

FACTORS INFLUENCING CHICK SURVIVAL IN THE WEDGE-TAILED EAGLE *Aquila audax*

LISA COLLINS and DAVID B. CROFT¹

School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052

¹Present address: UNSW Arid Zone Field Station, Fowlers Gap via Broken Hill, New South Wales 2880;

corresponding author: d.croft@unsw.edu.au

Received: 10 April 2006

Nest-site characteristics of the Wedge-tailed Eagle *Aquila audax* were studied in 1999 at Fowlers Gap, in arid western New South Wales, by measuring parameters of nest trees for five active nests and eight other nests. Parental and chick behaviour and prey items were recorded at five nests by remote time-lapse video surveillance, through the nestling period to fledging, and prey populations were surveyed. The five monitored nests were mostly in live gums *Eucalyptus* sp. in creeks, and the other nests were mostly in non-eucalypts in other habitats. Six clutches were all of two eggs; fledging success was 0.64 young per pair per year over 14 pair-years 1997–99. The eagles' breeding diet consisted of mammals (25% by number) and reptiles (72%): mostly juvenile kangaroos *Macropus* sp. (20%) and Bearded Dragons *Pogona vitticeps* (68%). By biomass, important prey were mammals (78%: kangaroos 73%) and reptiles (21%). Rabbits were scarce in the environment and in eagle prey; the eagles strongly selected juvenile kangaroos relative to their abundance, but took rabbits in proportion to their abundance. Parental and siblicidal behaviour is described. Sample sizes were too small to draw definitive conclusions, but tree canopy cover, human disturbance, sibling competition, and prey size and availability all appeared to have some influence on chick survival.

INTRODUCTION

Factors contributing to development and survival of eagle chicks may include the interplay between the offspring and their parents, between siblings, and between the chicks and the physical characteristics of the nest site. This study on the Wedge-tailed Eagle *Aquila audax* continues that of Silva and Croft (2007), by focussing on nest-site characteristics, prey selection, parental behaviour and siblicidal behaviour. Silva & Croft (2007) compared nest trees and non-nest trees; this study sought to compare successful and unsuccessful nests. The studies of Harder (2000) and Silva and Croft (2007) remain the only other quantified accounts of aspects of the eagle's breeding behaviour.

Chick survival from hatching to fledging may be affected by nest quality and parental quality. Nest quality may include nest and tree characteristics (e.g. cover, stability) and nest location, in relation to prey densities. Parental quality may include the rate of nest attendance and parental care, nestling dietary composition, and feeding rate. The nest environment may also be affected by sibling competition.

The Wedge-tailed Eagle is facultatively siblicidal; that is, siblicide (or cainism) is not invariable but seems related to food supply, as two (or rarely three) chicks can fledge in times of abundant food (Marchant and Higgins 1993; Olsen 1995). This aspect is little studied in Wedge-tailed Eagles though much studied in other *Aquila* eagles, notably obligate cainists that always fledge one chick from clutches of two eggs regardless of food supply (e.g. Gargett 1990; Meyburg 2002). Siblicide may be the greatest single cause of eaglet loss (Brown 1976).

This study sought to investigate some of the factors influencing chick survival in the Wedge-tailed Eagle: nest-site characteristics, diet and prey selection, and the level of parental care of the nestlings. The aims of the study were to identify characteristics of trees containing active nests; quantify prey items in relation to the availability of certain prey species;

describe and quantify parental behaviour in relation to chick age; and describe and quantify siblicidal behaviour.

STUDY AREA AND METHODS

Study site

The present study was conducted at Fowlers Gap Arid Zone Research Station (31°05'S, 141°45'E) in western New South Wales, as described by Silva and Croft (2007). The station, of 392 square kilometres, is semi-arid pastoral land running 5000–7000 sheep and a small number of cattle. The landscape varies from high sandstone ridges to grassy plains and chenopod shrublands, with eucalypts along ephemeral creeks, and *Acacia* and *Casuarina* on ridges, hills and plains away from creeklines. The mammal fauna is dominated by large kangaroos (Red Kangaroo *Macropus rufus*, Eastern Grey *M. giganteus*, Western Grey *M. fuliginosus* and Euro *M. robustus*). Common feral animals include Goats *Capra hircus*, Pigs *Sus scrofa*, Cats *Felis catus* and Foxes *Vulpes vulpes*. Rabbits *Oryctolagus cuniculus* were generally numerous, but their numbers were reduced by the calicivirus (Sharp *et al.* 2002) although small populations persist and are recovering. The avifauna is diverse (~100 species). There are at least 21 species of lizard (Magarey 1999), those of most relevance being the Central Bearded Dragon *Pogona vitticeps* and Shingleback *Tiliqua rugosa*.

Nests

The nests located by Silva and Croft (2007) in 1997 were revisited in 1999, and the study area was resurveyed as some of the previous nests had been destroyed by storms in 1997–98. A further eight inactive nests, in previously unsurveyed parts of the station, were located. Nests were recorded by GPS and plotted on a topographic map. Nests were visited in late June and classified as active (green foliage, adult or eggs on/in nest; n = 8) or inactive (no sign of activity), and categorised as 'ridge' 'creek' or 'downs' according to the criteria of Silva and Croft (2007).

Nest-site parameters were measured and categorised according to the methods and classification of Silva and Croft (2007). Characteristics of the newly discovered nests, and of those monitored in 1999, were added to the data set of Silva and Croft (2007). Characteristics of five active nests monitored through the breeding season in 1999 were compared with all nests (found in 1997 and 1999) in that habitat type. Data are given as mean \pm standard deviation. Available nest-occupancy and fledgling-productivity data for 1996 and 1998 were included in calculations of breeding success.

Behaviour and prey

Observations on diet and parental care were recorded by solar-powered time-lapse video, similar to the system described by Silva and Croft (2007), except that colour cameras were used. Cameras were installed at six of the eight active nests. Video recorders, with solar panels powering the camera and recorder, were used to monitor two nests continuously. These two VCRs were programmed to record from 30 minutes before dawn to 30 minutes after sunset at a time-lapse rate of 120 hours per three-hour VHS tape, so that tapes were changed every nine days. Nests not being videotaped were observed remotely from 500–800 metres away, via camera signal on the satellite band from a transmitter at the base of the nest tree. These nests were observed directly on a colour monitor at the receiver from early morning to sunset for seven days, and then the equipment (other than camera, left in place) was rotated to another nest (see Collins 1999 for details).

The video systems were initially set up at active nests in the prelaying or early incubation stage in June, but after breeding failure at three nests (one nest abandoned before laying, one clutch deserted, eggs not laid in one nest), five nests were monitored. Monitoring started when there were chicks in the nests, and ceased when a chick left the nest, for nearby branches, for the first time. Nests were visited only every third day.

Using the locality codes (i.e. Pair/Nest 1 and 2) of Silva and Croft (2007), Pair 1 (in a new nest in 1999) was monitored for nine days from hatching until the death of the chicks. Pair 2 (also in a new nest in 1999) was monitored for three days in week 4 until the chick died. Of the successful nests, Nest 3 was monitored from when the older chick was two weeks old until it fledged at about 11 weeks; Nest 4 chick from five weeks old to fledging; and Nest 5 chick at 3–4, 7–8 and 9–11 weeks old. Behavioural categories in this study were as described by Brooker (1974) for the Wedge-tailed Eagle, and Ellis (1979) for the Golden Eagle *Aquila chrysaetos*.

Instantaneous sampling (Martin and Bateson 1993), using the start of each minute as the instant for each sample point, was used to record and quantify behaviour. Parental behaviour and presence were classified as protection (brooding/shading), feeding (including delivery, tearing of food and removal of old food), allopreening the chick, nest maintenance (delivery and placing of foliage; eating food scraps), and standing (guarding?) when the parent was present but not performing these activities. When two parents were present, the behaviour of both was recorded. Only one observer (Collins) viewed and analysed the video footage.

Parental behaviour at successful nests (where at least one chick fledged) was analysed in one-week blocks according to the age of the chicks. The data set was augmented by reanalysing the results of Silva and Croft (2007) for their two successful nests. Chicks at unsuccessful nests lived for insufficient time to provide useful information; data for chicks at successful nests were analysed from age 2–3 weeks to 10–11 weeks. Parental behaviours (protection, feeding, preening, nest maintenance, standing on nest) were calculated as a proportion of the time a parent was present.

Instantaneous sampling, scoring behaviour at the start of each minute, was used to quantify jostling bouts between siblings. The number of pecks was counted, and parental presence or absence during these episodes was recorded. Only two nests (a small sample size) contained two chicks at the start of observations; these two nests were observed at different, non-consecutive stages of chick growth.

Prey brought to the five nestling broods was recorded by the video systems at the nests, and analysed according to the methods of Silva and Croft (2007). Prey items were identified and aged (e.g. juvenile kangaroo hindquarters) from the video footage. The duration of each feeding bout was recorded, as was the food type and the number of pieces offered to each chick by the parent.

Prey populations

Densities of adult and juvenile kangaroos, large birds (all species, flying and non-flying, >30 cm in length), rabbits and lizards around eagle nests were estimated at monthly intervals. These animals were surveyed by line transects, using the methods and assumptions of Buckland *et al.* (1993). Monthly transects were conducted four times from July to October at Nests 1 and 2, and three times from August at Nests 3 to 5, over the duration of the study. Transects, marked at 100-metre intervals, radiated for one kilometre on each of the four cardinal compass bearings (determined by a sighting compass) from each of the five nests. Each of the four nest subtransects was walked from sunrise on clear mornings, and all individuals in the prey categories were recorded. The transect data were analysed using Distance V3.5 (Thomas *et al.* 1998) to derive detectability functions and densities. Detectability of adult and juvenile kangaroos within 50–100 metres was typically close to 100 percent. Similar detectabilities for these animals were found between eagle nests for all strip widths (0–50, 0–100, 0–150 and 0–200 m), from ANOVA, therefore abundance counts from the 0–200 metre distance category could be analysed directly.

In September and October most transects were extended by up to two kilometres, and each resulting three-kilometre line (except where truncated by the property boundary or rugged terrain) was surveyed for dragon lizards (Agamidae), by motorcycle at 10 kilometres per hour in suitable conditions for diurnal lizard activity.

Animal carcasses (carrion) and rabbit warrens found along the transects were noted. Rabbit warrens were surveyed at all eagle nests over the four months of the study. An intensive search for rabbit warrens was conducted within an arbitrary

200-metre radius around each eagle nest, and the number of active warren entrances (after Myers and Parker 1975) was used to calculate an index of rabbit numbers using the regression equation of Parer and Wood (1986).

Prey selection was assessed by comparing the observed and expected frequency of prey items of each type at eagle nests with the calculated densities of these prey species as determined by the prey surveys.

Statistical analysis

Multi-dimensional scaling was used to plot the characteristics of all nests (including those of Silva and Croft 2007) in the 'creek' and 'downs' habitats. Successful and unsuccessful nests were plotted and compared within habitats, to determine whether they were typical of nest trees in that habitat. Local tree density was omitted from the analysis, as it served only to differentiate 'creek' (dense) from 'downs' (sparse) habitats.

Densities of adult kangaroos, juvenile kangaroos, rabbits and birds were compared between successful and unsuccessful eagle nests, and between the months in which transects were conducted, using ANOVA. Rabbit abundances (from warren data) within 200 metres of successful and unsuccessful eagle nests, and between months, were compared using ANOVA.

Parental behaviours (as a proportion of observation or parental presence time) were analysed by regression against chick age class. The feeding rates of chicks at successful nests, overall and by prey type, were compared by regression against age class. Graphical outputs of the regression analyses were provided by Collins (1999).

RESULTS

Eagle population and breeding

In 1999, there were approximately 10 pairs of eagles on the property of 392 square kilometres; six pairs laid eggs. The five monitored nests were in the 'creek' habitat ($n = 4$) and adjacent floodplain in the 'downs' habitat ($n = 1$). Of the eight newly discovered nests (three active, five inactive), six were in the 'downs' habitat and one each in the 'creek' and 'ridge' habitats.

Some of the new nests may represent pairs additional to those found by Silva (1998; data in Silva and Croft 2007).

In late June 1999, six of the eight examined active nests already contained eggs; the other two were lined with green foliage. The five monitored breeding attempts resulted in three successful outcomes (three broods of one), giving 0.6 young per attempt. The five pairs laid 10 eggs (five clutches of two eggs), of which seven eggs were known to hatch; in at least two cases both eggs hatched but only one chick fledged. Of the two failed attempts, one chick (of a brood of one) died at 4–5 weeks, and both chicks of the other brood died at 1–1.5 weeks.

These data exclude two or three cases of researcher-induced breeding failure: at the initial inspection stage to determine activity, one pair abandoned the nest before laying, another pair deserted the eggs (a clutch of two), and a third pair had lined the nest but did not lay (i.e. possibly abandoned after inspection). The deserted clutch was in a low (2–3 m) nest in a small tree, and was disturbed late in the day by installation of the monitoring equipment close by. Inclusion of these cases would lower the fledging rate to 0.5 young fledged per clutch started, 0.43 young per nesting attempt and 0.38 young per occupied nest in 1999.

Over four breeding seasons, 1996–99, the five monitored pairs usually rotated between their own alternative nests or used newly built nests (except for Pair 4 which used the same nest each year); over 14 pair-years for which the outcome was known, they had a success rate of 0.64 young fledged per pair per year (Table 1).

Nest-site characteristics

The monitored nests were situated in live River Red Gums *Eucalyptus camaldulensis* ($n = 4$) and a live Black Box *E. largiflorens* ($n = 1$). The new 'downs' nests were situated in Mulgas *Acacia aneura* ($n = 3$), Belahs *Casuarina cristata* ($n = 2$), and a dead tree ($n = 1$). The new 'creek' nest was in a Belah (a new nest-tree species for that habitat), and the new 'ridge' nest in a Mulga. The five monitored (active) nests were 140–210 centimetres wide x 75–150 centimetres deep (mean 188 ± 27.7 cm wide x 100 ± 30.6 cm deep); four of these were newly built, and the other (Nest 4) was used for at least three

TABLE 1

History of use of five monitored Wedge-tailed Eagle nests at Fowlers Gap, 1996–99, using data from Silva and Croft (2007) as a baseline (i.e. Silva's Pairs 1 and 2 used nests 1A and 2A, respectively, in 1997): nest code and outcome for each year. N = no. young fledged; ? = uncertainty/outcome unknown. No success data for 1996.

Pair	1996	1997	1998	1999
1	Nest B: ?	Nest A: 2	Nest C: 1	Nest D: 0
2	Nest B?: ?	Nest A: 1	Nest C: 1	Nest D: 0
3	Nest A: ?	Nest B: 0	Nest A: 1	Nest C: 1
4	Nest ?: ?	Nest A: 0	Nest A: 0	Nest A: 1
5	Nest A?: ?	Nest B: 0	Nest C: ?	Nest D: 1

TABLE 2

Mean monthly abundance of potential prey animals of Wedge-tailed Eagles at Fowlers Gap on radial transects (see Methods text) at each nest during the nestling period: number per standard transect. No rabbits sighted.

Nests	Large birds ^a	Juvenile kangaroos	Adult kangaroos
Unsuccessful (n = 2)	4.4	4	14.6
Successful (n = 3)	4.8	6.9	18.8

^a>30 cm in length

consecutive years (Table 1). With re-use and addition of material, Nest 4 increased in size from 1.9 x 1 metres in 1997 (Silva 1998) to 2 x 1.5 metres in 1999. The eight newly discovered nests were 120–210 centimetres wide x 55–125 centimetres deep (mean 154 ± 33.7 cm wide x 93 ± 24.5 cm deep).

The new nests (Appendix 1) were generally within or similar to the parameters of previously measured nests in their habitat categories (cf. Silva and Croft 2007). The monitored 'creek' nests (Appendix 1) were generally typical of previous 'creek' nests. The monitored 'downs' nest was typical of previous 'downs' nests except for greater crown depth and area, in which it resembled 'creek' nests; it was in a eucalypt, whereas other nest trees on 'downs' were mostly non-eucalypts (data in Collins 1999; Silva and Croft 2007).

There was little discernible difference in the parameters of successful (n = 3) versus failed nests (n = 2) monitored in 1999; successful nests averaged slightly greater in tree height (13.5 vs 9.7 m) and crown depth (10.7 vs 8.5 m), suggesting that they may have had more overhead cover.

Nest 4 (in a Black Box in 'downs') was atypical of the nest trees in 'downs' habitat: this nest was deep, with a large amount of crown cover, whereas other nests on 'downs' were typically shallow with a small amount of green crown cover, and commonly in Belahs or Mulgas.

Potential prey populations

The most frequently sighted animals were adult kangaroos, followed by juvenile kangaroos. Large birds (>30 cm) formed a small proportion of the potential prey, and no carrion or lizards were detected along the transects. The mean monthly number of animals per standard radial transect was slightly higher at successful nests than at unsuccessful nests (Table 2). However, prey populations did not change significantly over time, and prey abundance did not affect nest success (ANOVA: $P > 0.05$; details in Collins 1999).

The dragon surveys, extending up to three kilometres from eagle nests, produced only one sighting at 97 metres from nest 3. However, this result most likely reflects poor sightability (by humans) rather than low abundance, as Bearded Dragons are well camouflaged and 'freeze' flattened on the substrate, or

flee, at the sight or sound of approaching people or vehicles. The one-kilometre transects may also have been conducted before mornings had warmed sufficiently for reptile activity; reptiles may have been inactive (torpid) during the July and August transects.

Rabbit density was 0.3 animal per hectare in core warren areas around the active eagle nests, which were mostly in creeks (i.e. productive parts of the landscape), but may have been much lower over the landscape as a whole. The transects and warren data found no significant relationship between rabbit abundance and eagle nest success, nor a change in rabbit abundance over time (Table 3). However, the effect of rabbit density on nest success approached significance ($P = 0.08$; Table 3), although the sample size for successful and unsuccessful eagle nests was small.

Diet and prey selection

The eagles took mammals (25% by number) and reptiles (72%), with three percent of items unidentified (Table 4). Important prey were dragon lizards (68%) and juvenile kangaroos (20%). Rabbits formed only five percent of the diet by number, and no birds or lambs were recorded as food. Assumed or estimated masses were 1.5 kilograms for rabbits, 5 kilograms for juvenile kangaroos, 1 kilogram for unidentified mammals, 0.5 kilogram for unidentified (small) items, and 0.4 kilogram for reptiles. On this basis, mammals contributed 78 percent of dietary biomass (kangaroos 73%, rabbits 5%), and reptiles 21 percent (calculated from Table 4). Although eagles may have difficulty carrying a five-kilogram juvenile kangaroo (young at foot), the hindquarters were commonly brought to nests and it is likely that the adults shared, partly ate and dismembered such kills away from the nest before bringing the remainder.

Eagles strongly selected juvenile kangaroos in relation to their abundance; large birds (>30 cm) were avoided; and rabbits were taken in similar proportion to their abundance. That is, juvenile kangaroos and large birds were respectively taken significantly more than expected, and significantly less than expected, when compared with their densities (Chi-square, $P < 0.05$; Table 5). No index of abundance could be calculated for Bearded Dragons, but they were either strongly selected by eagles or they were abundant but not detected by the transect method.

Parental time-budgets

Parents spent less time at the nest during the day as chicks increased in age, from 2–3 weeks old to 10–11 weeks old. The average proportion of time no parent was present increased from 65 to 85 percent over this age interval ($F_{1,6} = 41.277$; $P < 0.01$), and the time only one parent was present decreased from 35 to 15 percent ($F_{1,6} = 22.312$; $P < 0.01$). The time both parents were present did not change significantly with nestling age, and formed only a small proportion of the day (2.5 to 1 percent over the observed age interval: $F_{1,6} = 2.629$; $P > 0.05$).

As a proportion of parental attendance time, nest maintenance decreased with nestling age from 0.6 percent to 0.4 percent over the age interval ($F_{1,6} = 16.806$; $P < 0.01$), as did protective behaviour (brooding/shading) from 19 percent to zero ($F_{1,6} = 18.413$; $P < 0.01$). Allopreening of chicks did not change significantly with nestling age ($F_{1,6} = 1.752$; $P > 0.05$), nor did feeding of the nestlings ($F_{1,6} = 0.6$; $P > 0.05$), but the proportion of parental attendance time spent standing on the nest (rather than brooding) increased from 51 percent to 70 percent over the age interval ($F_{1,6} = 11.115$; $P < 0.05$).

The average number of meals per day decreased significantly with increasing nestling age, from 39 to 8 percent of parental attendance time over the age interval ($F_{1,7} = 19.641$; $P < 0.01$). However, the average duration of meals did not change significantly with nestling age ($F_{1,7} = 0.374$; $P > 0.05$), nor did the average number of pieces fed per meal ($F_{1,7} = 0.89$; $P > 0.05$).

Parents provided fewer meals of juvenile kangaroo with increasing chick age (10 to 2.5 meals/day over the age interval: $F_{1,7} = 7.234$; $P < 0.05$). A similar trend applied to meals of Bearded Dragon (16 to 6 feeds/day: $F_{1,7} = 2.575$; $P < 0.05$), though fluctuating slightly in a manner complementary to that for kangaroo. The number of meals of rabbit did not vary significantly with nestling age ($F_{1,7} = 0.014$; $P > 0.05$).

There was little variation over time in the relative frequency of prey items brought to nests. The number of deliveries for all prey species did not vary significantly with chick age (Table 6).

TABLE 3

Two-factor ANOVA results for the effect of rabbit abundance within 200 m of eagle nests or along four radial 1-km transects from each nest, in monthly sampling periods, on Wedge-tailed Eagle nest success ($n = 5$ nests) at Fowlers Gap, in August–October 1999.

Parameter	DF	F	Significance (P value)
200 m radius:			
Nest success	1, 19	3.554	0.08
Period	3, 19	0.472	0.71
Success x period	3, 19	0.116	0.95
Radial transects:			
Nest success	1, 19	3.411	0.9
Period	3, 19	0.147	0.93
Success x period	3, 19	0.488	0.7

Dragons formed 68 percent of items delivered to nests, but only 45 percent of nestling meals; juvenile kangaroos formed 20 percent of items delivered, but 32 percent of nestling meals (probably a reflection of relative prey size). A positive correlation was found between the total number of meals and the number of meals in which Bearded Dragon featured ($F_7 = 30.234$; $P < 0.001$); that is, such small items were delivered frequently and eaten quickly. There was also a positive correlation between the proportion of time one parent was present and the number of meals of juvenile kangaroo ($F_{1,7} = 21.161$; $P < 0.01$); that is, a parent could remain on the nest and give multiple meals from a large prey item.

The above data apply to successful nests; few data were obtained for unsuccessful nests, which failed early in the nestling period.

Nestlings

Only two nests (Nests 1 and 3) were observed with two chicks. Nest 3 was observed from early August when the chicks were 2–3 weeks old, after a hatching interval of three days; only one survived to fledge. At Nest 1 the first chick hatched in mid-August; the second chick hatched three days later. Nest 1 failed soon after hatching, when the chicks were nine and six days old; the older (larger, dominant) one fell out of the nest and died (i.e. not pushed out by its sibling), and the younger died from unknown causes during the next night. The latter may have been preyed upon at night, as next morning only half its carcass remained, and the parent arrived early to deliver food although by then there were no live chicks.

At both nests, no pecking between siblings occurred when both parents were present. Eighty-nine percent of pecks occurred when no parent was present, and 11 percent when one parent was present. These proportions were the same at both nests, although the rate of pecking at Nest 3 (younger chick 8–11 days old) was six or seven times that at Nest 1 (younger chick 1–6 days old). The number of pecks increased with the age of the chicks as they became more coordinated and aggressive (Figure 1).

TABLE 4

Prey items observed brought to five Wedge-tailed Eagle nests at Fowlers Gap, nestling period, August–October 1999 (from video surveillance of nests; see text). Kangaroos were all young at foot; 'other' includes indeterminate vertebrate carcasses.

Species	No.	%
Rabbit <i>Oryctolagus cuniculus</i>	5	5
Kangaroo <i>Macropus</i> sp. (juvenile)	22	20
Unidentified mammal	1	<1
Total mammals	28	25
Central Bearded Dragon <i>Pogona vitticeps</i>	75	68
Other lizard	4	4
Total reptiles	79	72
Other (unidentified)	3	3
Total	110	100

TABLE 5

Prey selection by Wedge-tailed Eagles at Fowlers Gap through the nestling period ($n = 3$ successful nests), compared with local density of prey types (observed as prey vs expected from prey densities: Chi-square). Rabbit density from warren index (see Methods text). * $P < 0.05$.

Prey type	Mean density (n/ha)	Total deliveries	Expected deliveries	Standardised residual
Juvenile kangaroo	0.09	16	0.93	36.67*
Large bird ^a	1.13	0	12.28	-1.57*
Rabbit	0.35	1	3.79	0.28

^a>30 cm in length

There was little evidence of a hierarchy at Nest 1 in the early stages of the chicks' development (up to nine and six days old); each pecked the other, but they were uncoordinated. At Nest 3, the older chick (11–14 days old) delivered all of the pecks and appeared directly responsible for the younger chick's death. The older dominated the younger at feeding times: in the three days leading up to its death (at 11 days old), the younger received only 13 morsels compared with 529 pieces eaten by the older chick. The younger also spent much time on the edge of the nest, and was brooded for only 22 percent of parental brooding time. After its death, the parents fed it to the survivor.

Jostling bouts were more frequent during parental absence than when a parent was present: 75 percent of bouts versus 25 percent at Nest 1, and 93 versus 7 percent at Nest 3, respectively. However, bouts were often too short to record by the instantaneous sampling method. Aggression associated with food manifested when a parent was present, but such competition formed only a minor proportion of the total duration of aggressive interactions observed.

TABLE 6

Regression analysis of total prey deliveries versus nestling age for Wedge-tailed Eagle nests ($n = 5$) at Fowlers Gap.

Prey type	DF	F	Significance (P value)
Juvenile kangaroo	1, 7	0.511	0.498
Rabbit	1, 7	0.028	0.872
Mammal sp.	1, 7	0.134	0.725
Bearded Dragon	1, 7	0.008	0.931
Other lizard	1, 7	0.119	0.741
Unknown	1, 7	0.5	0.502

At unsuccessful Nest 2 the single chick was killed by infanticide at 4–5 weeks old, by an eagle thought to be the male parent after the female was apparently road-killed on the nearby highway. The Nest 2 female was not seen at the nest again, and the road victim resembled her in size and plumage. The presumed male ate the chick, returning to the nest once to continue feeding on it. No other food items in the nest at that stage were touched.

DISCUSSION

Clutches of two eggs, typical for the Wedge-tailed Eagle, were still common at Fowlers Gap in 1999 after the impact of the calicivirus (rabbit haemorrhagic disease) on local rabbit numbers (Sharp *et al.* 2001, 2002), although a reduction in clutch size might be expected if the food supply had been reduced (cf. Olsen and Marples 1992; Marchant and Higgins 1993). The hatching interval of three days was as expected from an inferred laying interval of 2–4 days, incubation starting with the first egg, and known asynchronous hatching (cf. Marchant and Higgins 1993).

Fledging success at Fowlers Gap in 1999, and in 1997–99, was lower than usually recorded elsewhere in Australia (cf. Marchant and Higgins 1993), even without the effect of researcher-induced desertion in this and the study by Silva and Croft (2007). Low fledging success at Fowlers Gap in recent years may reflect the reduction in rabbit populations (cf. Ridpath and Brooker 1986; Robertson 1987; Falkenberg *et al.* 2000; Sharp *et al.* 2001, 2002).

Inclusion of observer effects places fledging success at Fowlers Gap in 1999 among the lowest values recorded for this species (0.19–0.46 fledged per pair per year in the arid zone: Ridpath and Brooker 1986). Nest desertion in persecuted populations of large *Aquila* eagles, as in the Australian sheep belt, should be expected in response to human intrusion at nests at the lining or laying stage (Brown 1976; Mooney and Holdsworth 1991; Olsen 1995). In large, long-lived eagles, breeding attempts may be readily abandoned until the following year if conditions (whether environmental or disturbance-related) are likely to affect reproductive success adversely.

Nest dimensions and nest-site characteristics were generally similar to or within parameters previously recorded for the

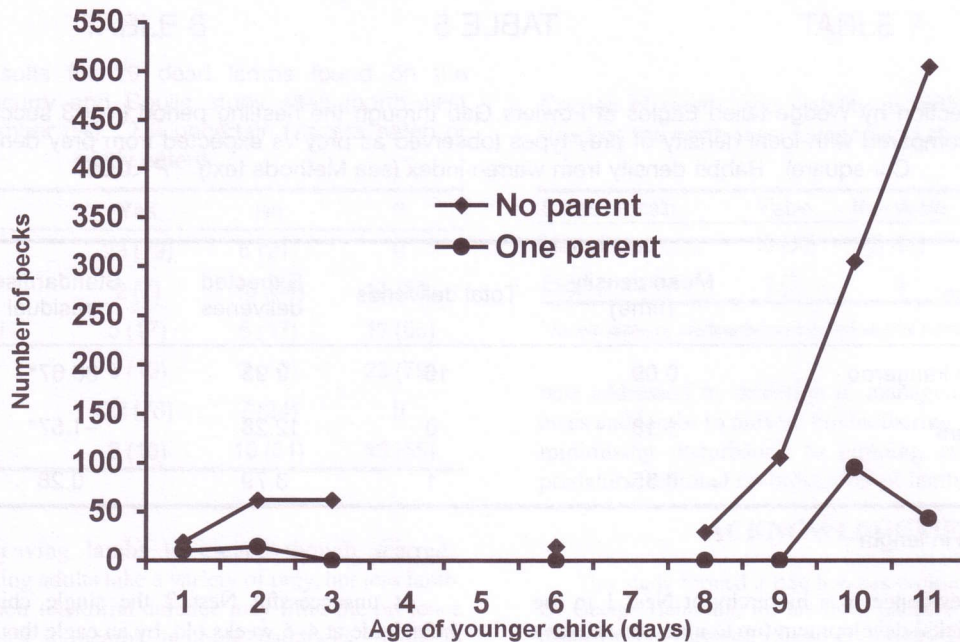


Figure 1. Siblicidal behaviour of Wedge-tailed Eagle chicks at Fowlers Gap: number of pecks versus chick age and parental presence, until death of younger chick (two broods: one with younger chick 1–6 days old; one with younger chick 8–11 days old). Lines join days of continuous monitoring.

Wedge-tailed Eagle at, or near, Fowlers Gap (cf. Sharp *et al.* 2001; Silva and Croft 2007). Patterns of nest use, rotation or re-use at Fowlers Gap were also generally typical for this species (cf. Marchant and Higgins 1993). Pair 4 may have repeatedly used one nest, despite the lack of success therein in 1996 and 1997, because other suitable trees were lacking in their territory. Most nest trees in this study were typical of previously recorded nest trees in the corresponding habitats at Fowlers Gap. Silva & Croft (2007) found that canopy cover and tree height were important in nest-tree choice, and that nest trees, although small (cf. Mooney and Holdsworth 1991), were nevertheless the largest trees available in that environment.

After the impact of the calicivirus on rabbits, the diet of the eagles at Fowlers Gap consisted of more lizards and fewer rabbits than in the study area in 1997, or elsewhere in the south-eastern arid zone, and an increased proportion of juvenile kangaroo, though still no lambs (cf. Leopold and Wolfe 1970; Baker-Gabb 1984; Robertson 1987; Sharp *et al.* 2002; Silva and Croft 2007). However, the eagles took no birds in 1999 (cf. Silva and Croft 2007). Sharp *et al.* (2002) found a similar pattern post-calicivirus, of changed dietary proportions and a strong increase in the number of Bearded Dragons taken, near Fowlers Gap. Increased predation on Bearded Dragons may reflect a lack of rabbits, or an increase in the population of these lizards following environmental change after the rabbits declined, as suggested for elsewhere in the study region (Sharp *et al.* 2002).

Although a variety of potential prey was available in the study area, the eagles concentrated on two species (lizard and juvenile kangaroo) from opposite ends of the eagle's prey weight spectrum. This result may reflect the abundance of these two prey species, the fairly small sample size of prey records, or a bias in the recording method (e.g. kangaroo hindquarters and whole lizards were easily identifiable on video footage,

whereas other prey items may have been less so). Prey remains and pellets may have revealed additional prey species.

Juvenile kangaroos were common in the study area, and were favoured prey in relation to their abundance. Rabbits were uncommon prey and taken in proportion to their abundance. Bearded Dragons are probably detected much more easily by airborne eagles than by earth-bound humans, and were probably abundant in the study area, though missed during surveys for prey. More effective surveys for cryptic reptiles (that avoid humans) may determine whether they are preferred prey. There was some indication that successful eagle nests occurred in productive parts of the landscape, in terms of densities of potential prey species (as suggested, for example, by Watson *et al.* 1992 for the Golden Eagle). Apparent prey availability, as a function of detectability and accessibility, may vary with vegetation cover.

Patterns of parental behaviour, care and nest attendance of the eagles at Fowlers Gap, including changes over time with chick growth, were consistent with previous information for the nestling period of this species, to the extent that comparable data are available (cf. Harder 2000; Silva and Croft 2007). Comparative, quantified data for the first 2–3 weeks of nestling life are lacking, but this stage is vulnerable to human disturbance.

Sibling rivalry in nests at Fowlers Gap, and its circumstances, were generally as previously described for the Wedge-tailed Eagle and other *Aquila* eagles, especially other facultatively siblicidal species (cf. Brown 1976; Cupper and Cupper 1981; Hollands 1984; Gargett 1990; Watson 1997; Marchant and Higgins 1993; Olsen 2005). Opportunity for siblicidal behaviour appeared to be related to the level of parental attendance, and was most intense during parental absence.

Infanticide appears to be rare in Australian diurnal raptors. It has been recorded once in the Wedge-tailed Eagle, by a still-dependent yearling that killed its parents' new chick (Olsen 2005). In the case at Fowlers Gap, it may have occurred because the male parent was unable to rear a chick of that age (requiring brooding and feeding) on his own, after the female died, or it may have been displacement behaviour under stress. Alternatively, the infanticidal eagle may have been a visiting individual and not the chick's father. The male at this nest was a brown immature in 1997 during the previous study (Silva and Croft 2007), and was probably the same inexperienced bird in 1999. By contrast, both adults at Nest 3 in 1999 were mature adults; both delivered prey and fed the chicks, and they may have been more experienced.

In this study, small sample sizes of successful and unsuccessful nests, and the truncated data on parental behaviour at failed nests, prevented firm conclusions on the role of nest quality and parental quality in the survival of Wedge-tailed Eagle chicks. Nevertheless, it was apparent that there were causes of chick death besides starvation or siblicide, and there was some indication that successful nest sites had superior physical characteristics or were located near abundant prey. Inexperience of the surviving parent may have been a factor in the case of infanticide. The chick may also have been hypothermic, starving and moribund, and not responding appropriately.

ACKNOWLEDGMENTS

This study formed a BSc Honours project by LC, who thanks the following people: Ian Rathbone, Johann Lonzer and Anke Frank for field assistance; personnel at Fowlers Gap, notably Emma Taylor, Will Evans and Nick Adams for technical assistance; Paul and Chris Adams and Amanda Bilton for their hospitality; LC's family (particularly Susie) for support; and Shaun Kelly for his support, encouragement and computing assistance. Dr Stephen Debus (Zoology, University of New England) prepared the manuscript. We thank Penny Olsen, Nick Mooney and two referees for critically reviewing drafts.

REFERENCES

- Baker-Gabb, D. J. (1984). The breeding ecology of twelve species of diurnal raptor in north-western Victoria. *Australian Wildlife Research* **11**: 145–160.
- Brooker, M. G. (1974). Field observations of the behaviour of the Wedge-tailed Eagle. *Emu* **74**: 39–42.
- Brown, L. H. (1976). 'Eagles of the World'. (David and Charles: Newton Abbot.)
- Buckland, S. T., Anderson, D. R., Burnham, K. P. and Laake, J. L. (1993). 'Distance Sampling: Estimating Abundances of Biological Populations'. (Chapman and Hall: London.)
- Collins, L. M. (1999). Factors Influencing Chick Survival in the Wedge-tailed Eagle, *Aquila audax*. BSc Hons thesis, University of New South Wales, Sydney.
- Cupper, J. and Cupper, L. (1981). 'Hawks in Focus'. (Jaclin Enterprises: Mildura.)
- Ellis, D. H. (1979). Development of behaviour in the Golden Eagle. *Wildlife Monographs* **70**.
- Falkenberg, I. D., Hurley, V. G. and Stevenson, E. (2000). The impact of Rabbit Calicivirus Disease on raptor reproductive success in the Strzelecki Desert, South Australia: a preliminary analysis. In 'Raptors at Risk' (Eds R.D. Chancellor and B.-U. Meyburg). Pp. 535–542. (Hancock House: Surrey, and World Working Group on Birds of Prey & Owls: Berlin.)
- Gargett, V. (1990). 'The Black Eagle'. (Acorn Books: Randburg, and Russell Friedman Books: Halfway House.)
- Harder, M. (2000). Diet and breeding biology of the Wedge-tailed Eagle *Aquila audax* at three nests in north-eastern New South Wales. *Corella* **24**: 1–5.
- Hollands, D. (1984). 'Eagles, Hawks and Falcons of Australia'. (Nelson: Melbourne.)
- Leopold, A. S. and Wolfe, T. O. (1970). Food habits of nesting Wedge-tailed Eagles, *Aquila audax*, in south-eastern Australia. *CSIRO Wildlife Research* **15**: 1–17.
- Marchant, S. and Higgins, P. J. (Eds) (1993). 'Handbook of Australian, New Zealand and Antarctic Birds', Vol. 2. (Oxford University Press: Melbourne.)
- Margarey, E. (1999). The Effect of Sheep Grazing on Lizard Assemblages in the New South Wales Arid Zone. BSc Hons thesis, University of New South Wales, Sydney.
- Martin, P. and Bateson, P. (1993). 'Measuring Behaviour'. (Cambridge University Press: Cambridge.)
- Meyburg, B.-U. (2002). On Cainism in the Lesser Spotted Eagle (*Aquila pomarina*) and a possible explanation for the phenomenon in this and other eagle species. In 'Raptors in the New Millennium' (Eds R. Yosef, M. L. Miller and D. Pepler). Pp 53–61. (International Birding and Research Center: Eilat, Israel.)
- Mooney, N. and Holdsworth, M. (1991). Effects of disturbance on nesting Wedge-tailed Eagles *Aquila audax fleayi* in Tasmania. *Tasforests* **3**: 15–29.
- Myers, K. and Parker, B. S. (1975). Effects of severe drought on rabbit numbers and distribution in a refuge area in semiarid north-western New South Wales. *Australian Wildlife Research* **2**: 103–120.
- Olsen, P. (1995). 'Australian Birds of Prey'. (New South Wales University Press: Sydney.)
- Olsen, P. (2005). 'Wedge-tailed Eagle'. (CSIRO: Melbourne.)
- Olsen, P. D. and Marples, T. G. (1992). Alteration of the clutch size of raptors in response to a change in prey availability: evidence from control of a broad-scale rabbit infestation. *Wildlife Research* **19**: 129–135.
- Parer, I. and Wood, D. H. (1986). Further observations of the use of warren entrances as an index of the number of rabbits, *Oryctolagus cuniculus*. *Australian Wildlife Research* **13**: 331–332.
- Ridpath, M. G. and Brooker, M. G. (1986). The breeding of the Wedge-tailed Eagle *Aquila audax* in relation to its food supply in Western Australia. *Ibis* **128**: 177–194.
- Robertson, G. (1987). Effects of drought on a breeding population of Wedge-tailed Eagles *Aquila audax*. *Emu* **87**: 220–223.
- Sharp, A., Gibson, L., Norton, M., Ryan, B., Marks, A. and Semeraro, L. (2002). The breeding season diet of Wedge-tailed Eagles (*Aquila audax*) in western New South Wales and the influence of Rabbit Calicivirus Disease. *Wildlife Research* **29**: 175–184.
- Sharp, A., Norton, M. and Marks, A. (2001). Breeding activity, nest site selection and nest spacing of Wedge-tailed Eagles, *Aquila audax*, in western New South Wales. *Emu* **101**: 323–328.
- Silva, L. M. (1998). Nest-site Spacing and Selection, Diet and Parental Care of the Wedge-tailed Eagle (*Aquila audax*) at Fowlers Gap. BSc Hons thesis, University of New South Wales, Sydney.
- Silva, L. M. and Croft, D. B. (2007). Nest-site selection, diet and parental care of the Wedge-tailed Eagle *Aquila audax* in western New South Wales. *Corella* **31**: 23–31.
- Thomas, L., Laake, J. L., Derry, J. F., Buckland, S. T., Borchers, D. L., Anderson, D. R., Burnham, K. P., Strindberg, S., Hedley, S. L., Burt, M. L., Marques, F., Pollard, J. H. and Fewster, R. M. (1998). 'Distance 3.5'. (Research Unit for Wildlife Population Assessment: University of St Andrews, UK.)
- Watson, J. (1997). 'The Golden Eagle'. (Poyser: London.)
- Watson, J., Rae, S. R. and Stillman, R. (1992). Nesting density and breeding success of Golden Eagles in relation to food supply in Scotland. *Journal of Animal Ecology* **61**: 543–550.

APPENDIX 1

Parameters of nest trees for Wedge-tailed Eagle nests at Fowlers Gap for newly discovered nests and nests monitored in 1999: mean \pm standard deviation. Numbers in parentheses for each category = sample size; in data field = range. Nest parameters according to the definitions and criteria of Silva and Croft (2007); tree density = number of stems per square metre.

Parameter	New (8) ^a	Monitored (5) ^b
Nest height (m)	3.3 \pm 1.5 (1.3–5.8)	7.2 \pm 2.6 (4.0–11.0)
Nest position (%)	43.8 \pm 13.2 (25.6–66.7)	54.8 \pm 18.4 (34.0–78.8)
Tree height (m)	6.9 \pm 2.3 (4.8–11.3)	13.9 \pm 5.2 (8.3–20.8)
Crown depth (m)	5.0 \pm 3.0 ^c (0.8–9.3)	11.5 \pm 4.8 (6.5–19.0)
Crown cover (%)	66.0 \pm 24.9 ^c (15.0–86.5)	78.6 \pm 12.1 (64.1–91.6)
Crown area	36.1 \pm 42.6 ^c (3.5–128.2)	128.5 \pm 80.7 (57.8–241.1)
Tree density (n/m ²)	386.1 \pm 232.9 (35.4–715.6)	3762.6 \pm 4537.5 (201.6–9550.2)
Tree condition	2	3.2

^aSix in downs, one in ridge, one in creek habitats

^bFour in creek, one in floodplain on downs (all in eucalypts)

^cMean of seven live trees, as one dead



S. Tredinnick

One adult delivering prey as the other looks on and the feathering chick lunges for the prey.