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Breeding Biology and Diet of the Wedge-tailed Eagle *Aquila audax* in the New England Region of New South Wales

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Summary

The breeding biology, behaviour and diet of the Wedge-tailed Eagle *Aquila audax* were studied by 156 hours of observation from nest-renovation to the post-fledging period, and by analysis of prey remains and pellets, at one nest in the New England region of northern New South Wales in 2005. Supplementary observations and collections of food remains were made at three and two other nests, respectively. Egg-laying occurred in June (n = 5 clutches). At one nest, incubation (by both sexes) lasted 43 ± 2 days, the nestling period lasted 90 days to first flight from the nest-tree (with the young venturing to branches in the nest-tree from 78 days), and the post-fledging dependence period lasted 4 months. Sex-roles, parental behaviour and time-budgets in each phase are described and quantified, and juvenile growth and behavioural development are described. Fledgling productivity was 1.2 young per pair (1.8 per successful pair) in 2005 (n = 6 pairs), and 0.8 young per pair per year in 2005–06 (n = 12 pair-years). The breeding diet at two nests near Armidale (on the Northern Tablelands of New South Wales) in 2005 was 74% mammals (56% Rabbits *Oryctolagus cuniculus*), 22% birds and 4% reptiles by number, and 89% mammals (40% Rabbits), 11% birds and <1% reptiles by biomass (n = 49 prey items). Hunting and attack behaviour are described; 80% of 10 observed strikes by experienced breeding adults were successful.

Introduction

Many aspects of the ecology of the Wedge-tailed Eagle *Aquila audax* have been extensively studied and quantified, notably its diet from most parts of Australia and certain breeding and population parameters (reviewed by Marchant & Higgins 1993 and Olsen 1995; recent studies by Davey & Pech 2004, Fuentes *et al.* 2004, Dennis 2006, Olsen *et al.* 2006a, Collins & Croft 2007, Parker *et al.* 2007, Silva & Croft 2007 and Winkel 2007). Its diurnal routines, displays and foraging behaviour have also been studied (Brooker 1974; Aumann 2001). However, there have been few quantified studies of breeding behaviour, such as sex-roles and parental time-budgets, with few nests observed, and in some cases for only part of the nestling period by video surveillance rather than direct observation (Harder 2000; Collins & Croft 2007; Silva & Croft 2007). Earlier accounts of breeding behaviour, based partly on captive birds, were anecdotal (Pizzey 1958; Cupper & Cupper 1981; Fleay-Thomson 2002). There have been few determinations of the incubation, nestling and post-fledging dependence periods, and little study of juvenile development in the post-fledging period.

Such a situation is remarkable for a large, spectacular and iconic species, given the much greater knowledge of these aspects for large *Aquila* eagles of conservation concern in other western countries (cf. Gargett 1990; Watson 1997; Ferrer 2001). Although the Tasmanian Wedge-tailed Eagle *A. audax fleayi* is endangered (e.g.

Olsen 2005), most published research has been conducted on the Australian mainland, and then largely in relation to the Eagle's possible impact on the sheep industry both historically and since the rabbit calicivirus potentially affected the Eagle's prey base.

This study describes and quantifies behavioural aspects of the breeding cycle of a family of Wedge-tailed Eagles from nest-refurbishment to independence of the juvenile. Allott *et al.* (2006) conducted a similar though unquantified study, and determined the duration of incubation, nestling and post-fledging phases, for one nesting event. Our study was supplemented by observations at three other nests, and the Eagles' breeding diet was quantified at two active nests. A previous dietary study in New England quantified a limited sample from one other nest (Debus & Rose 1999). Some aspects of the present study are not new, but they provide empirical support for some previous generalisations and inferences.

Study area and methods

The main part of the study was conducted at Armidale (30°30′S, 151°40′E), on the Northern Tablelands of New South Wales, in 2005. The area is an undulating plateau at an elevation of 1000 m, with remnant eucalypt woodland (mainly on ridges) amid cleared pasture and farmland (see Debus *et al.* 2006 for further details and references). The primary Eagles' nest (Armidale nest 1), from which most data were collected, was located in remnant eucalypt woodland adjoining Armidale State Forest (a plantation of Monterey Pine *Pinus radiata*). A second nest (Armidale nest 2), visited mainly for dietary data, was located in a woodland reserve (Imbota Nature Reserve, formerly Eastwood State Forest) of 220 ha (see Debus 2006 for further details and references). Both nests were at the locations of a previous study on the Little Eagle *Hieraaetus morphnoides* (Debus 1983, 1984). The current and alternative or old nests of a total of six Wedge-tailed Eagle pairs around Armidale were examined in 2005 for their general site characteristics.

A secondary study, also of two Wedge-tailed Eagle nests in 2005, was conducted at Tamworth (30°05′S, 150°55′E) on the North-west Slopes of New South Wales, 100 km south-west of Armidale. One of these nests was at the site described by Debus *et al.* (2005), and the other was in similar rural habitat within 10 km.

Observations at Armidale nest 1 were conducted by rotating teams of observers, from an unconcealed position 330 m from the nest, using binoculars and telescopes (25×, 20–40× zoom). At this distance the adult Eagles ignored human activity. The nest was watched for a total of 19 h over 19 days (mostly mornings) in the month leading up to laying (late May to late June); 22 h over 19 days throughout the 6-week incubation period (daily in the latter half of the final week, to pinpoint the hatching day); and 94 h over 68 days in the 3-month nestling period. The nestling was watched daily in weeks 1–2, on 5–6 days per week in weeks 3–7, on 2 days in week 8, on 4–6 days per week in weeks 9–11, and daily in weeks 12–13, with two or three watches per day on the final 9 days, to pinpoint fledging. The Eagle family was also observed for 21 h over 21 days in the first four weeks of the post-fledging period, and then for usually an hour on one or two days in each of weeks 5–10. Casual monitoring, partly by local landowners (S. & R. Trémont), was undertaken thereafter, until the last sighting of the juvenile. Nest-based observations until fledging totalled 135 h, distributed through the day but least in the early mornings (Table 1); the nest area was often fog-bound, with poor visibility, until 0800–0900 h in the cooler months. Most nest-watches were for an hour, rarely 0.5 h (around sunset) or 1.5–2 h in some weeks of the nestling period that had <7 observation days, especially week 8. Watches were opportunistic, but the start times were varied, and team members observed sequentially or on different days.

Armidale nest 2 was visited by SD twice in the nestling period (large downy chick stage, feathered nestling stage when fledging imminent in 2005), and five times at weekly to fortnightly intervals in the first two months of the post-fledging period until the last sighting, with a further three checks over the following six weeks.

Tamworth nest 1 was observed by binoculars from a vehicle (serving as a hide) at roadside points 80 m from the nest (if the 'tame' female was on the nest) or by telescope at 200 m if

Table 1

Observation schedule at Wedge-tailed Eagle nest in nest-building, incubation and nestling periods (May–November 2005), Armidale, NSW (nest 1: see text), during each 2-hour interval of daylight hours.

0600–0800	*0801–1000*	*1001–1200*	*1201–1400*	*1401–1600*	*1601–1800*
Building:					
0	9.8	7.1	1.7	0	1.0
Incubation:					
0	2.8	5.8	6.2	4.5	2.7
Nestling:					
2.6	29.7	21.5	11.1	13.9	14.8

the warier male was present, for an hour on each occasion. The nest was watched on two days during the incubation phase and five days throughout the nestling phase by SD (with an additional check on one day during each phase), and on two days during the 'branching' stage by N. Marshall. Tamworth nest 2 was observed by telescope at ~500 m; it was watched on three days in the incubation period, for an hour each time, by SD.

Incubation, hatching, and brooding/feeding of new chicks were inferred from parental behaviour. Parental time-budgets at Armidale nest 1 and both Tamworth nests were quantified by continuous focal-animal sampling, i.e. observing and recording the start and finish times (duration) of each behaviour, to the nearest minute. At those three nests the adults were readily sexed because each pair had an adult and an immature member (age criteria from Ridpath & Brooker 1986); when together, the sexes were identified by relative size (cf. Brooker 1996). At Armidale nest 1 the male was a fully 'black' adult and the female was a brown immature; at Tamworth nest 1 the female was a black adult and the male was a final-stage immature in 2004 and almost black in 2005; at Tamworth nest 2 the male was a pale immature and the female was almost black. Distances between focal points in nesting territories were measured with a range-finder; heights of nests above the ground were estimated from a 2-m person standing beside the tree-trunk; and tree diameter at breast height was calculated from the circumference measurement.

Pellets and prey remains (orts) were collected from below the two Armidale nests and the surrounding roosting perches during two or three visits each at the end of the nestling period, with a few items also from below Tamworth nest 1 at the stage of 'branching' behaviour (fledglings venturing to branches in the nest-tree). Prey items were identified by ABR, by microscopic examination of fur if necessary, from comparison with a reference collection. For each nest, the minimum number of prey individuals was calculated from orts, pellets and observed prey items pooled. That is, species in pellets were counted only if they were not represented in orts, and items seen brought to nests were counted only if they were not represented in orts or pellets, taking into account the age distribution of items in orts and pellets, and the number of sight records compared with orts. We did not assume that one pellet equals one prey individual and, *contra* Sharp *et al.* (2002), we did not double-count items that were represented in both orts and pellets.

For prey biomass calculations the wastage factors adopted by Brooker & Ridpath (1980) were used, i.e. 20% for prey ≤1 kg, 30% for prey >1 kg, and 50% for lambs and similar or larger animals.

Results

Most of the nest-based behaviours described for parent and juvenile Golden Eagles *Aquila chrysaetos* (Ellis 1979) were observed in Wedge-tailed Eagles. Many of these have been illustrated for the Wedge-tailed Eagle (e.g. Cupper & Cupper 1981; Olsen 1995, 2005), and definitions or descriptions of these action patterns are not repeated here.

Table 2

Nest-site characteristics of Wedge-tailed Eagle nests at Armidale and Tamworth, NSW, 2005. Nest-tree species: 1 = Manna Gum *Eucalyptus viminalis***, 2 = Blakely's Red Gum** *E. blakelyi***, 3 = Yellow Box** *E. melliodora***, 4 = Silvertop Stringybark** *E. laevopinea***, 5 = Forest Ribbon Gum** *E. nobilis***.**

Pair/nest no.	*Nest-tree characteristics*				*Height of nest above ground (m)*
	Species	*Height (m)*	*Diameter at breast height (cm)*	*Position*	
Armidale:					
1a	1	20	76	SW slope of hill	15
1b	2	20	54	NW slope of hill	16
2	3	23	57	N slope, on W flank of gully	15
3	2	24	115	Creek bank	13
4a	4	20	62	S slope, on E flank of gully	16
4b	4	24	64	S slope, on W flank of gully	20
5	1	22	70	W-facing slope	11
6	5			Upper reaches of W-facing gully	
Tamworth:					
1	3	22	124	Minor drainage line	11
2	3	20	130	Open flat	12

Eagle population

At Armidale, there was an active Eagle nest (pair/nest 3) offset between pairs 1 and 2 (4 km SE of nest 1 and 7 km NNE of nest 2), with probably another pair in between. There was also an active nest (pair/nest 4) 4 km north of nest 2; these two pairs were apparently nearest neighbours. Two other known nests (Table 2) were not the nearest neighbours of nests 1–4 or of each other. There were at least 10 pairs, probably more, in a semicircle of radius 20 km (i.e. 628 km^2) centred on Armidale.

Nest 1 was known since summer 1998–99 (i.e. established at least 7 years), when a brown subadult Eagle attended what then appeared to be a newly built nest. Pair 2 was a young pair recently established since Imbota was gazetted as a reserve in 1999; a brown immature male was first seen in spring 2002 (after intensive, daily fieldwork by SD since 2000) and the nest was built subsequently, after the reserve was kept locked to exclude vehicles and human disturbance. Both parents were final-stage (slightly brown) immatures in spring 2005. Nest 3 was known since spring 1980 when it contained a nestling; the nest was thus at least 25 years old. After an apparent lapse in occupation for several years, the territory was occupied in 2005–06 by a pair of final-stage immature Eagles.

Armidale pair 1 ranged 1.3 km south-west of the nest, 1 km west, 2 km north-west, >2 km east, and >1 km south-east of the nest, giving a likely home-range of >10 km^2. Tamworth pair 1 consisted of the same 'tame' adult female in 2004–06 inclusive, and the same individually recognisable (by his facial features and moult/plumage pattern) maturing male in 2004 and 2005.

Nest-sites

Eagle nests were sited in common local eucalypts in woodland patches, with apparently no preferred orientation or topographic position other than a tendency to be midslope on the side of a gully (Table 2). Nests were all in the top half (commonly the top one-third) of large old trees, usually within or under a leafy canopy.

Armidale nest 1 was on a wooded hill in the zone of high-density rural smallholdings (mainly grazing land) within 5 km of outer Armidale city; it was 400 m from the nearest farmhouse (at the observation point) and ~500 m from another, both in full view. The adults had several favoured roosting and perching trees: three live Rough-barked Apples *Angophora floribunda*, with solid bare limbs (below which they left orts and pellets), along the contour of the hill 20, 30 and 35 m north of the nest, and a live Manna Gum *Eucalyptus viminalis* 40 m south-west of the nest. There was a disused (alternative) nest 400 m north of the active nest.

Armidale nest 2 was on the boundary between the reserve woodland and cleared land, out of sight of farmhouses, and 6 km from the edge of Armidale city. There were no regular perches within the reserve near the nest, as the Eagles appeared to spend much time on adjoining private land.

Tamworth nest 1 was located in a eucalypt-lined minor gully 25 m west of the edge of a minor public road in agricultural land; it was 300 m west of a farmhouse, in full view. The adults used a dead perch-tree 40 m west of the nest and a live tree 50 m east of the nest, and the male used a live perch-tree 100 m south-west of the nest. The landowner (a cattle grazier, with little incentive to notice or persecute eagles), despite regularly driving past, was unaware of the nest, which was inconspicuous in the live tree-canopy though almost opposite his driveway.

Tamworth nest 2 was the nest in the 'eagle tree' described by Debus *et al.* (2005), i.e. a live old Yellow Box *E. melliodora* in a paddock, directly under the flight-path of light aircraft taking off and landing at Tamworth airport.

Armidale pair 1 did not re-use their 2005 nest in 2006; the part of the tree-canopy above the nest was recently dead, with a few dry leaves remaining, in 2005 and was bare in 2006. Armidale pair 2 re-used the 2005 nest (in a live tree) in 2006. Pair 4 used a new nest in 2005, after their regular nest-tree (used annually for many years) was dead and leafless; an older, abandoned nest was in a long-dead tree. Tamworth pair 1 re-used their 2005 nest (in a live tree) in 2006. Thus, it appeared that nests were usually abandoned within a few years of the nest-tree dying, although Armidale pair 4 re-used the 2004 dead tree in 2006.

Breeding chronology

In 2005 the adults at Armidale nest 1 were building or lining the nest by late May and laid egg(s) in the last week of June; the young hatched in early August and fledged in early November. Armidale pair 2 had large downy chicks in mid September, large feathered young near fledging in late October, and fledglings by mid November (the same timing as pair 1, i.e. laying in late June). Tamworth pair 1 had eggs in the second week of June and in mid July, and large downy chicks in early August; the chicks fledged in mid October. Tamworth pair 2 incubated in mid July and early August before failure. In 2006 Armidale pair 2 failed at the chick stage in early August, therefore laying was in June; nest 4 fledged a juvenile in mid November, therefore laying had occurred by early July. Tamworth

nest 1 was unattended on 9 June and the female was incubating on 16 June. Thus, in this region, laying occurred from early to late June (n = 5) or by early July (n = 1), with another clutch present by mid July.

Nest-building and prelaying phase

Armidale nest 1 was already well built-up in late May 2005. In the month until egg-laying in 2005, the pair mostly brought green foliage for nest-lining. Both sexes, mainly the male, brought material to the nest. During 18.5 h over 19 mornings, the male brought one stick and seven green sprays, and the female brought one green spray (total 0.5 item/h; 0.4 and 0.1/h for male and female respectively). Material was carried in the feet. On one occasion the male plucked greenery from a treetop with his foot.

During this phase the male attended the nest for 5% of observation time and the female for 12%. The male also perched in the nest-tree for 3% and the female for 1%. Both sexes arranged nest-material, crouched, shuffled and turned around in the nest; the male positioned sticks by shaking them with his bill as he inserted them in the structure, and formed the nest-cup by sitting and raking with his feet. Sometimes when the male arrived, the female moved aside while he worked in the nest. In the initial fortnight the female was not roosting on the nest on one check at sunset. In the final fortnight the adult Eagles were vocal, often calling ('yelping') on and around the nest, and in the final week the female often stood or sat in the nest.

At this stage the pair often soared high over the nesting territory, and descended to the trees on the nest hill in stages, by undulating dives ('pot-hooks', cf. Marchant & Higgins 1993); the male also performed vigorous undulating dives of equal ascending and descending amplitude, either alone or when soaring with the female. On one occasion the pair appeared to perform a boundary display, first soaring over the ridge on the skyline 1 km east of the nest, then flying north along the ridge and gliding high over the nest area to soar, with the male undulating, over the ridge on the skyline 1 km west of the nest, before finally returning to soar high over the nest. Other aerial courtship manoeuvres were not observed at this stage, but in the final week of the nestling period the pair flew past the nest hill together, with the female repeatedly turning upside down under the male; both had their legs extended, but did not touch feet. At Armidale nest 3 in the pre-egg stage in 2006, the male swept past the perched female (in a treetop) in a series of undulating dives.

Courtship (supplementary) feeding was not observed, but on one morning the adults of Armidale pair 1 returned to the nest area together with full crops, apparently having shared a food item. Food was not seen brought to, or eaten at, the nest during this phase. Although not seen during the prelaying phase, in the nestling period the male allopreened the female's nape when she lowered her head to feed the chick, and also when she arrived with prey and placed it on the nest. At Tamworth nest 2, after the nesting attempt failed at the egg or hatchling stage, the pair touched bills briefly at the nest when arranging material.

During the final week before laying, Armidale pair 1 copulated three times (in trees on the nest hill) in 4 hours over four mornings (0.8 copulation/h in this phase). Mating, obscured from view by foliage, was initiated or accompanied by loud, slow yelping calls, apparently from the female. Tamworth pair 1 copulated during the downy chick stage: after the adults arrived together on different branches

Adult Wedge-tailed Eagles mating, Blue Mountains, NSW

Plate 18 Photo: Steve Tredinnick

of the dead tree near the nest, the male alighted beside the female, they mated for ~1 minute, without calling, then he dismounted on the higher side; they continued perching side by side for 8 minutes before he retreated to the other branch.

Territorial advertisement and defence

At Armidale nest 1 during the building phase, when a juvenile Wedge-tailed Eagle soared in the valley, the female left the nest and soared as the juvenile departed. Later in the building phase, after the pair had been soaring and the male performed undulating dives, he descended to the trees in a series of undulations and the female continued to soar and perform a series of shallow undulations.

When the female was incubating, the male frequently soared and undulated over the nesting territory. During one such display he stooped at Australian Ravens *Corvus coronoides* flying over the nest hill. On five occasions the incubating male left the nest to soar and undulate before returning to sit. On at least three of these occasions, the display was directed at intruding conspecific(s): once he flew towards and undulated near two other Eagles soaring over the western ridgeline; on other occasions he performed this behaviour when there was a raptor-related disturbance in that area, or when he flew purposefully towards the area as if he had seen an intruder; and once he stood and called (yelping notes), then left to soar and

undulate over the nest hill. Similarly, the incubating female once left the nest to soar and undulate with the male, in the direction of an intruding Eagle on the eastern ridgeline, then back over the nest hill. After this and many subsequent bouts of high aerial activity throughout the breeding cycle, the adults dropped steeply to a perch, descending with the legs lowered, body nearly horizontal, and wings almost furled with the carpals held out from the body.

Australian Ravens bred on the Eagles' nest hill, and frequently mobbed the Eagles in the airspace over the Eagles' nest. In the early stages of the Eagles' nestling period, weeks 1–4 (from the hatching day onwards), the male Eagle stooped at or chased a Raven on four occasions, apparently in defence of the eaglet. In week 3 the female left the nest and soared with the male when an intruding Eagle appeared high overhead; after undulating, the male stooped towards the nest hill and chased a Raven that was flying past. In week 4 a light aircraft flying past appeared to stimulate the male to leave the nest and soar. In week 5 a Pied Currawong *Strepera graculina* swooped the Eagles' nest, apparently at the chick, as the male perched in the nest-tree; he moved to the nest as the female arrived on the rim. Also in week 5, an adult White-bellied Sea-Eagle *Haliaeetus leucogaster* appeared, soaring over the ridgeline ~1 km away; the male Wedge-tailed Eagle soared towards the Sea-Eagle, which turned away and retreated. In week 7 a Brown Goshawk *Accipiter fasciatus* landed on a branch above the Eagles' nest, and both Eagles appeared immediately from the hill trees: the female to the nest, the male soaring above, as the Goshawk left.

Reaction to disturbance

Armidale pair 1 appeared habituated to routine agricultural activity on the smallholdings in the valley, as the adults frequently soared over farmhouses. Local residents were aware of, and tolerated, the Eagles. During the prelaying phase the Eagles were apparently not disturbed by the landowner chainsawing firewood ~200 m downhill from the nest. However, during this phase they did not attend the nest while two people repaired a fence, with much loud pounding, on the hilltop ~100 m away, and they were absent when there was much loud discharging of heavy firearms within ~1 km, apparently during military training exercises in the state forest. The brooding female did not flush when a familiar person approached on horseback ~200 m from the nest, nor when a familiar vehicle approached a similar distance. When brooding or feeding the chick, she tolerated an observer's approach to within ~60 m of the nest before flushing (which happened twice, inadvertently, but the male immediately took her place as the observer retreated).

Tamworth nest 1 was discovered when council staff, working on a culvert opposite the nest (30 m away), noticed the incubating female in 2004; the nest later contained a downy chick. In 2005 the pair appeared habituated to routine agricultural activity and road traffic: the incubating female did not show any reaction to cars or trucks passing by; she watched as heavy machinery went past, but otherwise appeared undisturbed. At the chick stage, both adults (male in a roadside tree, female in the nest-tree then on the dead tree near the nest) tolerated a small excavator driving past. However, at the juveniles' 'branching' stage the male parent appeared uneasy about a car stopping and its occupants watching him, and he flushed from his perch-tree at ~100 m. Tamworth pair 2 (male in the nest-tree, female on the nest) ignored light aircraft landing past the nest-tree at treetop height. Subsequently, the male flew from the nest to a branch in the nest-

tree (possibly flushed) as a plane flew past, but he returned to the nest.

Armidale nest 2 could not be approached through dense woodland without the female flushing before the observer was within suitable viewing distance (hence, nest-watches were not conducted and the nest was not visited until the chicks were close to fledging).

Incubation

At Armidale nest 1, incubation was estimated to have started on 29 June ± 2 days (prelaying activity on 26 June, incubation in progress by 2 July). Incubation was still in progress on 10 August and a chick had hatched on 11 August, giving an incubation period of 43 ± 2 days.

Both sexes shared diurnal incubation, although the female performed most. At Armidale nest 1 the female incubated for 81% of observation time (22 h), and the male for 16%; the eggs were uncovered for 3% of time, and the nest was unattended by either adult for 2%. The female also stood on the nest for 1% of time, and the male for < 1%. The female's incubation stints always extended beyond the start or finish of watches (or both, i.e. often > 60 min.; also > 75 min., > 113 min.). The male's timed stints averaged 21 minutes (range 3–38 min., n = 6), but there were also occasions when his stints exceeded watch times (> 54 min., > 60 min.).

During some 1-hour watches the female occasionally (once per watch) stood for 1–2 minutes, changed orientation and resettled, but on others she incubated continuously. She also left the nest for 1–2 minutes to perch in nearby trees, apparently to defaecate, and once for 5 minutes to defend the territory against a conspecific. The incubating male was more restless, leaving the nest unattended for 2–3 minutes (once 9 minutes) to defend the territory against conspecifics, in the female's absence, before he returned to sit; he also occasionally changed orientation and resettled. When relieving the female, the male brought greenery and placed it on the nest while she stood and departed as he settled (two occasions); once he brought greenery and gently beaked the sitting female's wing, but she resettled after standing, then he left. On another occasion, the male arrived and nudged the sitting female with his bill until she rose; she fed for 7 minutes on a prey item on the nest while he stood, then she resettled and he departed. Twice, the relieving female arrived at the nest, and the male stood and departed while she settled. Once, after being relieved, the male soared and performed a series of undulations in a pendulum fashion over the nest area.

During the incubation period, the male brought three items of greenery in 22 h (= 0.1 delivery/h). No prey deliveries were observed; it appeared that the female mostly fed herself away from the nest during her extended absences (> 50 min.; three entire 1-h watches) while the male incubated.

At Tamworth nest 1, during two 1-hour watches, the incubating female stood once for 1–2 minutes and either preened or stretched and arranged fresh greenery before resettling; once she appeared to roll the eggs as she resumed sitting. On another day she was off the nest for > 20 minutes, perching in the rain 400 m from the nest, in the male's absence. At Tamworth nest 2 the male arrived after 30 minutes and gently nudged the sitting female's back; she stood aside while he beaked the nest contents, but he then retreated to the branch and she remained on the nest. On a later day the female incubated for the entire 1-hour watch.

Adult female Wedge-tailed Eagle at nest, Blue Mountains, NSW
Plate 19 Photo: Graham Cam

Nestling period: parental behaviour

At Armidale nest 1 both sexes shared parental duties, with the female performing most of the care of the chick. Her nest-attendance routine changed through the nestling period, from mostly brooding in the first three weeks, to standing on the nest or perching in the nest-tree (guarding) in the middle stages, to being mostly absent in the final weeks (Table 3). She first stood on the nest, rather than brooding, for >60 minutes on the warm, sunny afternoon of day 14; she appeared to cast her shadow on the chick. The male's attendance pattern showed a similar trend, although he brooded little, mostly in week 2 (Table 3). Both parents were on the nest together for a small proportion (usually <10%) of observation time, peaking just after day-brooding ceased. Both sexes tore prey and fed the chick bill to bill, until fledging though with low frequency in the later stages; the male's contribution complemented that of the female (Table 3). These trends in parental attention parallelled the growing and feathering chick's ability to thermoregulate and feed itself on prey stored in the nest (cf. Table 5).

In week 1 the female brooded almost constantly, standing, feeding the chick or eating for periods of 3–18 minutes. The male sometimes tried to feed the chick, or brooded it, while the female fed herself. On day 7 the nest was unattended for 1 minute when she left briefly for the hill trees and the male then arrived. Her brooding stints extended beyond the start or finish times (or both) of watches, i.e. often >60 minutes, though she occasionally rose and resettled. Behaviour was similar in week 2, except that the female left the nest for the hill trees as the male arrived in the nest-tree. The male seemed anxious to brood, once bringing greenery and waiting but the female did not relinquish her position; he brooded for one stint of >30 minutes when she left the nest. In week 3 the nest was unattended by either parent for periods of up to 9 minutes, but the female was usually in the hill

Table 3

Parental time-budgets of a Wedge-tailed Eagle pair at Armidale, NSW (nest 1: see text) in the nestling period, August–November 2005: % observation time (total 94 h) spent in each activity. Stand = adult standing on or beside nest (includes adult feeding itself); in tree = adult perched elsewhere in nest-tree; absent = female away from nest; unattended = neither adult at nest. Numbers in parentheses = no. of hours observation in each week. Week 1 = first week after hatching.

Sex/activity	*Week*												
	1 (7.0)	*2 (8.5)*	*3 (7.0)*	*4 (6.0)*	*5 (5.0)*	*6 (5.0)*	*7 (6.0)*	*8 (4.5)*	*9 (6.7)*	*10 (5.0)*	*11 (6.0)*	*12 (14.2)*	*13 (12.8)*
Female:													
Brood	79	67	74	4[a]			11[b]						
Stand	9	17	5	36	31	55	21	19	7	3	4	11	17
Feed chick	12	7	1	17	10	14		10	14				<1
In tree		1	1		1		10						5
Absent	<1	9	19	43	59	31	58	71	80	97	96	89	79
Male:													
Brood	<1	6	<1										
Stand	4	6	14	33	15	13	4		4		7	3	5
Feed chick			1			<1	5				3		
In tree	<1	1	2	6	12							3	5
Unattended	<1	1	9	11	57	30	58	55	75	97	87	87	74
Both at nest	4	5	5	9	8	12	5	15				2	

[a]Day 22, but not thereafter

[b]Large chick partly under brooding female at dusk on day 43 and during storm on day 48

trees within 100 m (except once when both defended the territory). During her longer absences, the male was usually on the nest or in the nest-tree. Sometimes, when she left for the trees, she called and he went to the nest. The female preened the chick in week 2, and the male appeared to do so in week 3.

Day-brooding ceased early in week 4 (except for a stormy afternoon in week 7), and night-brooding continued until at least week 7 (Table 3). From weeks 4 to 6, if the female left the nest the male sometimes stood on it, and if the nest was unattended an adult was often in the nest-tree, in the hill trees or soaring over the nest area. Thereafter, the chick was often left alone although an adult was sometimes in the hill trees or soaring. The female was on the nest at sunset, apparently to roost, in week 9, but by week 12 she roosted in the hill trees. On a warm morning in week 5, when the chick was panting in the sun, the female arrived and moved between the sun and the chick so that her shadow fell on the chick, though she did not spread her wings. The panting chick was not shaded in week 9.

The duration of feeding sessions, and the amount of food taken by the chick, gradually increased as the chick grew (Table 4). After week 6, the parents rarely fed the chick bill to bill. Feeding sessions occurred throughout the day, in all 2-h time blocks; the frequency of feeding sessions was higher in the early mornings,

Table 4

Parental feeding of nestling Wedge-tailed Eagle, Armidale, NSW, August–November 2005 (nest 1, see text): chick's meal sizes and morsel consumption rates. F = female, M = male parent.

Week	*Length of parental feeding bout*	*No. morsels taken by chick*
1	F: 3 min. to >11 min. (n = 8)	25 morsels in one 9-min. session (= 2.8/min.)
2	F: >8 to >15 min. (n = 3)	35 morsels in one 10-min. session (= 3.5/min.)
3	M: 3 min. (n = 1); F: >3 min. (n = 2)	Eight pieces, larger than before, in 3 min. (= 2.7/min.).
4	F: 38 min., 10 min. (n = 2)	In 38 min. peak rate was one piece per 4–5 sec. over 8 min.; also 47 pieces in 10 min. (= 4.7/min.)
5	F: 30 min. (n = 1)	145 pieces in 30 min. (= 4.8/min.)
6	No data (F)	At end of feeding session, replete chick intermittently took food over 49 min., but sometimes refused F's offerings; in two other sessions took food at usual rate of one piece per 4–5 sec.
7	M: 18 min. (n = 1)	One piece per 3 sec.
8	F: the longer of two feeding sessions lasted >21 min.	Usual rate (one piece per 4–5 sec.)
9	F: 6 min. (n = 1)	As for week 8, then chick fed itself; during another session feeding was intermittent over 49 min., during which chick sometimes fed itself.

0600–0800 h (2.6 sessions/h) than in the other time-blocks (0.3–0.5 session/h; see Table 1 for number of observation hours in each block). The frequency of parental feeding sessions declined through the nestling period, as the chick became capable of feeding itself. In 3-week blocks from weeks 1–3 to weeks 10–12 and in week 13, the number of parental feeding sessions per hour was 0.6, 0.8, 0.3, 0.1 and 0.1 session/h respectively (see Table 3 for number of observation hours per week).

The adults frequently ate prey or scraps on the nest, and took prey remains from the nest into the hill trees (at a rate of 0.1 item/h), where they dumped the remains. The male twice took a whole rabbit from the nest into the hill trees, and the adults occasionally brought pieces of prey from the trees, where the items had apparently been cached, to the nest. The female once took a pellet, in her bill, from the nest into the trees, and once tossed a pellet out of the nest.

Throughout the nestling period the adults brought nest-material at a combined rate of 0.1 item per hour of observation time (94 h): six green sprays and a long strip of bark by the male, three green sprays and two sticks by the female. Greenery was observed brought to the nest in weeks 1–5 and week 12, and fresh green foliage was on the nest in weeks 6, 7, 11 and 13 (fledging day). Items were often carried in the feet (e.g. bark strip by the male, large green spray by the female), but the female brought a twiggy branch in her bill.

Behaviour at Tamworth nest 1 was similar. At the large downy chick stage, when not standing on the nest the adults were in the nest-tree or their nearby perching trees, or absent. The female collected greenery from the nest-branch in her bill. At the feathered nestling stage, the male was standing on the nest when

Wedge-tailed Eagle chick, Blue Mountains, NSW

Plate 20 Photo: Steve Tredinnick

the female left prey for the young to feed themselves; after the older nestling had eaten, the male fed the begging younger one bill to bill (~25 pieces in 8 minutes = 3.1/min.). In the nestlings' final fortnight and at the stage of venturing to branches in the nest-tree, the adults (if present) were in the nest-tree or perch-trees.

Nestling period: development of young

At Armidale nest 1, one chick fledged from an undetermined number of eggs or hatchlings, although there may have been a second chick until day 8 (Table 5). The chick was downy for its first five weeks, with remiges emerging in week 3; from week 6 feathers gradually appeared dorsally, ventrally, then finally on its head, until at 11 weeks it was mostly feathered with some down on the neck (Table 5). Down persisted on its underwings until fledging at 13 weeks, when its primaries and tail were still incompletely grown. From hatching on 11 August to first flight from the nest-tree on 9 November gave a nestling period of 90 days, although the juvenile jumped and flapped from the nest to adjacent branches in the nest-tree (= 'branching') from 78 days old.

The chick could sit up and raise its head above the nest-rim in week 3; it defaecated over the rim at that stage, and possibly earlier (day 8: Table 5). It walked around the nest-rim and flapped its wings in week 4; pecked at nest-material in week 6; and practised 'killing' objects in the nest from week 8. It first fed itself, on prey left in the nest, on day 60. From week 7 it jumped and flapped on the nest; in week 11 it engaged in much pre-flight practice, with venturing to branches in the nest-tree in week 12 (Table 5).

Table 5

Growth and development of nestling Wedge-tailed Eagle, Armidale, NSW, August–November 2005 (nest 1: see text). Chick not sufficiently visible in weeks 1–2 to ascertain plumage details. F = female parent, M = male.

Week	*Day*	*Comments*
2	8	Small jet of whitewash from within nest, originating from in front of brooding F: chick defaecated over rim? F brooding second chick?
3	16	Chick moving on nest.
	17	Downy chick's raised head visible above rim.
	18	Chick sat up and nudged F's bill.
	21	Chick downy with dark trace on wing edges; defaecated over rim.
4	24	Active; walked around nest-rim.
	26	Downy with dark rear edges to wings; flapped clumsily.
5	31	Primaries emerging.
	34	Remiges and rectrices emerging, cere visible.
	35	Scapulars and upperwing-coverts emerging.
6	37	Flapped wings.
	40	Wings feathering.
	42	Upperwings feathered, tail emerging, pins on hindcrown, gape yellow; pecked stick.
7	43	Flank/thigh feathers emerging.
	44	Feathered dorsally except head; head pins burst.
	48	Ventral feathers emerging; jumped and flapped wings.
8	55	Head feathering but still partly downy.
	56	Crown feathers emerged, underwings downy, remiges and rectrices well ensheathed; yelping calls; foot-stabbed at branch.
9	60	Chick fed itself: stood on prey, tore, ate pieces with similar frequency to F; gagged on large piece of food before giving up and being fed by F; played with stick.
	61	Well feathered; some down around nape, chin and throat; gape yellow, cere cream.
10	64	Still some down on neck.
	66	Underwings downy, primaries and tail short, downy nape-stripe and neck-stripes.
	70	Wings and tail slightly longer; bill-stabbed in nest, tossed pellet with bill, beaked and footed sticks and branches.
11	73	Downy on nape and underwings.
	74	Flapped on nest-rim, lifted 15 cm into air several times; flew across nest with two buoyant leaps, then with one buoyant bound 30 cm into the air; rearranged greenery.
12	79	Bounced around nest, lifting off higher than before (>30 cm); once perched in small branches 60 cm above nest, balancing with open wings, ungainly.
	80	Vigorous flapping and rising from nest, 60 cm above and maintaining position briefly; later hovering briefly; F dropped prey on rim as she arrived, young seized prey with foot.
	82	Fully feathered, primaries and tail short; jumped to nest-branch and back, performed 'killing' behaviour towards stick, repeatedly crouched with half-spread wings in flight-intention posture, sunned on nest with wings spread.

Table 5 Continued

Week	*Day*	*Comments*
12	83	Repeatedly jumping to branches in nest-tree, flapping on branch; 'attacked' greenery delivered by M.
	84	Frequent flight-intention movements; more sunning.
13	85	Pounced on delivered prey (small Rabbit), tore, ate; then jumped on it and performed 'killing' behaviour with feet.
	86	Repeatedly jumped to branches 1–1.5 m above nest, in treetop, and back to nest; flapped and rose 50 cm off branch. Primaries and tail still short.
	87	Chased harassing Grey Butcherbird *Cracticus torquatus* off nest; more jumping and flapping to high branch in nest-tree.
	88	Repeatedly jumped and flapped to high branch and back to nest; underwings downy.
	90	Last day on nest before flying from nest-tree on day 91.

Nestling behaviour and development at Tamworth nest 1, which fledged two young, were similar to those at Armidale nest 1 (cf. Table 5). At the large downy stage, with primary pins, the chicks sat high in the nest, pecked at objects, preened, stood, and tottered around the nest (the younger with the aid of its wings). There was no sign of rivalry or pecking, although one was larger than its sibling. At the feathered stage, the older one fed on delivered prey while the younger waited its turn; if the older nestling returned for more food, the younger sibling retreated. About a fortnight from the stage of 'branching' behaviour, one nestling played with dry greenery then jumped and flapped; both nestlings had a yellow cere and gape, and pale-yellow feet. At the 'branching' stage they repeatedly jumped and flapped between the nest and nest-branch, lifted off the nest (40 cm) and flew from one side to the other, made flight-intention movements, flapped on the branch, and ventured to other branches around the nest. At that stage their primaries and tail were still noticeably short.

Fledging

Early in the morning of the fledging day the Armidale 1 juvenile was on the nest, calling (yelping begging-calls), as the male perched in the nest-tree in the female's absence. After the male flew to the trees on the nest hill, the juvenile jumped and flapped on the nest, calling. After ~30 minutes, in the absence of the parents, it suddenly launched off the nest north over the treetops along the nest hill, flapping continuously at first, then gliding before turning into the trees where the adults often perched. There was no calling or other behaviour by the adults, and the juvenile flew competently for ~100 m. Over the ensuing 10 minutes, while the juvenile perched, there was no detectable calling or other behaviour from any of the Eagles. In late morning the nest was vacant and the adults appeared from the hill trees, soaring then departing; the male returned with prey and took it to a tree near the nest.

In the late afternoon the juvenile was back on the nest with both parents; the adults departed then returned (female to the nest-branch, male to the nest), and the male delivered prey. After clutching and tearing at the prey, the juvenile jumped on it and performed 'killing' behaviour. At sunset the adults remained perched at the nest while the juvenile fed.

Wedge-tailed Eagle feathered nestling, Blue Mountains, NSW

Plate 21 Photo: Steve Tredinnick

Young Wedge-tailed Eagle 'brancher', Blue Mountains, NSW

Plate 22 Photo: Steve Tredinnick

At Tamworth nest 1, the juveniles were performing 'branching' behaviour vigorously on 11 October, on 12 October one was in the nest-tree and one in the nearby dead tree (40 m away), and on 14 October neither could be found in the immediate nest area (N. Marshall pers. comm.).

Post-fledging period

At Armidale nest 1, in its first week the juvenile mostly perched in the hill trees, but was mobile between the nest and trees; on day 3 it was with both parents on the nest. It roosted in live trees in the nest area or (on day 6) back on the nest. On day 3 its wings and tail appeared almost adult in proportion; by size (compared with its parents) it appeared to be a male. At fledging, the juvenile was darker sooty brown ventrally, and richer rufous dorsally, than its blonde-naped, brown mother's worn plumage. However, during the post-fledging phase the female started moulting and acquired some blacker feathers.

In weeks 2 and 3 a dead paddock tree ~250 m south-east of the nest, halfway between the nest and a farmhouse, became the focus of post-fledging activity. However, the juvenile roosted on the nest on day 9 and in the nest-tree on day 10. From week 2 it accompanied its parents at kills in the nest area (within 300 m), and was fed on the focal dead tree. It first soared in week 2 (day 11), in spirals on day 12, and high with its parents in week 4. By this stage it ranged 500 m from the nest. Thereafter, it ranged increasingly farther and became more competent at soaring, but was still dependent until the last sighting in week 19 (day 129; Table 6). It attained adult proportions in week 2 or 3, apart from broader wings, and from week 3 its rich colours started to fade so that it contrasted less with the blonde female. In week 4 the male and juvenile interacted briefly when they approached closely in high soaring flight.

In the early stages of the post-fledging period, as in the nestling period, the adults were alert to human approach towards the nest or fledgling. The male often soared over to observe an intruder, and both guarded the new fledgling. In the post-fledging period an approaching farm vehicle flushed the trio; the juvenile flew to the focal dead tree and, when an observer was ~100 m away, the female alarm-called (loud, slow contralto yelps with the emphasis on the higher second syllable, almost hoarse) and the juvenile flew off.

At Armidale nest 2 the two large feathered juveniles were almost at the stage of 'branching' behaviour on 22 October (exact age unknown), and had fledged by 15 November when they could not be located in the immediate nest area. On 29 November they appeared adult in proportion, with creamy yellow cere, gape and feet, and were at a similar stage to the Armidale 1 fledgling (i.e. fledged ~3 weeks). One was back on the nest, and the other was on the ground ~50 m from the nest with a full crop, having fed; it flew competently to a tree near the nest-tree. At ~4 weeks after fledging, both were perched on logs on the ground, in a paddock within 50 m of the nest; they flew off, one >200 m into the woodland around the hillside. At ~5 weeks one was in a tree near the nest then flew off, joined by both adults. At ~6 weeks one juvenile gave begging-calls from woodland ~300 m from the nest, and at ~8 weeks one was on a log in woodland ~250 m from the nest. They thus stayed close to the nest for longer than the Armidale 1 fledgling, in more extensive woodland cover; the one seen on the last two occasions appeared (from its size) to be a female. The begging-calls of this individual were loud and insistent, its yelping calls interspersed with a long chittering note. At ~11 weeks and thereafter, the juveniles could not be located in the reserve, but

Table 6

Development of juvenile Wedge-tailed Eagle in post-fledging period, Armidale, NSW, November–December 2005 (nest 1: see text). J = juvenile, F = female parent, M = male. Focal dead tree = tree in paddock (sparse woodland) ~250 m SE of nest (see text).

Week	*Day(s)*	*Comments*
2	8	Flew 300 m, made gliding turn, circuit back to nest-tree, slightly clumsy landing in tree. Jumped and flapped on nest. Still slightly short in wings and tail; appeared short-tailed, broad-winged in flight (cf. adults). J roosted in live tree near nest-tree.
	9	Family (M, F, J) in focal dead tree in nest area; J roosted on nest.
	10	J in hill trees; flew strongly (round-winged, short-tailed). Roosted in nest-tree, below nest.
	11	J soared, to several times treetop height (50–100 m); appeared more adult-shaped, tail wedged when spread.
	12	J soared in spirals on set wings, to ~100 m, 5 minutes; gliding descents. Adult-like shape, slightly 'wobbly', lowered feet.
	13	Family on ground with prey (at Rabbit warren); then with prey in focal dead tree. F fed first, then M; J waiting.
	14	Family in focal dead tree; adults perch-hunting above warren? J appeared adult in shape and proportions, rich tawny colour (redder than blonde F), with pale tail-tip.
3	15–17	Family on focal dead tree; day 16 M and F roosted in nearby live tree, J still on dead tree (roosting?). J tawny colour fading from day 16: more blonde (like F). Day 17, J tail appeared adult in length.
	20	J on focal dead tree, F delivered prey.
4	22	J alone 500 m E of nest.
	25	J soared high competently with parents; adult proportions, but broader wings (longer secondaries). J performed minor manoeuvres with M when wind-soaring.
5	29	Family together 800 m E of nest, in tree after sharing kill on ground.
	34	Family together 1 km E of nest; often in this area subsequently (R. & S. Trémont pers. comm.).
8	51	Family together 1 km E of nest (R. & S. Trémont pers. comm.).
9	60	M, F soaring together, J in loose association.
10	69–70	Family soaring high together, 1 km E of nest (S. Trémont pers. comm.).
11	74	As above; J calling (begging?) (S. Trémont pers. comm.).
12	79	Family soaring high together; J mildly harassed intruding yearling (moulting) Eagle that passed high through territory.
14	95	Parents soaring high in nest area; J soared very high, competently like adults; no longer in close association as trio.
19	129	Family together on ground, apparently with prey; J begging (S. Trémont pers. comm.). Last sighting of J.

they may have been on adjoining private land. The post-fledging dependence period thus lasted at least 2 months, and probably longer.

In another Eagle territory near Armidale in late February 2005 (~3.5 months after local fledging time), an advanced juvenile accompanied its foraging parents as they descended into a gorge then soared up quartering the cliff-face, apparently hunting Brush-tailed Rock-Wallabies *Petrogale penicillata*. The adults quickly rose up beyond the gorge-rim, but the juvenile lagged well behind on the ascent as it

seemingly struggled to master the updraughts, before finally joining the soaring adults and giving begging-calls.

At Armidale nest 1 the post-fledging dependence period, from 9 November to the last sighting on 17 March 2006, lasted just over 4 months. Thereafter, in early April, dispersal of juvenile Eagles was observed when a 'wave' of >5 single individuals passed along a wooded ridge in the region, gliding out of sight in the same direction, over several minutes. In mid April the adults of pair 1 were in the nest area: the male undulating and the female soaring high, with no sign of the juvenile.

At Armidale nest 4 in early March 2007, the 2006 juvenile soared competently in an adult-like manner, alone, up to ~1 km from the nest, almost 4 months after fledging. At Armidale nest 1 in early April 2007, the 2006 juvenile (apparently female by size) was still begging and associating closely with its parents almost 5 months after local fledging time. By this stage the female parent was blacker than in 2005–06, especially ventrally, with adult-like pattern on the underwing and wing-shape, though still some dorsal brown (rusty rather than blonde nape, darker and narrower brown band on the upperwing). By mid April the juvenile was not seen with the adult pair.

Breeding productivity

Combining the fledging results herein for Armidale nests 1 (brood of one) and 2 (brood of two) and the two Tamworth nests (brood of two, nil) with those for Armidale pairs 3 (did not breed) and 4 (brood of two) in 2005 gave seven young in six pair-years or 1.2 young per pair. Three of four successful pairs raised two fledglings (1.8 per successful pair). Nest 4 over many years has usually hatched two chicks but fledged one young annually; in 2005 this pair used a different nest (G. Hannon pers. comm.). In 2006, Armidale pairs 1–4 raised one (in an alternative nest), nil, nil and one young respectively, and Tamworth pairs 1 and 2 raised one and nil young respectively (= three young in six pair-years or 0.5 young per pair). The combined result for 2005 and 2006 was 10 young in 12 pair-years, or 0.8 young per pair per year.

Feeding rates

At Armidale nest 1, no prey deliveries were observed until the nestling period, when 12 prey items were delivered to the nest in 94 h of observation (0.1 delivery/h or ~1 per day). However, deliveries at possible peak hunting times (the first 1–2 h of daylight) may have been missed, as only five watches started before 0800 h and only two by 0730 h, but parental chick-feeding sessions peaked before 0800 h. Observed deliveries ranged from none in a week to two in a day, but there was usually fresh prey on the nest (sometimes one fresh item when stale remains were dumped). There was sometimes a surplus of food, as suggested by the chick's occasional disinterest at fresh prey deliveries. The male occasionally arrived without prey then fed on an item in the nest.

The male delivered five items, of which he was observed to catch two, and the female delivered seven items, of which she was observed to catch four (see Diet and hunting section for descriptions of prey captures witnessed). Of the remainder, the male was seen eating one item in the hill trees before he brought it to the nest; the female brought two items apparently retrieved from caches in the hill trees; in one case both adults arrived together, with the male bringing partly eaten prey

(the pair apparently having shared a kill); and in one case both adults brought parts of a prey item possibly from a cache or a shared kill. The female's first two deliveries, in weeks 2 (day 11) and 4, were apparently from caches (in the male's absence she went to the hill trees and returned immediately with prey); her first observed kill was in week 5 (day 30).

In the first three weeks of the post-fledging period, the adults brought five prey items to the juvenile in 18 h of observation (0.3 delivery/h). The male brought two items to the nest in weeks 1–2, the female brought one item to the nest area in week 1 and to the juvenile on the focal dead tree in week 3, and late in week 2 the female ate part of a kill before the male ate some then gave the remainder to the juvenile on the dead tree. Thereafter, the juvenile accompanied the adults to their kills away from the nest area.

Diet and hunting

Twenty-eight intact pellets averaged 66 × 32 mm (36–98 × 26–43 mm). The Eagles' diet at the two Armidale nests consisted of 74% mammals (56% Rabbit), 22% birds and 4% reptiles by number, and 89% mammals, 11% birds and <1% reptiles by biomass (Table 7, which gives scientific names). Introduced lagomorphs contributed 56% of prey biomass (Rabbit 40%, Hare 16%), and macropods much of the remainder (25%). Livestock was unimportant by number or biomass, and at least one of the three items (two lambs, one kid) was carrion.

At Armidale nest 1, proportions in orts were 92% mammals (19 Rabbits, one Hare, one Goat kid), 4% bird (one Australian Magpie) and 4% lizard (one dragon). In pellets (n = 41) Rabbit occurred in 38 (93%), and Goat, wallaby and Magpie in one each (2% each, or mammals in 98%). Observed prey items delivered to the nest or juvenile Eagle were 19 Rabbits (73%), one Australian Wood Duck (4%), one Noisy Miner (4%), one unidentified bird (4%), and four unidentified items (e.g. parts of prey brought from caches; 15%) that were assumed to be represented in orts or pellets. Additional items observed being eaten in the nest area, but not taken to the nest nor found in orts or pellets, were one half-grown Eastern Grey Kangaroo (unknown whether live prey or carrion) and one lamb (carrion): mammals thus formed 88% and birds 13% of 24 identified observed items. There was fairly close agreement between the three methods of prey detection, with each method detecting a few species not detected by the other two; 19 observed Rabbits were matched by 19 individuals in orts.

At Armidale nest 2, proportions in orts were 61% mammals (eight Rabbits, three Hares) and 39% birds (one each of fowl, turkey, Wood Duck, Straw-necked Ibis, Tawny Frogmouth, and two Magpies); in nine whole pellets Rabbit occurred in five (56%), Hare in three (33%) and Magpie in one (11%), or mammals in 89%. Among ~39 pellets (including ~30 fragmented ones), mostly of Rabbit, Hare and bird in approximately these proportions (i.e. ~56, 33 and 5% respectively), lizard scales and lamb's wool occurred in one pellet each (3% each of total pellets). Orts revealed more prey species than in pellets, but two species in pellets (wallaby, lamb) were not detected in orts. The origin of the wool (i.e. from a kill or scavenging) could not be determined, but there was no lamb in orts.

Incidental prey items below an Eagle nest 140 km north-west of Armidale in December 2005 were Common Brushtail Possum *Trichosurus vulpecula* and Australian Wood Duck remains. Incidental prey items at the Tamworth 1 nest were one Rabbit observed brought to the nest, and subsequently Rabbit remains

Table 7

Breeding diet of Wedge-tailed Eagle at Armidale, NSW (nests 1 and 2: see text), 2005: minimum number and percentage (% n) of prey individuals from orts, pellets and observations pooled (rabbits and hares by skull and bone count; birds by bone or remex/rectrix count; lizard by jawbone). [O] = observed, [R] = orts, [P] = pellets. For biomass and percentage (%), figures are minus the appropriate wastage factor for the species' body weight (following Brooker & Ridpath 1980). Prey weights from Debus (1984), Marchant & Higgins (1990) and other *HANZAB* volumes, Strahan (1995) and Winkel (2007), adjusted (by estimate) for age of individual as appropriate (kangaroo, kid).

Prey species	*Weight (kg)*	*Nest 1*	*Nest 2*	*Total*	*% n*	*Biomass (kg)*	*%*
[O]Eastern Grey Kangaroo *Macropus giganteus*	20	1		1	2	10	14
[P]Red-necked Wallaby *Macropus rufogriseus*	16	1		1	2	8	11
[ORP]Rabbit *Oryctolagus cuniculus*	1.5	19	8	27	56	28.4	40
[RP]Brown Hare *Lepus capensis*	4	1	3	4	8	11.2	16
[OP]Lamb *Ovis aries*	3.5	1[a]	1	2	4	3.5	5
[RP]Goat kid *Capra hircus*	3.5	1		1	2	1.8	3
Total mammals		**24**	**12**	**36**	**74**	**62.9**	**89**
[R]Domestic Fowl *Gallus gallus*	1		1	1	2	0.8	1
[R]Domestic Turkey *Meleagris gallopavo*	5		1	1	2	3.5	5
[OR]Australian Wood Duck *Chenonetta jubata*	0.8	1	1	2	4	1.3	2
[R]Straw-necked Ibis *Threskiornis spinicollis*	1.4		1	1	2	1.0	1
[R]Tawny Frogmouth *Podargus strigoides*	0.3		1	1	2	0.2	< 1
[O]Noisy Miner *Manorina melanocephala*?	0.06	1		1	2	0.05	< 1
[RP]Australian Magpie *Gymnorhina tibicen*	0.3	1	2[b]	3	6	0.7	1
[O]Unidentified bird	0.5[c]	1		1	2	0.4	1
Total birds		**4**	**7**	**11**	**22**	**8.0**	**11**
[RP]Tree Dragon *Amphibolurus muricatus*	0.05	1	1[d]	**2**	**4**	**0.08**	**< 1**
Total		**29**	**20**	**49**	**100**	**71.0**	**100**

[a]Carrion: Eagle seen eating carcass of lamb that had died

[b]One juvenile (262 g)

[c]Weighted mean of identified birds

[d]Dragon scales, probably this species

Adult Wedge-tailed Eagle hunting, Blue Mountains, NSW

Plate 23 Photo: Steve Tredinnick

in orts (two individuals) and a pellet, and feral Rock Dove *Columba livia* feathers.

At Armidale nest 1 the adults were observed hunting or capturing prey on 11 occasions in the nestling and early post-fledging periods:

1. Nestling week 2, 1430 h: the male (in the nest-tree) left, soared and undulated in display over a paddock (near ewes and lambs) for 2–3 minutes; after soaring for 1–2 minutes he made a drop-attack onto a Rabbit, clutching it on the ground for 1 minute then taking it (via hill trees, where he opened the carcass) to the nest. The female (on the nest) had flown towards his kill, but returned to the nest before he did.

2. Nestling week 5, 0905 h: the female, apparently perched on the nest hill, flew directly at treetop height then made a long, slanting glide-attack onto prey on the ground in a paddock >500 m away. After 1 minute she carried large prey (possibly Rabbit) to the hill trees then, after 3 minutes, to the nest. The male (which had been in the nest-tree) had followed her to the kill, but returned to the nest before she did.

3. Nestling week 6, 1405 h: the male (on the nest) peered and bobbed, then flew low to the ground amongst nearby trees (within ~100 m), followed by the female (from the nest); both returned to the nest hill, unsuccessful.

4. Nestling week 7, 1540 h: the female was on the ground and logs (near a Rabbit warren) 1.3 km from the nest, trying to catch prey that had eluded her first strike and had taken refuge. She gave up and returned to the nest.

5. Nestling week 9, 1245 h: the male, soaring for an undetermined time (<20 min., partly out of sight), dropped towards the ground within 100 m of the nest and made a strike from a steep glide-attack, with his wings retracted; he took small prey to the hill trees then (after 4 min.) to the nest.

6. Late nestling period: the male, ~1 km from the nest, made a fast, shallow, low-level attack, around dense sapling regrowth, at free-range poultry within 100 m of a house, but was unsuccessful (S. Trémont pers. comm.).

7. Nestling week 11, 0905 h: the female was on the ground below the nest (~50 m away), apparently having failed to complete her first strike; she chased and caught a (possibly disabled) Rabbit on foot after a few steps, tore at it and plucked it on a log (where the male waited beside her), then took the prey to the nest.

8. Nestling week 13, 0655 h: the female, which had been in the nest-tree, made a long, low glide-attack onto a small Rabbit in a paddock 500 m away; she made a last-second adjustment and brief chase as the prey tried to dodge her strike, but she clutched and pecked it, then took it to the nest.

9. Nestling week 13, 1150 h: after high aerial activity (male undulating), both adults soared for 8 minutes; the male, then female, dropped into ridge woodland and made a fast, shallow glide-attack low to the ground, in tandem (outcome unseen).

10. Post-fledging week 1, 1800 h: the male left the nest-tree on a direct flight low into woodland >500 m away, followed by the female; 2 minutes later he returned to the hill trees with a small Rabbit, then (after 3 min.) gave this to the fledgling on the nest (to which the female had returned).

11. Post-fledging week 2, 0620 h: the pair left the nest hill and soared together over a ridge for 4 minutes, wind-hanging in characteristic hunting posture with head bent down, wings and tail fanned, carpals held forward and alulae projecting; the female made a drop-attack amongst the trees, followed by the male, then after 1 minute she rose with a small Rabbit and took it to the hill trees, followed by the male, which undulated as he arrived.

Thus, of 10 observed strikes, eight were successful (80%); opportunistic forays often resulted in a quick capture. For eight observed search-and-attack sequences, four glide-attacks were launched from a perch and four attacks from soaring flight, in which the Eagle dropped onto prey (twice) or dropped into a low-level glide-attack (twice).

The adults were observed feeding on carcasses in the nest area on two occasions in the nestling period:

1. The brooding female left the nest (relieved by the male) and soared, then descended to a paddock where she fed on a dead lamb; on that day the ewes and lambs were in the adjoining paddock. (This was the first occasion, on day 10, that she was seen foraging after the chick hatched.)

2. Both adults were at the nest; the female left, followed by the male, and flew directly to the fresh (already opened) carcass of a young Grey Kangaroo in a paddock ~300 m away; the female fed while the male stood beside her on the ground. They appeared to be revisiting a known food source, probably killed (by an unknown agent) earlier in the day.

Discussion

Breeding biology

This study and other recent data (Harder 2000; Allott *et al.* 2006; Collins & Croft 2007; Silva & Croft 2007) confirm that in south-eastern Australia the Wedge-tailed Eagle lays eggs mainly in winter (June–July), a little earlier than the July–August peak shown by Olsen (1995). However, the latter data were from egg collections rather than precisely determined laying dates. Recently determined incubation periods (~43 days, mean 44 days, 42 days: this study; Harder 2000; Allott *et al.* 2006) add to the previously small sample, and support a duration of 42–43 days per egg (Olsen 2005); they suggest that longer reported values of up to 48 days are per clutch rather than per egg, given that hatching is asynchronous (cf. Marchant & Higgins 1993). Nevertheless, 43–45 days may be reasonable (as for the Golden Eagle, cf. Watson 1997), though further data are required.

Recently determined nestling periods (90 days, mean 79 days, 87 days: this study; Harder 2000; Allott *et al.* 2006) also add to the previously small sample, and confirm that time to first true flight from the nest-tree is 11–13 weeks. Lower values of 10–11 weeks probably represent 'branching' behaviour before first true flight (e.g. at 72 days: Silva & Croft 2007; cf. Marchant & Higgins 1993). Conversely, fledglings may return to the nest and behave as if they had not yet fledged (as also observed by Allott *et al.* 2006), leading to possible overestimates of the nestling period unless observations are frequent at fledging time.

Fledgling productivity in New England in 2005 was at the high end of the recorded range for this species, with over half of successful pairs raising two young (cf. Marchant & Higgins 1993; Harder 2000; Davey & Pech 2004; Fuentes *et al.* 2004; Dennis 2006; Collins & Croft 2007; Silva & Croft 2007). Productivity was low in 2006, but the average for 2005–06 combined was typical for this species in the temperate zone (cf. Marchant & Higgins 1993). However, long-term data for New England, from a larger sample of nests, are needed. The rabbit calicivirus has had negligible effect in New England, where Rabbits are still abundant (SD pers. obs.).

Breeding behaviour

The Eagles' displays were much as previously described (cf. Marchant & Higgins 1993; Olsen 1995, 2005), with this study adding some context. Elements of courtship and copulation were also much as previously described, and in some cases occurred through the breeding cycle. Sex-roles, parental time-budgets and the frequency of various activities (prey delivery, foliage delivery, removal of food remains) in the incubation and nestling periods were similar to those previously recorded, including trends in parental care and nest attendance during the chick's growth (cf. Harder 2000; Collins & Croft 2007; Silva & Croft 2007). These aspects were previously unquantified for the prelaying period.

Although the sample of nests in this study was small, it enhances the composite picture from other small samples. It is apparent that males are closely involved in all aspects of nest-based parental care (though taking a minor share of incubation and brooding), that they have a substantial role in nest-renovation and maintenance, and that relations between mates are amicable. The Eagle trio reported by Cupper & Cupper (1981) was probably the adult pair (rather than two females) at the nest, and an unattached, non-territorial bird (perhaps a previous offspring) associating loosely. Furthermore, observer presence may have prevented the male from visiting another nest observed by Cupper & Cupper (1981); in our study, the male delivered prey to the nest rather than the female leaving the nest to take prey from him.

Juvenile development

Nestling growth stages were similar to those previously reported (cf. Marchant & Higgins 1993; Harder 2000; Olsen 2005; Allott *et al.* 2006), with this study adding detail to previous descriptions of the behavioural development of Wedge-tailed Eagle nestlings. There was no indication that adults performed enticement behaviour (e.g. with prey) to induce young to fledge, but rather continued to deliver prey to the nest after the young had fledged. Feathered nestlings and fledglings in this study had cream to yellow bare parts (cere, gape and feet; *contra* Marchant & Higgins 1993).

It is worth noting that the photographs of an 'immature' Wedge-tailed Eagle and a 'pair… at nest' in Olsen *et al.* (1993: pp. 71–72) are, respectively, a prematurely fledged juvenile and two sibling fledglings. Much historical disagreement and confusion over juvenile versus adult or at least parental plumage characters has been confounded by the fact that some Eagles breed in immature plumage; new fledglings are darker ventrally and more richly coloured dorsally than subadult parents in worn brown plumage. In this study, initially immature (brown) breeders acquired blacker plumage over successive years, as found by Cupper & Cupper (1981).

Fledging and post-fledging behaviour were much as described by Allott *et al.* (2006). The post-fledging period and independence of juvenile Wedge-tailed Eagles have been little studied; our results seem typical for the Wedge-tailed Eagle, so far as is known (cf. Marchant & Higgins 1993; Olsen 2005; Allott *et al.* 2006). It appeared that, at Armidale, the latter stages of the post-fledging period, until independence, included accompanying the parents to their foraging grounds and kills. Aerial interaction between a male and fledgling (this study), and between a female and fledgling (Debus 1978), may have been as described by Ferrer (2001); that is, parental assessment of the juvenile's aerial competence, including soaring ability, and thus its readiness for independence and cessation of parental food-delivery. Soaring ability indicates the juvenile's capacity to locate carrion, a stopgap while it hones hunting skills (Ferrer 2001). However, other interpretations of parent–offspring aerial interactions are possible.

Diet and hunting

The diet of the Eagles in this study was dominated by mammals, especially in biomass, as is typical for the species, and was similar to previous results for the New South Wales tablelands (reviewed by Olsen 2005; also Debus & Rose 1999; Davey & Pech 2004; Fuentes *et al.* 2004; Olsen *et al.* 2006a,b). However, in recent times the Eagle's diet on more southerly parts of the tablelands has shifted towards macropods and away from lagomorphs, as the relative abundance of these prey species has changed (Davey & Pech 2004; Fuentes *et al.* 2004; Olsen *et al.* 2006a). A diet shift could also cause a shift in the time of breeding.

At Armidale there was close agreement in the composition of orts, pellets and observed prey at nest 1, particularly if (as is likely) all or most of the unidentified observed items were mammals. There was less agreement between orts and pellets in the smaller sample at nest 2. However, there was close agreement between pellets from nests 1 and 2. There are biases associated with orts and pellets, e.g. sharing of (or multiple meals from) large prey items; differential ingestion or digestion of prey parts; differential persistence of large or robust remains; consumption of food away from nests (e.g. scavenging); and removal of remains by the Eagles or scavengers (see Sharp *et al.* 2002; Parker *et al.* 2007; Winkel 2007). Our results suggest that the best representation of diet is obtained by calculating the minimum number of individuals (without double-counting) from all sources, i.e. orts, pellets and observations pooled, as each method can detect prey species that the others may not (see also Seguin *et al.* 1998 for a review).

Foraging and attack behaviour of the Eagles at Armidale was much as previously described (e.g. Marchant & Higgins 1993; Aumann 2001; Olsen 2005; Olsen *et al.* 2006b), with this study adding several examples and some data on hunting success, which is evidently high for experienced adults. It was apparent

that the adults were alert to each other's attacks on prey, often hunted together (perhaps co-operatively at times), shared kills, and the male sometimes guarded the food-bearing female to the nest. The adult Eagles at Armidale occasionally scavenged during the breeding cycle when foraging for themselves, although there was no evidence that they brought carrion to the nest to feed the young.

Conclusions

Wedge-tailed Eagles in New England appear, where they are not persecuted, to be habituating to human activity on the rural fringe of cities. Creation and greater protection of reserves, by excluding disturbance, are also enabling wary individuals to establish new nesting territories. It appears that the Eagles, in the absence of persecution, are becoming bolder and more willing to nest near humans (provided that they have foraging grounds and prey), and that this propensity augurs well for their future.

Behavioural aspects of the Wedge-tailed Eagle's breeding cycle, and nestling and fledgling behaviour, seem typical for large *Aquila* species (cf. Gargett 1990; Watson 1997; Ferrer 2001; Margalida *et al.* 2007). The general principles determined by Ferrer (2001), González *et al.* (2006) and Soutullo *et al.* (2006a,b,c), on aspects of the post-fledging period, independence and dispersal phase, probably apply to the Wedge-tailed Eagle, though confirmation is required.

Most aspects of the biology of the Wedge-tailed Eagle have been well studied, with the notable exception of survival and recruitment to the breeding population, social organisation by individual marking, and dispersal, home-range and habitat use by radio-tracking (Olsen 2005). There is also scope for further quantification of hunting behaviour and success. There is much scope for improvement on the 'snapshot' nature of this study, with greater sample sizes than in existing behavioural studies, by a more rigorous approach that might include, for instance, systematic observation in time-blocks throughout the day, in all phases of the breeding cycle of several pairs. Observational or remote video studies should take care to avoid disturbance to the Eagles, especially when nests are visited or approached closely (cf. Collins & Croft 2007; Silva & Croft 2007). Tasmania is an appropriate location for further research, as most of the gaps in knowledge, when filled, would have direct conservation and management application for the most threatened Wedge-tailed Eagle population. Finally, mortality of large *Aquila* eagles (and other raptors) at windfarms is a growing issue, and will require investigation with respect to the Wedge-tailed Eagle (cf. Walker *et al.* 2005; Dennis 2006; Fielding *et al.* 2006).

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Postscript: A possible model study is that by Margalida *et al.* (2007), 'A long-term large-scale study of the breeding biology of the Spanish Imperial Eagle (*Aquila adalberti*)', *Journal of Ornithology* **148**, 309–322.