumes and elongated crown and nape feathers which could also be raised. There was no sign of a post-nuptial moult towards the end of the nesting season, as in the Cattle Egret *Ardeola ibis* (McKilligan unpub. data). The basal three-fifths of the bill was red during laying and incubation, and the tip yellow. The red areas gradually became maize-yellow then orange-yellow by the time the chicks were three weeks old. The initially blue-green lores and circumorbital skin faded more slowly but were all yellow when the chicks fledged at about six weeks. These breeding colours of bill and lores were progressively replaced by small scattered patches of yellow. The iris was red with a yellow inner margin in prelaying birds and all yellow in those with full clutches. It became a distinctly paler yellow by the nestling stage. The prelaying bird had a red tibia, red and black tarsus and blackish toes, except for one which had predominantly red legs and toes. The red changed to yellowish and the black to brown during incubation. Small differences in colour between egrets did not appear to be sex-related.

Nest building

The male brought all the sticks to the nest and gave them to his female who placed them, except for two placed by him. She used a 'tremble-shove' (Blaker 1969b) action to insert them into the nest. He collected these dead sticks from the ground (in 1987) and water (1989) close to the nest tree. Nest 3 was initially only half-built and received 50 sticks over two days. The other nests received 0 to 18 sticks per day during prelaying and laying. Advanced chicks and adults brought a few sticks to their nests from nearby abandoned Cattle Egret nests.

Copulation

Of the ten intrapair copulations recorded, three were at the half-built Nest 3, two at Nest 2 with two and three eggs and one each at Nests 4, 5 and 6. Eight copulations occurred within 30 minutes of the female's return to the nest and two after 100 minutes had elapsed. The male of Nest 2 attempted extrapair copulation once on both the female and the male in Nest 1. Each 'victim' struggled under the intruder, apparently thwarting the attempt. The Nest 2 male had a complete extrapair copulation with a female at a more distant nest while her mate was searching for a nest stick. On several occasions the males of Nests 2 and 4 flew from their nest tree to circle over or perch within a few metres of the unattended female at Nest 1. She responded by either sitting on the nest or threatening the approaching male.

Time investment by the sexes

Pre-incubation. In Nests 3, 4, 5 and 6 males attended the nest from 67–100 per cent ($\bar{x}$ = 82.4%) of the day and females 14.7–63.4 per cent ($\bar{x}$ = 42%) (Table 1). The female was left unattended at Nests 3, 4 and 5 for up to 33 per cent of the day.

TABLE 1

Attendance at the nest by the sexes of Intermediate Egret during pre-incubation as a percentage of observation time (Nests 3, 4, 5 and 6).

	% Attendance at nest			
	3	4	5	6
Male	72.8	70.7	94.8	100.0
Female	63.4	31.9	44.5	14.7
Observation time (mins)	1 442	1 442	1 442	720

Post-incubation. Both the male and female at Nest 1 attended until the two surviving young became independent at 9–10 weeks and at Nest 2 at least until its surviving chick fledged, after six weeks. There were no obvious sex-related differences in nest attendance from incubation onwards, with the overall attendance of the male slightly exceeding the female's in Nest 1 and vice versa in Nest

2 (Table 2). Gross differences between Nest 1 and Nest 2 in the attendance percentages for the 3–7 week stage partly come from more prolonged guarding at Nest 2, but also from the disproportionate allocation of observation time at Nest 2 to the early weeks of this stage.

Incubating, brooding and guarding behaviour

There was some overlap in nest attendance during early incubation when the male brought nest sticks to the female or simply stood by the nest, but thereafter the mates spent no more than a minute or so together, at the change over. The male and female turned/moved the eggs with about equal frequency (three times each in Nest 1, and male 9 times and female 13 times in Nest 2), with 11 turns recorded in Nest 2 in one day.

The adults of each sex protected their chick(s) from the elements (brooded) by sitting and entirely covering it, to 12 days old, and then crouching over it with wings drooped and held out somewhat. Up to 19 and 20 days old the chicks in Nest 1 were protected thus in the early morning, when it rained and when the wind blew strongly. Brooding continued intermittently with the chick in Nest 2 until it was 26 days old. When it was hot adults and chicks fluttered their gular membranes.

Nest attendance by adults when not feeding or brooding is termed 'guarding' and was seen first when the adult stood on its nest beside the chicks aged 8-12 days during the warmer part of the day. It spent longer standing or sitting on the nest beside 19- or 20-day old chicks, and as they grew larger and more importunate in their food begging, it perched up to 6 m from the nest. All-day guarding was not seen at Nest 1 after the chicks were 19 and 20 days old and at Nest 2 after the chick was 24 days old. The former two were guarded for part of the day at 25 and 26 days old but not thereafter, whereas the single chick at Nest 2 had an adult in part-time attendance for several hours of the day until it was at least 37 days old.

The Intermediate Egret defended its nest against too close an approach by Cattle Egrets and once against a Brown Goshawk *Accipiter fasciatus* which landed a few metres away. In the latter instance the male egret flew from its distant perch to crouch over its 29-day-old chick with its plumes raised and wings partly extended, uttering a throaty 'kroo-kroo . . .', each 'kroo' lasting approximately 1.5 seconds. This alarm (or threat) call was similar to, but less prolonged than, the alarm 'kreow' of the Cattle Egret. The Goshawk flew off after a minute or so without incident.

TABLE 2

Attendance at the nest by the male and female Intermediate Egret from incubation through fledging, as a percentage of observation time (Nests 1 and 2).

	% Attendance at each stage			
	Incubation	Nestling (<3 wks old)	Brancher (>3 wks, <7 wks)	Post-Fledging (>7 wks, <10 wks)
Nest 1				
Male	64	45	9.4	1.1
Female	43	55	3.7	0.7
Observation time (min)	1 858	2 430	3 835	867
Nest 2				
Male	58	48	33	—
Female	53	52	29	—
Observation time (min)	3 300	2 980	987	—

Feeding behaviour

Feeding visits occurred from 0555 h to 1825 h, with more in the morning than after 1200 h (23 v. 16 at Nest 1 and 8 v. 2 at Nest 2) for the all-day observation sessions.

When feeding young chicks the parent stood on the nest with its head lowered to hold its bill almost vertically downwards, so that its tip was close to the nest, just in from the edge. After the chicks were about ten days old, the adult held it's bill progressively higher and angled it less steeply.

At both nests the adults regurgitated within a few minutes of walking on to the nest and, at Nest 1, delivered their food boluses over periods ranging from 1–83 minutes. The duration of feeding sessions fell dramatically once the adults stopped all-day guarding, reducing from a mean value of 26 minutes with chicks up to 20 days old ($n = 14$, $SD = 21$) to 6.4 minutes from 25 to 48 days ($n = 26$, $SD = 3.7$) (Welch's test, $t = 3.44$, $P < 0.01$, $v = 13$).

TABLE 3

Food delivered by male and female Intermediate Egret parents to chicks in Nest 1 and Nest 2 (per day for chicks aged to 48 days in Nest 1 and to 24 days in Nest 2, but from the sum of shorter observation periods thereafter).

Ages of chicks (days)	Number of feeding visits (regurgitates) by male	by female
Nest 1		
6,5,2	2 (11)	2 (7)
12,11,8	2 (16)	2 (12)
20,19	3 (6)	2 (7)
26,25	2 (9)	4 (9)
34,33	3 (8)	4 (10)
40,39	2 (8)	4 (11)
48,47	4 (6)	3 (6)
52–69	5 (12)	2 (4)
TOTAL	23 (76)	23 (66)
Nest 2		
4,2	1 (3)	1 (3)
10	2 (9)	1 (4)
16	1 (6)	1 (9)
24	2 (3)	1 (3)
29–51	2 (6)	4 (6)
TOTAL	8 (27)	8 (25)

Feeding investment by male and female

Each sex made an equal number of feeding visits (range 2–5 per day) at both nests, but the males regurgitated more food boluses than their mates (15% more at Nest 1, 8.0% at Nest 2) (Table 3). The two males reingested uneaten food after five regurgitates and the females after ten. Daily variations in food delivered by the male and female did not form any obvious pattern. The larger daily amounts of food delivered to Nest 1 correlated with the larger brood in this nest (McKilligan 1990b).

The distribution of food by each parent among the chicks was assessed from the number of boluses the chick ate from and, more accurately, from a score based on an estimate of how much of the bolus a chick received, in which six points were given for a whole bolus and 5–1 points for portions of a bolus (Table 4). In Nest 1, Chicks 1 and 2 received similar scores when feeding on regurgitates from the male and female parent, but Chick 3 did better with the male's, in that it fed from 28.3 per cent of the male's boluses securing 27 per cent of the food in these, compared with 18.9 per cent of the female's boluses and 20.4 per cent of their food.

TABLE 4

Distribution of food among Intermediate Egret chicks in Nests 1 and 2 by the male and female parents (see text for method of calculating the feeding score).

Age of chicks (days)	Bolus delivered by:	No. of boluses eaten from and (feeding score) Chick 1	Chick 2	Chick 3
Nest 1				
2–12	Male	18 (43)	20 (65)	15 (40)
	Female	17 (40)	13 (42)	7 (21)
2–62	Male	48 (229)	44 (197)	—
	Female	38 (165)	38 (177)	—
Nest 2				
2 and 4	Male	2 (6)	2 (6)	
	Female	2 (6)	2 (6)	
2–30	Male	—	27 (156)	
	Female	—	25 (138)	

DISCUSSION

The male Intermediate Egret spent about twice as much time at the nest during the pre-incubation period as the female, on average. The sexes shared incubation, brooding and guarding the young approximately equally. Thus, overall, the male may spend about 22 per cent more time at the nest than the female (assuming a pre-incubation period of ten days). By contrast, van Vessem and Draulans (1986) found about equal nest attendance by male and female Gray Herons *Ardea cinerea*, averaged over the season. They counted the male as absent when on prolonged stick searching, however, whereas in the present study all stick searching is counted in with nest attendance. The latter approach seems more appropriate in a study of nesting investment.

In calculating the energetic investment in breeding by the sexes, Werschkul (1982) found that the food energy foregone by the male Little Blue Heron in pre-incubation nest guarding exceeded the female's greater energy investment in gametes by a factor of 2 or 3, so that the male's investment was much greater than the female's up to hatching. This seems likely to apply also to the Intermediate Egret. The male Intermediate Egrets' food provisioning of chicks was 8 and 15 per cent greater than their females', and if this is a real difference, it would further shift the energy cost of parental care on to the male.

Van Vessem and Draulans (1986) found greater variation in nest attendance between pairs than within pairs, and this and the small number of nests observed requires the results of the present study to be interpreted with caution. Nevertheless, the male Intermediate Egret does appear to spend more time at the nest than the female. This sex difference in time investment seems an inescapable consequence of the male's high level of nest attendance at pre-incubation, most probably aimed at guarding his female against extrapair copulation when she is at the nest and preventing stick theft while she is absent. Extrapair copulation was observed in this study and it may be that, as in the Cattle Egret (McKilligan 1990a), it can potentially increase or decrease a male's breeding success by a significant amount. The possibility that the female Intermediate Egret's breeding behaviour is adapted to exploit the male (Krebs and Davies 1984, p.267) by her contributing less food for the chicks deserves further study.

As in other bird species (O'Connor 1984), the smaller Intermediate Egret brood was brooded longer than the larger one. This single chick was also guarded (intermittently) for a longer period, possibly because its food needs were more easily satisfied than those of two chicks, leaving the parents with time to spare.

The third chick in Nest 1 fed from fewer of the boluses and received a lesser share of the food provided by the female than from its male parent. This inequality occurred during indirect feeding, however, and thus seems unlikely to result from a bias by the female against feeding this chick.

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BOOK REVIEW

Taronga Zoo's Guide to the Care of Urban Wildlife. Erna Walraven, 1990. Allen & Unwin Australia Pty Ltd. 157 pp., rrp $19.95 paperback, $24.95 hardback.

Erna Walraven is the wildlife rehabilitation officer at Sydney's Taronga Park Zoo. Apart from her personal expertise and qualifications in this area, she has been in the enviable position of being able to draw upon the wealth of knowledge possessed by her colleagues to compile this guide.

The seven chapters are written in an easy to read format which explore just about all of the needs and problems facing native fauna in the urban environment. The book is packed with useful information the average person will find helpful in understanding the environmental needs of wildlife and how to modify the existing environment to better suit and attract native species. The book also provides extensive, but very basic, information on first aid and short-term care of sick, injured and orphaned animals. I am pleased to note that the author does point out that in the interests of any animal rescued, the assistance of experienced foster carers should be sought at the earliest opportunity.

The guide is nicely rounded-off with a number of appendices which provide information on legal obligations and telephone numbers and addresses of State and Territory fauna authorities, organizations involved in wildlife rescue and rehabilitation and of suppliers of various products mentioned in the text. Finally, a useful list of other references is provided, under various sub-headings, for those who may wish to further their knowledge after whetting their appetite with this book.

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