

THE BREEDING BIOLOGY OF THE INTERMEDIATE EGRET. PART 1: THE PHYSICAL AND BEHAVIOURAL DEVELOPMENT OF THE CHICK, WITH SPECIAL REFERENCE TO SIBLING AGGRESSION AND FOOD INTAKE

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The development and behaviour of marked chicks in two broods of the Intermediate Egret *Egretta intermedia plumifera* are described. Incubation was 26 (± 1) days, the chicks flew at six and seven weeks old, and were fed at the nest until about ten weeks, when they left the heronry. The rate of food bolus delivery to the nest was greatest when chicks were 8–16 days old but the frequency of feeding visits increased after brooding finished (chicks older than 20 days). About twice as much food was delivered to the nest with twice as many chicks. Feeding success was directly related to age and to success in fights among three siblings to 12 days old. Older siblings seldom fought and had about equal feeding success overall. Aggressive and begging displays which may enhance feeding success are described.

INTRODUCTION

The breeding biology of the Intermediate Egret *Egretta intermedia* is known only from a partial description of its breeding displays (Blaker 1969a) and fragmentary pieces of information summarized in Ali and Ripley (1968), Cramp and Simmons (1977), Hancock and Elliot (1978) and Brown *et al.* (1982), which refer to *E. i. intermedia* and *E. i. brachyrhyncha*. These observations of the subspecies *E. i. plumifera* in eastern Australia extended from the completion of the clutch to the independence of young at two nests where each adult and chick was uniquely marked. They describe the chick's growth, pterylosis, skin colours, and the development of locomotory, agonistic, vocal, comfort and feeding behaviours. Each chick's share of the food brought to the nest was estimated. The parental behaviour and nesting investment of the adults are described in Part II (McKilligan 1991).

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. These nests were in a heronry near Gatton in south-east Queensland (described in McKilligan

1985), in which the Great Egret *Egretta alba* and, predominantly, the Cattle Egret *Ardeola ibis* also nested that summer.

The chicks in both nests were distinguished by ink or paint marks on their plumage until about 20 days old, when a numbered patagial tag was attached to each wing. Up to about three weeks old, or their earlier death, the chicks were weighed and their culmens and tarsi measured at least every second day for chicks in Nest 1 but less frequently for those in Nest 2. Chick 1 of Nest 1 was measured opportunistically when 40 days old.

Observations of the nests were made from a hide on a platform which was initially 3.5 m high but was raised to 5.5 m after 19 days to allow Nest 2 to be observed also. The nests were each 4 m above the ground and were about 5 m (Nest 1) and 7 m (Nest 2) from the front of the hide. Observations were made at least once a week, and during the hatching to fledging (Nest 1) and hatching to 4 week old chick (Nest 2) stages they continued from about 0530–1900 h (sunrise + 30 mins to sunset + 30 mins). At earlier and later breeding stages the observations ranged from one to 11 hours in duration. Total observation time was 153 h.

A complete record was attempted for food ingestion by chicks at both nests and for begging and aggressive interactions among chicks in Nest 1. Feeding events were voice taped and transcribed at the end of the feeding session. Behaviour other than feeding was written down as it occurred. The limits to the precision of the chronology obtained for the age of onset of different behaviours were set by the intervals between observation days and by the spread of chick ages.

RESULTS

Two eggs were broken by accident in Nest 1 and replaced by two of about the same age. The incubation period was determined accurately only for Egg 3 in Nest 2 and was 26 (± 1) days. The four eggs in Nest 1 and two of the three in Nest 2 hatched. One of Nest 2 was pecked into by the adult when it was splashed with yellow paint in an attempt to mark this bird. The parent then threw the broken egg out of the nest. Chicks 1 and 2 of Nest 1 and Chick 2 of Nest 2 survived to leave the heronry between 69 and 75 days, 68–74 days and 62–70 days, respectively. Chick 3 of Nest 1 disappeared between 12 and 14 days old, and Chick 4 was found dead in the nest aged about two days. Chick 1 of Nest 2 disappeared between four and nine days.

Chick Growth

The body weight growth curve among the surviving three chicks suggests a sigmoid form, while the rates of increase in lengths of culmen and tarsus appear more linear over this 20–24 day period (Figs 1, 2 and 3). Judged by the measurements of one chick at 40 days, the rate of growth slowed considerably between 20 and 40 days in each of the three parameters.

All three non-surviving chicks were lighter just before their death/disappearance than were the surviving ones when at the same age. Chick 3 of Nest 1 started to lose weight about four days before it disappeared, and this was accompanied by a slowing in the growth of its culmen and tarsus. All chicks had infestations of the larval stage of the tick *Argas robertsi* and may also have been fed on by the nymphal and adult stages of this tick.

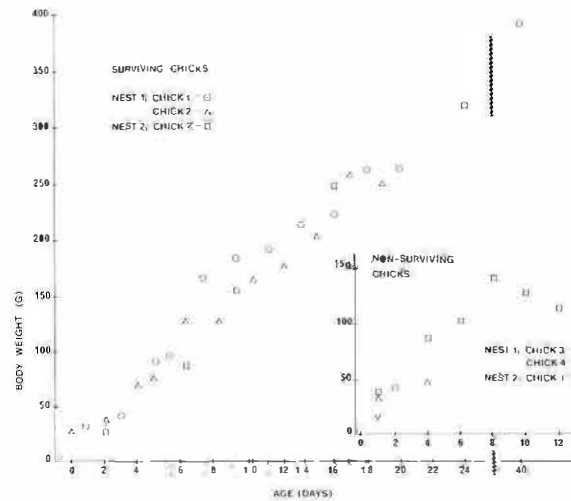


Figure 1. Growth in body weight of surviving and non-surviving chicks.

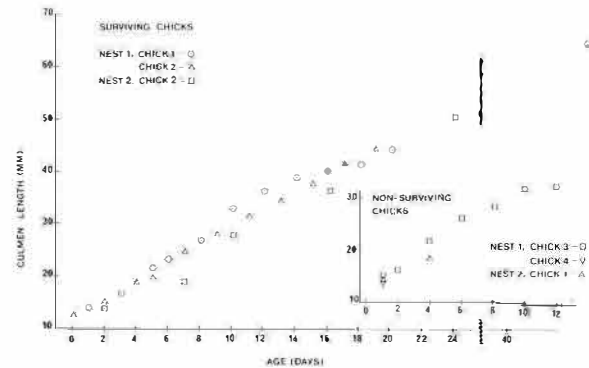


Figure 2. Growth in culmen length of surviving and non-surviving chicks.

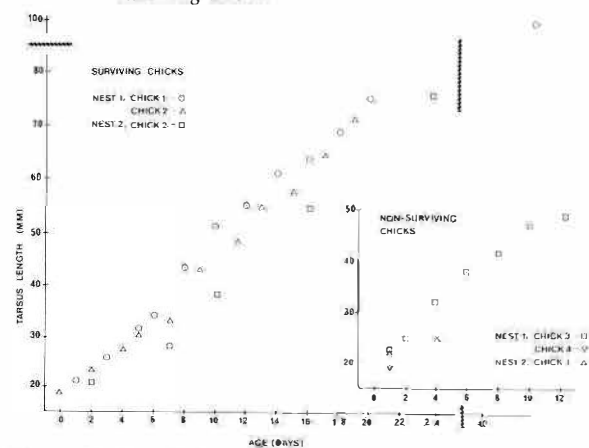


Figure 3. Growth in tarsus length of the surviving and non-surviving chicks.

Plumage and Skin Colours

In this and subsequent sections where among the (surviving) chicks there is some variation in the age at which a physical or behavioural feature was first observed, the youngest age is usually given.

The chicks have down feathers on hatching. Pin feathers first appear on the spinal, ventral, humeral and wing feather tracts at four days of age and on the capital and femoral tracts at six days (Figs 4 a and b). The pin feathers first start to unsheath on the humeral tract at eight days and on the others at ten days, except for those on the capital and upper spinal tracts, which unsheath at 12 days. Two powder down patches appear at 17 days on the rump flanking the preen gland. By 24 days of age a second pair of ventral feather tracts develop lying parallel with and medial to the first. By this age the chicks appear well feathered, but filoplumes still protrude through the head feathers at 40 days.

The bill is initially yellow with a dark margin to both mandibles and in some a brownish subterminal smudge across the upper mandible. By ten days the mandible between the nares and lores also has become brownish. This colour pattern remains through fledging but with proportionately smaller areas of brown on the now orange-yellow bill. The lore is yellow or yellow-green throughout the chick stage. The circum-orbital skin is brighter yellow than the lore. The iris goes from yellow-white at hatching to pale yellow in the first week. The palate and tongue are dark brown, but the rest of the buccal skin is pinkish at first, becoming purplish by ten days. The skin of the body and leg is olive-green except for a yellowish rump, tarsal joint and posterior tarsus. By 14 days the tibia and under toes have become a paler green than the rest. The tarsal joint, posterior tarsus, tibia and under toes are green or grey-green by fledging, whereas the anterior tarsus and upper toes have darkened to blackish.

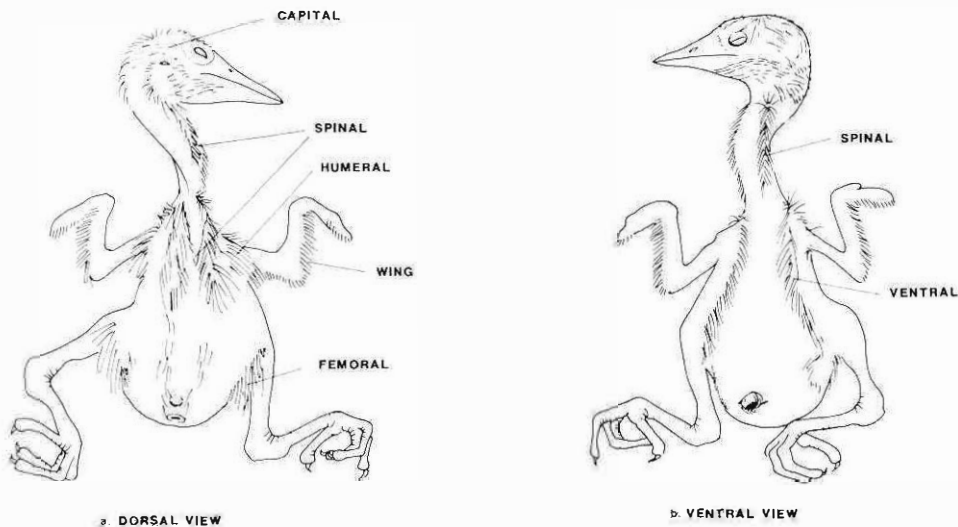


Figure 4 a and b. Dorsal and ventral views of the eight day old Intermediate Egret chick drawn from photographs.

Locomotory Development

The chick could shuffle around the nest on its tarsi at two days, but this was limited to small relocations and reorientations required in feeding. From 12 days it could stand on its digits, and it walked, unsteadily, at 17 days. Chick 2 of Nest 1 walked onto an adjacent vacant nest at 24 days, and by 33 days it was climbing onto nearby branches using its bill and feet to haul itself up. Chick 2 of Nest 2 did not leave its nest until 37 days old, possibly because of its awkward location in a fork of a tree.

Dual wing flapping (Wing Exercising, O'Connor 1984) took place as soon as the chick could stand and became more prolonged and vigorous when it was able to perch in a less confined situation away from the nest. Chick 2 of Nest 1 progressed to flapping while it jumped between branches at 39 days and flew 4 m at 42 days. Its sibling flew between 48–53 days and the chick in Nest 2 flew between 37–45 days.

As their locomotory skills developed the chicks spent progressively less time in the nest, preferring to perch up to 4 m away on a branch or an abandoned Cattle Egret's nest. Their first flights were to the ground, where they searched for food, and to nearby trees, and then to a lagoon 80 m away.

Voice

When begging the young Intermediate Egret chick gave a high pitched, repeated sing-song 'chi-chi' call, which became a lower pitched 'cro-cro' or 'khe-khe' as it became older. The rate of calling sometimes decreased as the feeding session continued, in older chicks at least.

In greeting its sibling, a chick returning to its nest gave a throaty 'kroh', which is repeated more slowly (at about 2 per second) than the begging call. The threat call given to an intruding bird is similar but harsher. On stabbing with its bill towards an antagonist, the young chick gave a single sharp 'chee' and the older one a duller 'thok', with each stab.

Comfort Behaviour

The four-day old chick preened the pin feathers of its ventral tract, and at six days preened its back and underwing feathers. At 47 days it rubbed the side of its head in the vicinity of a powder down patch and then onto its wing feathers, and at 52 days it nibbled its preen gland.

Scratching took place from 17 days onwards, with the toes being vigorously moved up and down against the side of the head as the bird stood. While standing, from 12-days old, the chick fully extended one wing laterally and then the other (sideways stretch). At 16 days it raised its unfolded wings until they almost touched above its back and tilted its body forward with head outstretched to hold this position for roughly ten seconds (upward stretch). This 'bowing' action would stretch the upper wing, neck, body, and legs simultaneously. From 26 days the leg and wing on the same side were extended posteriorly but not the rectrices.

From six days old the chicks gular fluttered when it was hot. Defaecation was recorded once per day per chick for chicks aged 11–43, except on one day for one chick when it may have been overlooked. The faeces was directed over or onto the edge of the nest.

Agonistic Behaviour

Overt aggression mostly comprised a hard stab with the bill at the head of another bird. Chicks occasionally fenced bills and frequently grabbed one another's bill, but the latter usually appeared to be part of the begging display, and neither action is counted as being aggressive here unless it resulted in withdrawal of one of the combatants.

Between five and 12 days old the chicks in Nest 1 gave an aggressive display in which a bird raised its body, fully extended the neck vertically and directed its downwards inclined bill towards a sibling (Stiff Necked Upright Display, Meyer-riecks 1960); the latter sometimes returned the display. Such a confrontation ended after a few seconds with one of the birds lowering its head and facing away with closed or half-closed eyes, sometimes after receiving a single hard peck from the other. Older chicks were not seen giving this display and only twice pecked one another. They did however, jockey for the centre position on the nest.

When left unguarded, from about 21 days old, the chicks threatened the parent as it returned to the nest. In this, their heads were held low and bills stabbed horizontally towards the parent, wings lifted from their sides, the crown feathers raised and splayed in a central parting, and the upper

breast and back feathers raised (Forward Display, Meyerriecks 1960). Between stabs they lowered their wings and gave a series of hoarse croaks. This display was also given to other intruding birds. Chicks from four to ten days old stabbed at the observer. From about ten to 20 days old they cowered, but when older attempted to escape.

Of the 48 aggressive encounters among chicks in Nest 1, 46 were when there were three in the nest, aged 2–11 days, and only two were between the surviving Chicks 1 and 2, aged 40 and 48 days. On the day the chicks were six, five and two days old, all three interacted aggressively, whereas at 12, 11 and eight days of age only the younger two did so. Chick 1 won all of its 35 'fights', four of them by display only, while Chicks 2 and 3 won ten and three respectively (Table 1). On at least four occasions Chicks 2 and 3 initiated fights with an older sibling. Eighty-three per cent of these fights occurred outside feeding bouts (defining a bout as a period of continuous begging).

Food and Feeding Behaviour

Some food items were identified as they were being ingested by the chicks and others when the chicks regurgitated them while being handled for measurement. For chicks aged four to 24 days, these comprised five dragonfly nymphs, one cricket, two grasshoppers, three frogs, 13 skinks and three fish. The adult regurgitated food boluses, all of which were eaten indirectly (i.e., off the nest) by chicks up to six days old. Chicks took some items directly from the end of the parent's bill at eight days and had converted entirely to feeding from the parent's gape by 18 days. In Nest 1 Chick 1 stole large food items from the bill of Chick 3 when they were six and two days old respectively.

The chicks jockeyed for a good feeding position between the parent's feet, orientating out towards the edge of the nest and the parent's lowered bill. They gaped and pecked with closed mandibles at the back of the parent's bill, and by two days were mandibulating its end. As they seized the bill further up they initially held it between their mandibles in an over-and-under grip. The chicks seemed unable to maintain this hold for more than a few seconds and their bills then slid down and off the end of the parent's in a stroking action. From six days old the chicks were seen

TABLE 1

Outcomes of fights among chicks 1 (C_1), 2 (C_2) and 3 (C_3) in Nest 1. The first mentioned chick of the dyad appeared to initiate the fight. Outcome of fight refers to first mentioned chick.

Ages of Chicks (days)		C_1	C_1	C_2	C_2	C_3	C_3
		v	v	v	v	v	v
		C_2	C_3	C_1	C_3	C_1	C_2
6, 5, 1	Win	24	7	0	1	0	3
	Lose	0	0	1	0	2	1
12, 11, 8	Win	0	0	0	8	0	0
	Lose	0	0	0	0	0	0
40+	Win	1	—	0	—	—	—
	Lose	0	—	1	—	—	—

repositioning their hold from over and under to grasping the sides of the parent's bill (Scissoring, Mock *et al.* 1987), and by 11 days they were applying this sideways grip to the top of the parent's gape overlapping the lores. This was the pole position and to dislodge it, the other chick tried to gain a higher hold over the parent's lores and eye.

Begging behaviour also involved erratic nodding and shaking of the head with the neck flexed. A chick often held one or both partly unfolded wings level with its back and sometimes flapped them alternately. At least in older chicks (from 30 days) the feathers of the crown and nape were erected and parted mid-dorsally as in aggressive display. When the adult put its bill out of the chick's reach by raising it or, with older chicks, walking off the nest 30 cm or so, a chick often seized another's bill. Less frequently, up to 12 days old, they sometimes seized the adult's lower leg or toe, or the head or wing of a sibling, or pecked at or fenced bills with a sibling. No food was gained by such behaviours, and these and begging displays ceased when the adult commenced brooding or moved a metre or more off the nest.

Food Intake

The chicks in Nest 1 were fed 4–5 ($\bar{x}=4.3$, $n=3$ days) times per day to 20 days of age when brooding ceased, and then 6–7 ($\bar{x}=6.5$, $n=4$ days) times per day to fledging after which all day observations finished. At Nest 2 the chick(s) was fed three times per day up to 24 days old ($n=4$ days). The number of food boluses delivered were readily counted until the chicks fed from the top of the

parent's gape when the only indication of bolus transfer was a series of rapid jerking pulls by the chick on the parent's bill. From 12 to 28 boluses were regurgitated per day at Nest 1 ($\bar{x}=18$) and from six to 15 at Nest 2 ($\bar{x}=10$) (Table 2), with from one to nine ($\bar{x}=3.6$) boluses per adult feeding visit. Most boluses were brought to Nest 1 when the chicks were 8–12 days old and to Nest 2 when its chick was ten and 16 days. Uneaten food was reingested by the parent from Nest 1 after three regurgitates and from Nest 2 after 12 regurgitates, eight of them given to the ten day old chick. This surviving ten day old chick in Nest 2 did not beg on the first arrival of an adult to feed it. The adult regurgitated a bolus and then reingested it when the chick continued to show no interest.

It was possible to roughly compare how much food each chick ingested by awarding a score of six for each whole bolus won and from 5–1 points for parts of shared boluses. This ignores reingestion by the adult and the fact that some boluses were noticeably smaller than others. At one and two days old the chicks' food intake scores ranged from 12–14 (Table 2); however, Chick 3 of Nest 1 would have scored about as high as its six and four day old nest mates (ca. 36 points) had Chick 1 not stolen food from it. From five to 47 days old

the chicks' feeding scores ranged from 32–90 points per day. While there were considerable differences in the daily food scores of Chicks 1 and 2 of Nest 1, their total scores to fledging were very close (358 and 340 respectively). When aged 52–69 days, Chick 2 spent more time away from the nest tree than Chick 1 and missed three of the eight recorded feeding sessions, with Chick 1 gaining a score of 72 and Chick 2 only 36 points from these.

The number of times each chick in Nest 1 seized its parent's bill during feeding was recorded as fully as the flurry of activity then permitted. Among the three chicks at 6, 5 and 2 days old, the oldest seized 70 per cent of the time, but when they were 12, 11 and 8 days, these frequencies were 48, 31 and 21 per cent respectively, and by 20 and 19 days of age the two surviving chicks had similar bill seizing frequencies (Table 2). By the ages of 20 and 19 the elder was only 6 per cent heavier than its nest mate compared to a 19 per cent body weight advantage when they were 12 and 11 days old.

As the chicks grew larger, and better able to hold onto the parent's bill, the number of bill seizures per day decreased to 25 per cent of their greatest number, and about half of the seizures then yielded a regurgitated bolus.

TABLE 2

Feeding data for Nest 1 and Nest 2 calculated per full day of observation.

Chick ages (days from hatching)	No. of feeding visits	No. of boluses regurgitated	No. of reingestions by parent	Feeding Score (Number of bill seizures)		
				Chick 1	Chick 2	Chick 3
<i>Nest 1</i>						
6, 5, 2	4	18	2	56(28)	36(8)	14(4)
12, 11, 8	4	28	0	57(59)	75(38)	47(26)
20, 19	5	13	1	38(37)	40(41)	chick missing
26, 25	6	18	0	41(27)	67(28)	—
34, 33	7	18	0	66(19)	42(18)	—
40, 39	6	19	0	66(14)	48(10)	—
48, 47	7	12	0	34(15)	32(10)	—
Mean daily rate	5.6	18	0.4	54.8	48.6	30.5
Mean hourly rate	0.42	1.35		Mean No. of chicks fed = 2.29		
<i>Nest 2</i>						
2, 1	3	6	3	12	12	
10	3	13	8	chick missing	78	
16	3	15	0	—	90	
24	3	6	1	—	36	
Mean daily rate	3	10	3	12	54	
Mean hourly rate	0.22	0.75		Mean No. of chicks fed = 1.25		

DISCUSSION

The growth in weight of the surviving chicks of this study was closely similar to that of tick-free chicks in a subsequent, unpublished, study, whose weights at 20 days ranged from 208–285 g. Tick infestation may therefore not have depressed growth in these chicks, although it may have contributed to the loss of their siblings. Weights of Intermediate and Cattle Egret chicks are also very similar over the first 20 days, comparing the present data with those of Siegfried (1973) and my unpublished observations on the Cattle Egret. The tarsus and culmen of the Intermediate Egret grow faster than those of the Cattle Egret, however, reaching lengths of about 75 and 45 mm in the former species and 60 to 38 in the latter at 20 days. This allometric growth of Intermediate Egret appendages is expected, given the differences between the adults of these species.

From a larger sample of Intermediate Egret chicks than that available to this study, Maddock (1989, pers. comm.) described beak colours from all-yellow through yellow-black to all black. His chicks of about three weeks and older had black palates, and the one with the black bill had black lores.

In the Intermediate Egret underwing preening first occurred about 12 days earlier than in the Cattle Egret (Blaker 1969b), but the chronologies of other comfort behaviours were similar. The ritualized aggressive display used by the young Intermediate Egret chick, but not seen in the adult, seems identical to the Stiff-necked Upright Display of the adult Green Heron *Butorides virescens* (= *B. striatus*) (Meyerriecks 1960). This display may have its antecedents in the upright posture assumed during fights by the chicks of some other herons (Blaker 1969b; Wershkul 1979). In the Intermediate Egret a younger sibling sometimes attacked an older one, whereas this is said not to happen among Cattle Egret siblings (Blaker 1969b; Fujioka 1985).

Bill grabbing between siblings seems best interpreted as a redirected food begging activity, with the focus of action being transferred from the adult's bill to the sibling's when the former is out of reach. Its pattern of occurrence does not suggest 'play' or 'ritualized duel' (Wershkul 1979). Such bill grabbing never induced regurgitation by a sibling, in contrast to the Grey Heron

Ardea cinerea (Lowe 1954). Its immediate cessation on the departure of the adult suggests its function is to stimulate the adult to resume feeding the chicks.

The number of feeding visits to a nest and food boluses regurgitated were in direct proportion to the number of chicks being fed, as these events were about twice as frequent at Nest 1 as Nest 2. The adults at Nest 2 appeared to take some time to adjust their feeding rate downwards after the loss of a chick, judged by their unsolicited regurgitation and eight reingestions of food off the nest of the surviving ten day old chick. As in the Cattle Egret (Fujioka 1985), the number of feeding visits increased after brooding ceased at Nest 1. In some herons such a rise is followed by a fall in the number of visits (Wershkul 1979; Fujioka 1985), and there was an indication of this with the Intermediate Egrets siblings aged 47 and 48 days.

Clearly sibling competition provides a method of brood reduction in this species. Food stealing must reduce the food sharing benefit of the indirect method of feeding where food items are small enough to be swallowed quickly by the oldest chick, but not the youngest. Direct fratricide occurs in the Cattle Egret (Fujioka, 1985) and Great Egret *Casmerodius albus* (= *Egretta alba*) (Mock *et al.* 1987), but was not seen in the present study. Most serious for Chick 3 of Nest 1 may have been the increased indirect competition for food when its older siblings started to feed directly from the parent. Within a few days of this Chick 3 started to lose weight, and it disappeared aged from 12 to 16 days.

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DAILY FOOD CONSUMPTION OF TWO CAPTIVE LITTLE EAGLES

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Two Little Eagles *Hieraaetus morphnoides* were fed *ad libitum* over two and 12 months in an outdoor enclosure in which they could exercise. In winter, daily food consumption averaged 122 g (10% of body weight) for the female and 78 g (11% of body weight) for the male. The female's mean daily food consumption ranged between 122 g and 163 g (10-15% of body weight, \bar{x} =12%) in the other three seasons, during which she was gaining weight, replacing feathers, or both.

Daily food consumption rates are of ecological interest, but have been obtained for few Australian raptors (Swamp Harrier *Circus approximans*: Baker-Gabb 1982; Wedge-tailed Eagle *Aquila audax*: Brooker and Ridpath 1980) and not previously for the Little Eagle. I therefore took the opportunity to measure the daily food intake of two wild Little Eagles, a male and a female, while they were being held in captivity following injury.

MATERIALS AND METHODS

Two eagles were kept sequentially (female April 1986 to April 1987, male June to August 1987) in an outdoor enclosure at the University of New England, Armidale, New South Wales. The aviary measured approximately 7 m long \times 3 m wide \times 3.5 m high, with the western third enclosed by fibro sheeting against the prevailing

winds. The remainder was wire mesh lined inside with hessian. Perches were provided at each end, and fresh water was provided *ad libitum* in a dish large enough for the birds to bathe in. Accommodation was less than optimum (cf. Olsen and Olsen 1981), but the birds did have access to sun and rain and were able to exercise, and environmental conditions thus approximated those in the wild.

The eagles were fed *ad libitum*, for convenience mainly on freshly killed adult wild rabbits (>1 300 g), although these were larger than prey items normally taken in the wild (<1 000 g: Debus 1984). They were occasionally fed on fresh road-killed rabbits or birds. The eagles were fed once per day on more of a rabbit carcass (gutted) than they could consume. Each portion of rabbit (forequarters or hindquarters, complete with fur) was weighed before being given to an eagle, and