

Breeding biology of the reverse-dichromatic, co-operative parrot *Eclectus roratus*

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Abstract

The breeding biology and social system of the eclectus parrot *Eclectus roratus*, a species with a unique form of sexual dichromatism (red and blue females, green males) was examined. Our 4-year study at Iron Range National Park on Cape York Peninsula, Australia, showed that females guarded their nest hollows in emergent rainforest trees for up to 9 months each year, often starting well before they laid their first clutches early in the dry season. During this time they rarely left the nest and relied on males for food, both for themselves and their nestlings. Intrasexual competition for scarce hollows and the threat of egg destruction by other eclectus parrots may explain this extreme guarding behaviour. Reproductive success was low. The combined effects of egg and chick loss to conspecifics and predators, brood reduction and flooding of hollows from heavy rain meant that only 18% of eggs and 27% of clutches produced a fledgling. Over 4 years, reproductive success amongst females was strongly skewed: 39% of females were never successful, and only 29% produced more than one fledgling per year. Eclectus parrots were found to breed co-operatively with as many as five males feeding a single female at the nest. Multiple mating, involving one female and four males, was observed once. Despite an even sex ratio at fledging, the adult sex ratio was strongly male-biased, suggesting higher mortality of females. Our data shows that reproductive variance for females is high, and suggests that a shortage of tree hollows and eligible females may enforce co-operative breeding amongst males.

Key words: *Eclectus roratus*, nest hollows, reproductive success, co-operative breeding, dichromatism

INTRODUCTION

Parrots are known for their bright colours and gregarious behaviour. However, despite roosting communally and spending at least part of the year in conspicuous flocks, most are socially monogamous with long-term pair-bonds. Their apparent monogamy is reflected in a general lack of sexual dimorphism (either colour or size); sex differences when they do occur are usually slight (Forshaw & Cooper, 1989; Juniper & Parr, 1998). Both sexes are involved in parental care, although the female is often solely responsible for incubation. Clutch sizes vary from just one egg in the largest parrots (e.g. some cockatoos, Cacatuinae; Saunders, 1982) to 10 eggs in smaller species (e.g. budgerigars *Melopsittacus undulates*; Wyndam, 1981). Most parrots nest in pre-existing tree hollows. Although the conservation implications of these requirements have been explored in temperate Australia (e.g. Saunders, Smith & Rowley, 1982; Mawson & Long, 1994; Nelson & Morris, 1994), very little information is available for the nesting requirements and breeding biology of tropical

Australasian species (see Marsden, 1992; Marsden & Jones, 1997 for rare examples).

Eclectus parrots *Eclectus roratus* are large (500–600 g) birds found in the Moluccan Islands in Indonesia, the coastal area and offshore islands of New Guinea, the Bismarck Archipelago, the Solomon Islands, and Cape York Peninsula, Australia. Across this range they are divided into as many as 12 sub-species; all are found in lowland and lower montane rainforest (Forshaw & Cooper, 1989; Higgins, 1999). Eclectus parrots are in the Psittacidae, and in the absence of clearer taxonomic affiliation are grouped with the genus *Geoffroyus* in the ‘unplaced’ tribe Psittaculini (Higgins, 1999). They are frugivorous and nest in large hollows in tall trees that emerge above the rainforest (Forshaw & Cooper, 1989).

Eclectus parrots exhibit a variety of traits that set them apart from other parrots, and indeed from other birds. Most obvious is their extreme dichromatism: male and female eclectus parrots are so differently coloured that they were originally classified as different species (Forshaw & Cooper, 1989). Females are a spectacular red and blue, while the larger males are shiny green with a bright

orange beak. The gaudy plumage of females suggests that sexual selection has operated on females as well as males, in contrast to the majority of birds and mammals in which higher reproductive variance for males has led to their being the sex with elaborate secondary sexual characters (Andersson, 1994). Reversed size dimorphism or dichromatism is rare in birds, and is usually associated with reversed sex roles (see examples in Andersson, 1994). However, this is not the case in eclectus parrots because, in typical parrot fashion, the male provides food for the incubating female, and later for nestlings. In few other parrot species is the female brighter than the male, and in all such species the differences are only slight (e.g. Ruppell's parrot *Poicephalus rueppelli*).

Eclectus parrots also differ from most other parrots in their social system. In contrast to the social monogamy seen in most parrots, anecdotal reports suggest that several males feed the breeding female at the nest (Forshaw & Cooper, 1989). Other parrots with unusual social or mating systems include polyandrous vasa parrots *Coracopsis vasa* (Wilkinson, 1994), communally nesting golden conures *Guaruba guaruba* (Oren & Novaes, 1986; Juniper & Parr, 1998); polygamous keas *Nestor notabilis* (Juniper & Parr, 1998), and lekking kakapos *Strigops habroptilus* (Best & Powlesland, 1985). None of these species have marked sexual dichromatism, and only the keas and kakapos show strong sexual dimorphism, with males being larger than females in both species.

Finally, analyses from captive birds show that female eclectus parrots have remarkable control over the sex of their young, and often produce long unbroken strings of one sex (20 males in one case) before switching to the other (Heinsohn, Legge & Barry, 1997). This is one of the strongest statistical departures from parity in sex allocation reported amongst birds (see, Komdeur *et al.*, 1997; Cockburn, Legge & Double, 2002), but the adaptive significance of such control remains unknown.

Despite great interest in eclectus parrots from aviculturalists and evolutionary biologists alike (Forshaw & Cooper, 1989; Grafen, 2000), little is known about their ecology, breeding biology, or social organization (see Higgins, 1999). The aim of this paper is to provide the first report of their natural history based on our long-term study at Iron Range National Park, Cape York, Australia. Here we confirm that eclectus parrots breed co-operatively, describe the factors that affect their reproduction, and provide the foundation for future interpretation of their unusual social and physical features.

METHODS

Our ongoing study is being conducted on the sub-species *E. r. macgillivrayi* at Iron Range National Park on Cape York Peninsula, in far north Queensland, Australia (12°45'S, 143°17'E). The national park is located in an area of lowland rainforest of c. 500 km², which constitutes about one-half of the entire range of this sub-species. The rainforest occurs as patches in a complex mosaic that

includes eucalypt woodland and heath. The mean annual rainfall for the national park is 2780 mm (M. Blackman, pers. comm.) with most rain falling during a distinct 'wet' season from December to April.

This study began in July 1997 and the data presented covers 4 breeding seasons (1997–2000), with some additional information from the beginning of the breeding season in 2001. To find nest trees, we walked along tracks and creek beds listening for eclectus parrot vocalizations. Females call loudly at the beginning of the breeding season, apparently to advertise their presence at the nest hollow. Fourteen nest trees (with 23 hollows) were located during July–September 1997, 16 additional nest trees (with 17 hollows) in 1998, and a further 3 nest trees in 1999 and 2000. Nest trees are used every year, giving a total of 33 nest trees (with 45 hollows) monitored in this study. Most such nest trees ($n = 26$) occurred in a block of c. 30 km² of rainforest in the Claudie River drainage and comprised all nest trees in that area. Our demographic data are most complete for the eclectus parrots associated with these trees.

Nest hollows were found in the trunk or a major branch between 15 and 30 m above the ground. Single-rope techniques were used to gain access to the nests and each nest tree was climbed once every 2 weeks to monitor breeding activity. For each nest visit, records were made of the presence or absence of the breeding female, the number of males seen attending her, and the number of eggs or nestlings in the nest. The lay date of eggs was established (± 3 days) by 'candling' with a small light. The progress of the nestlings was monitored and they were sexed using either down or feather colour. Retrospectively it was established that female nestlings have darker grey down than males. Eclectus parrot nestlings develop directly into their adult plumage colours. From the age of c. 27 days, the presence of either green or red pin feathers on the head indicates their sex. The chicks were banded on our last visit to each nest when they were c. 8 weeks old. On every nest visit, the condition of the nest hollow, in particular whether it was dry and suitable for breeding or whether it was damp or flooded due to rain, was also noted.

Permanent 'hides' were built c. 20 m above the ground in trees neighbouring 6 nest trees, and on the ground at 2 nest trees where the hollow was clearly visible. These hides ranged from 30 to 60 m from the nest hollows and enabled us to observe the birds at the nest without being detected. Observations of female presence or absence, group sizes, and individual identities of colour-banded individuals were made from these hides. Although eclectus parrots are difficult to catch, we are able to report the nest-site fidelity of 8 banded breeding females over multiple years. It was not possible to distinguish reliably through natural markings individuals that were not colour-banded. Briefly, our capture methods entail hoisting mist nets into breaks in the canopy within 60 m of the nest. When captured, birds were colour banded with 1 coloured stainless steel band on each tarsus. These bands were painted using industrial strength methods (powder-coating) to ensure maximum duration of the colour.

Table 1. Characteristics of 33 nest trees and 45 nest hollows of *Electus roratus*. Tree species include: *Alstonia scholaris* (9), *A. actmophylla* (2), *Castenospermum australe* (5), *Ficus albipila* (5), unidentified (dead) *Ficus* sp. (1), *Eucalyptus tessellaris* (1), *Tetrameles nudiflora* (1), *Endospermum myrmecophilum* (1), *Palaquium galactoxylum* (1)

Genus	<i>n</i> trees	<i>n</i> nests	Mean height (m)	Mean hole depth (cm)	Mean entrance width (cm)	<i>n</i> facing sideways
<i>Alstonia</i>	11	14	24.6 ± 3.6 SD	85.0 ± 30.6 SD	32.9 ± 9.6 SD	11/14
<i>Castenospermum</i>	5	7	22.0 ± 3.2 SD	87.1 ± 28.7 SD	34.3 ± 11.3 SD	7/7
<i>Ficus</i>	6	9	24.9 ± 3.7 SD	103.0 ± 30.8 SD	31.8 ± 16.2 SD	8/9
<i>Melaleuca</i>	5	6	19.0 ± 1.9 SD	76.7 ± 10.3 SD	35.0 ± 10.5 SD	2/6
<i>Syzigium</i>	1	2	21.0 (range 6)	70.0 (range 20)	40.0 (range 20)	2/2
<i>Lophostemon</i>	1	2	16.0 (range 4)	90.0 (range 20)	30.0 (range 0)	2/2
<i>Eucalyptus</i>	1	2	15.0 (range 2)	75.0 (range 10)	40.0 (range 0)	1/2
<i>Tetrameles</i>	1	1	20.5	65.0	35.0	1/1
<i>Endospermum</i>	1	1	18.0	80.0	42.0	1/1
<i>Palaquium</i>	1	1	28.0	50.0	45.0	1/1
Total	33	45	22.4 ± 4.3 SD	84.4 ± 27.2 SD	34.1 ± 10.7 SD	36/45

RESULTS

Nest tree and hollow characteristics

All nests were found in hollows in trees that emerged above the surrounding canopy. Overall, 10 genera of tree were used by eclectus parrots, but just four genera (*Alstonia*, *Castenospermum*, *Ficus*, *Melaleuca*) accounted for 36 out of 45 hollows in 27 out of 33 nest trees (Table 1). Most nest trees were completely surrounded by rainforest, except for the *Melaleuca* sp. and *Eucalyptus tessellaris* that were on the edge of rainforest patches that bordered on open woodland or swamp. The mean height of nest hollows above ground was 22.4 m ± 4.3 SD. Most hollows (35/45) faced sideways whereas 10/45 opened skywards. Hollows averaged 84.4 cm ± 27.2 SD deep and the mean entrance width was 34.1 cm ± 10.7 SD (Table 1). Two trees had three simultaneous nests, six trees had two nests, and the remaining 27 trees had one nest hollow.

The breeding season

Breeding began in the dry season and ended in the wet season (Fig. 1a,b). All females laid their first clutches between June and December, and no eggs were laid after February. There were considerable differences between years in clutch initiation dates; for example, no female laid before September in 1997 whereas over half the females laid their first clutch between June and August in 2001. Laying dates may have been related to the persistence of rainfall in the early part of the 'dry' season, as females laid earlier in years when rainfall was lower from May to June (Fig. 2). However, our sample of 5 years is too small to confirm this statistically.

Anecdotal reports suggest that breeding usually starts from June (e.g. Forshaw & Cooper, 1989), but this was only true in 1 of 5 years. Such reports are most likely an artefact of the birds' behaviour. In each year of our study, females occupied their nest hollows at least from July onwards, regardless of when they laid eggs. This behaviour is potentially misleading as females occupy hollows well

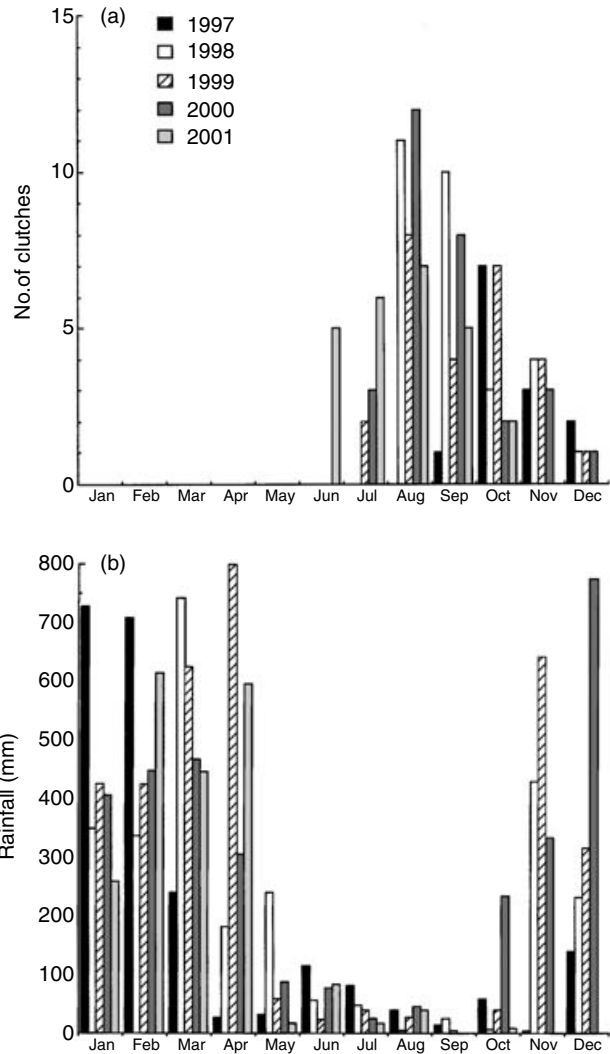


Fig. 1. (a) Initiation of first clutch by each female *Eclectus roratus* vs. month across five breeding seasons. (b) Monthly rainfall records and mean rainfall for same period.

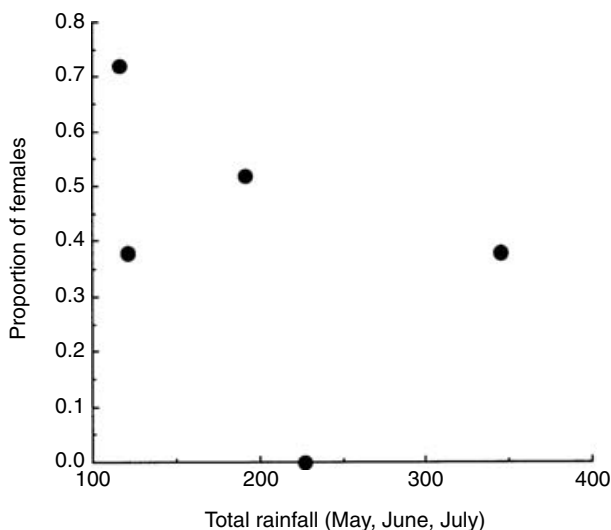


Fig. 2. Proportion of female *Euclestus roratus* that initiated clutches by August against dry season rainfall (May–July).

before they breed, so hollows must be inspected to gain reliable data.

Incubation and nestling periods

Nest trees were not climbed regularly during incubation to avoid disturbance. The incubation period was 30 days on five occasions when we were present the day an egg was laid and just after the same egg hatched. In nine clutches where precise timing of hatching was known, hatching intervals between first and second eggs ranged from 1 to 7 days (mean = 2.8 days \pm 1.9 SD). In other nests, laying and hatching dates were estimated from candling eggs and ageing chicks. The mean nestling period for females was 79 days (range = 72–86 days) whereas that of males was 86 days (range = 79–97 days). Our overall sample of fledged chicks was 51 (24 males, 27 females). Most clutches were of two eggs, but occasionally a clutch had one egg (Table 2).

Breeding behaviour

Most females were continually present at their nest hollows for at least 7 months, and some for as long as 9 months. In all 107 female breeding-years, each female

Table 2. Distribution of *Euclestus roratus* clutch sizes over 4 years

Year	Clutch size = 2	Clutch size = 1	Total clutches	Total eggs
1997–98	13	4	17	30
1998–99	41	8	49	90
1999–00	31	4	35	66
2000–01	38	7	45	83
Total	123	23	146	269

was already present at the nest tree on our first visit to the nest in July and August each year even if they had not laid eggs. Females were at the nest hollow on every occasion the nest was visited ($n = 5$ –22 visits per female breeding season) in 81 out of 107 female breeding-years. Females in the remaining 26 female breeding-years were present on between 74% and 95% of visits. Females in 98/107 breeding years were still consistently present at their nest hollow in February, and females in 36/107 breeding years were still present in March. None of a limited sample of females were present in their hollows when checked in April or May each year (1998, $n = 12$; 1999, $n = 11$; 2000, $n = 10$; 2001, $n = 8$). It was confirmed that females were present continuously at their hollows throughout the day by using four all-day watches on two nests in October 1998, and 18 3-h watches on eight nest trees (including 12 nests) from September to December in 1998 and 1999.

During this prolonged nesting period, the females were fed by at least one attending male. These flew either to the rim of the hollow or to a nearby branch, and regurgitated food directly to the begging female. Males were never observed feeding chicks directly; females always did this once they had acquired the food from the males. However, females always stayed at the nest hollow after chicks fledged either to attempt further reproduction or to continue guarding the hollow, while the fledglings and accompanying males went elsewhere. Males seemed to take on all responsibility for feeding fledglings. Such observations were rare, but recently fledged juveniles were seen with males on eight occasions, and never in the company of their mothers.

Nest site fidelity, female turnover and recruitment

Nest site fidelity data was obtained for eight colour-banded breeding females over multiple years. Given various capture dates, it was found that 18 out of 21 females returned to occupy and breed in the same nest in subsequent years. One additional female returned to the site to find that her nest tree had fallen over but she remained in the area. Two females did not use the nest again; one had died in the hollow from mysterious causes (see below), and the other disappeared from the study area and was presumed to have died (Table 3). When five banded and unbanded females died and two disappeared during the breeding season, their nests were never taken over by new females until the following year (Table 4). It was therefore assumed that hollows with unbanded females were occupied by the same female throughout the season. It was also assumed that unbanded females were faithful to nest sites between years, though we cannot rule out the possibility that some changes may have occurred during the non-breeding season.

Of all females, only seven were known to have died or disappeared over 107 female breeding-years. Two of these were preyed upon by amethystine pythons *Morelia amethystina* in the nest (one 3-m and one 4-m python, both with large bulge, found in hollow). Two were found dead but uneaten in the nest, and one was found dead

Table 3. Nest site fidelity for eight colour-banded *Eclectus roratus* females. Data were taken until the beginning (July) of the 2000–01 breeding season

Female, year captured	Subsequent years	Nest site fidelity?
Lofas old hole, 1997	1998–2001	Yes
Lofas new hole, 1998	1999–2001	Yes
Smugglers high hole, 1998	1999–2001	Yes
Mamas, 1998	1999–2001	Yes*
Syzigium, 1998	1999	Yes
	2000	Died
Catfish, 1998	1999–2000	Yes
	2001	Died
Smugglers low hole, 1999	2000–2001	Yes
Scrub Itch, 2000	2001	Yes

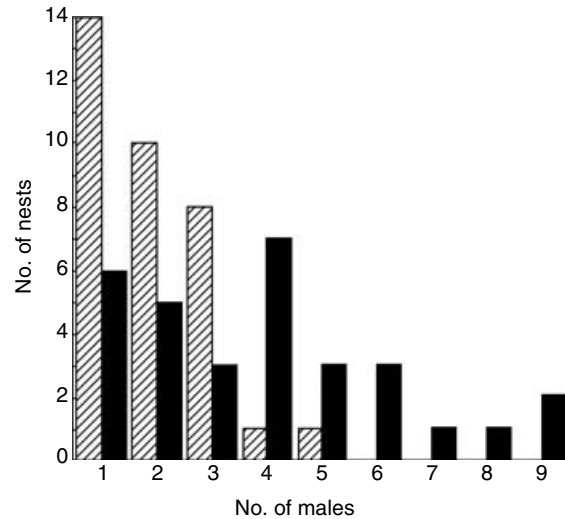
* Nest tree fell over in 2001 but female remained at site.

at the base of the nest tree having apparently died from a broken neck. We suspect that the three females found dead at or near the nest were victims of female–female aggression.

Three females that were banded as nestlings occupied nest hollows and sang to advertise their presence in later breeding seasons (two in 2000, one in 2001). One was banded in the first year of the study, and was in her third year when she bred. She dispersed 6.9 km to occupy a hollow that faced skywards in a branch of a dead tree to which we could not gain access, but we know she was not successful at reproducing. She was not seen again the following year. Another female was banded in 1998; in her second year (the 2000 season) she occupied a hollow in the same tree as another female, *c.* 1.8 km from her natal hollow. She lost two clutches of eggs, and returned to that hollow in the 2001 breeding season. The third female was banded in 1997, and was seen in her fourth year (2001/02 breeding season) occupying a shallow (*i.e.* inadequate) hollow in her natal nest tree, although she did not lay a clutch.

Social group size and composition

Usually, there was only one female associated with each nest hollow. However, females additional to the number of nest hollows were seen near resident females without

**Fig. 3.** Number of nests against the mean (hatched bars) and maximum (shaded bars) number of male *Eclectus roratus* observed attending females at those nests.

aggression on more than three occasions during a nesting period in 23/107 female breeding-years across eight nest trees. The lack of aggression suggests they may have been offspring from previous seasons. These additional females were never seen feeding the breeding female entering the nest.

The number of males seen around each nest fluctuated and is summarized in two ways. Figure 3 shows the mean number of males (rounded to the nearest male) observed over a minimum of 10 observations from egg laying to fledging of young, and also the maximum number of males observed in any one visit over the nesting period. The mean number of males attending the female ranged from one (in more than a third of nests) to five. In contrast the maximum number of males observed ranged from one at six nests up to nine males at two nests.

Co-operative breeding and multiple mating

Females were fed at the nest by more than one male at 20/34 nests (at 26 nest trees). The greatest number of males seen feeding females was five; the occasions when more

Table 4. Deaths and disappearance of *Eclectus roratus* females, and take-over of nesting hollows

Nest, year	Circumstances of female death	Take-over same season?	Take-over following season?
Funnyslow, 1997	Female dead at base of nest tree	No	Yes
Funnyslow, 2000	Predation by python in nest	No	Yes
Scrub Itch, 1997	Female dead in nest	No	Yes
Syzigium, 1999	Predation by python in nest	No	No
Tree from hell, 1999	Female dead in nest	No	Yes
Catfish, 2000	Female disappeared	No	No
Noisy buggers, 1999	Female disappeared	No	Yes

Table 5. Causes of egg and nestling loss and number of *Eclectus roratus* fledglings produced over 4 years. Figures are expressed both as percentage of total eggs and total clutches laid. Percentages of clutches sum to >100% because some processes (e.g. one egg lost to hatch failure and the second to flooding) applied at the same nest

Year	Eggs/ clutches	Total	Hatch failure	Egg damage	Egg disappearance	Flooding of nest	Partial brood loss	Whole brood loss	Fledged
1997	Eggs	30	3 (10%)	4 (12%)	10 (33%)	4 (13%)	3 (10%)	2 (7%)	5 (17%)
	Clutches	17	2 (12%)	2 (12%)	5 (17%)	2 (12%)	3 (18%)	1 (6%)	4 (23%)
1998	Eggs	90	11 (12%)	10 (11%)	21 (23%)	9 (10%)	5 (6%)	19 (21%)	15 (17%)
	Clutches	49	7 (14%)	6 (12%)	12 (24%)	6 (12%)	5 (10%)	12 (24%)	13 (26%)
1999	Eggs	66	7 (11%)	4 (6%)	20 (30%)	8 (12%)	5 (8%)	13 (20%)	9 (14%)
	Clutches	35	7 (20%)	2 (6%)	10 (29%)	5 (14%)	5 (14%)	7 (20%)	7 (20%)
2000	Eggs	83	10 (12%)	1 (1%)	29 (35%)	15 (18%)	2 (2%)	6 (7%)	20 (24%)
	Clutches	45	8 (18%)	1 (2%)	16 (36%)	9 (20%)	2 (4%)	4 (9%)	15 (33%)
Total	Eggs	269	31 (12%)	17 (6%)	80 (30%)	36 (13%)	15 (6%)	40 (15%)	49 (18%)
	Clutches	146	24 (16%)	11 (8%)	43 (29%)	22 (15%)	15 (10%)	24 (16%)	39 (27%)

males were observed at the nest did not entail all of the males feeding the female. We interpret the mean number of males observed as a conservative approximation of the stable group size, and the larger numbers of males observed as temporary. Aggression between males at the nest was common, and they often displaced each other at the rim of the hollow when attempting to feed the female.

Groups did not form through natal philopatry of grown offspring. In 4 years, none of the males banded as nestlings that fledged successfully ($n = 24$) remained as helpers in their natal groups. Male attendants were probably unrelated to the breeding female and were seeking mating opportunities. We observed multiple mating on one occasion during the 2000 breeding season. The 'Mamas' female, who had fledged two chicks 3 weeks earlier, mated with four males in quick succession over the space of *c.* 4 min. Each mating occurred as a single episode, and took between 8 and 15 seconds. There was no apparent aggression between the males on this occasion. All female chicks that fledged successfully ($n = 27$) also disappeared from the natal area, at least for a number of years; three were observed attempting to breed for the first time (see above).

Adult sex ratio

Eclectus parrots on Cape York are believed to have a strongly male-biased adult sex ratio (Forshaw & Cooper, 1989). This is mostly because of the clear predominance in males seen flying to and from nest trees by most observers, and the fact that females are rarely seen away from the nest trees. However, no attempts at quantifying the adult sex ratio have been made. Using the information above, a range of possible values from 1.47 to 2.87 males per female was constructed.

The conservative value (1.47) divides the sum of the mean numbers of males seen at each of 26 nest trees by the number of females associated with that tree; additional females are included if they were seen on at least three occasions in the course of a breeding season. Females are treated in this manner as they are less observable;

unlike males, they are not constantly seen returning to feed the breeding female. The maximum value (2.87) divides the maximum number of males ever seen at the nest tree by the maximum number of females. The first value (1.47) may be too low because it only scores the number of males seen together at the nest tree, and must therefore underestimate the number of males attached to that tree. However, the maximum value is probably too high as such large numbers of males are only seen at a nest tree when a female is approaching her fertile period. Preliminary radio-tracking data confirms that some males repeatedly visit other nest trees (pers. obs.), so we favour the lower figure (1.47) as the best conservative estimate of the adult sex ratio. In either case, males clearly outnumber females.

Reproductive success

Overall, reproductive success was low, as only 18% of eggs in 27% of clutches resulted in a fledgling. The causes of failure at the egg and nestling stages were unexplained hatching failure, egg damage, egg disappearance, flooding of the nest hollow, and whole and partial brood loss. Results for each of these categories, both as percentage of eggs laid and as percentage of clutches, are given for each year in Table 5. Table 6 expresses losses resulting from flooding, and partial and whole brood loss as a percentage of the total nestlings that hatched.

Twelve per cent of 269 eggs failed to hatch; half of these did not have a visible embryo and were possibly infertile. A further 6% failed to hatch because of damage (e.g. breakage) from unknown causes. Other *eclectus* parrots probably caused this damage as the eggs were not eaten. Infertility seemed to be constant across years, whereas egg damage was most apparent in 1997 and 1998 (Table 5).

Sudden disappearance of clutches accounted for 30% of all eggs laid. Note that females did not leave damaged eggs in the nest for more than *c.* 3 days, so that it was often not possible to ascertain whether these eggs had disappeared because of predation or because of interference from other *eclectus* parrots.

Table 6. Causes of *Electus roratus* nestling loss over 4 years. Figures are expressed as percentage of total chicks hatched and percentage of total clutches that hatched at least one chick

Year	Nestlings/ broods	Hatched	Flooding	Brood reduction	Whole brood loss	Fledged
1997	Nestlings	12	2 (17%)	3 (25%)	2 (17%)	5 (42%)
	Broods	9	1 (11%)	3 (33%)	1 (11%)	4 (44%)
1998	Nestlings	43	4 (9%)	5 (12%)	19 (44%)	15 (35%)
	Broods	34	4 (12%)	5 (15%)	12 (35%)	13 (38%)
1999	Nestlings	31	4 (13%)	5 (16%)	13 (42%)	9 (29%)
	Broods	21	2 (10%)	5 (24%)	7 (33%)	7 (33%)
2000	Nestlings	33	5 (15%)	2 (6%)	6 (18%)	20 (61%)
	Broods	24	3 (13%)	2 (8%)	4 (17%)	15 (63%)
Total	Nestlings	119	15 (13%)	15 (13%)	40 (34%)	49 (41%)
	Broods	88	10 (11%)	15 (17%)	24 (27%)	39 (44%)

Loss of eggs and chicks as a result of flooding of the nest hollow from heavy rain accounted for 13% of all eggs laid. Loss to flooding was highest in the 2000–01 breeding season. Partial brood reduction (loss of just one

chick) was relatively rare, accounting for 6% of all eggs laid (or 13% of nestlings hatched). Whole brood loss, attributed to either predation or interference, was higher and accounted for 15% (7–21%) of eggs laid (or 34% of nestlings) over 4 years.

Over all 107 female breeding-years, 68 failed to produce any fledglings, 22 produced one fledgling, 13 produced two, and one produced three fledglings (in two broods) in 1 year (Fig. 4a). Of the females that failed in 68 breeding-years, 38 laid and lost two consecutive clutches, six laid and lost three clutches, and two laid and lost four clutches. Of the 22 females that produced one fledgling, six had already lost one clutch, and of the 14 females that fledged two or more young, one had already lost one clutch.

There was high skew in reproductive success between breeding females. Of 28 females monitored for at least 3 years, 11 (39%) fledged no young, whereas eight (29%) averaged over one fledgling per year. Three out of 28 (11%) breeding females averaged over two fledglings per year (Fig. 4b). Only four females successfully produced a chick in every year they were monitored; these are referred to as ‘super-females’.

Only five females attempted a second brood in the same season after successfully fledging a first brood. Four of these were the super-females mentioned above. Two of these females succeeded; the Lofas female fledged an additional young in 2 consecutive years, and the Smugglers Bat Hole female succeeded once. Table 7 lists the success or failure of these five females and, if they failed to fledge the second brood, the stage at which they failed.

DISCUSSION

Our monitoring of 146 clutches laid over 107 female breeding-years at Iron Range National Park yields a comprehensive picture of the breeding and social biology of *electus* parrots, an unusual species that has never been systematically studied in the wild. Our data reveals specific nest hollow requirements and seasonality of breeding. Unusual behaviour has also been observed at the nest including continuous guarding of the hollow by females and co-operative breeding and multiple

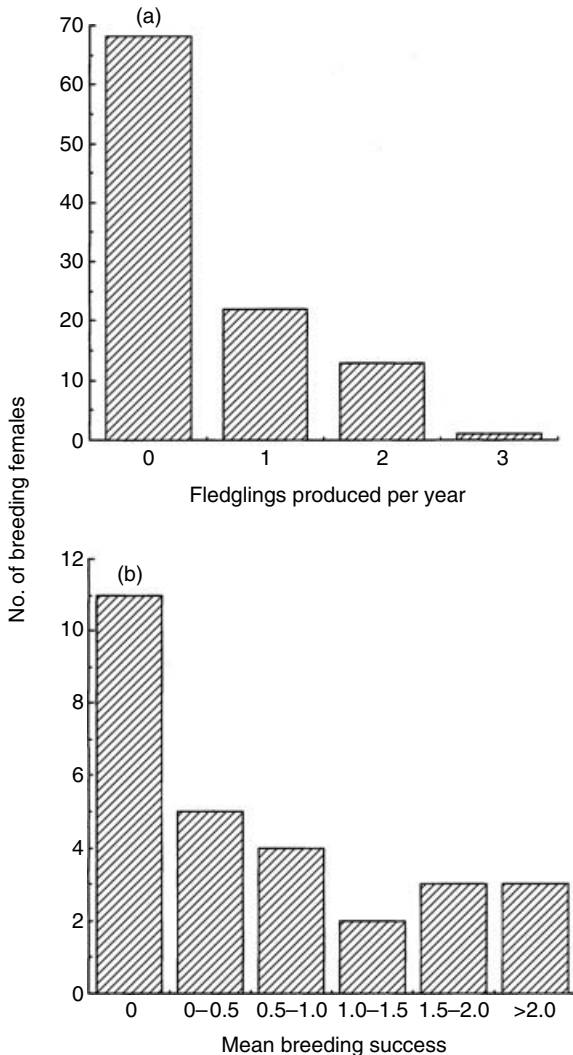


Fig. 4. (a) Number of *Electus roratus* fledglings produced in each of 107 female breeding seasons. (b) Number of females with mean breeding success (over 3 or 4 years) in six categories.

Table 7. Details of 10 attempts to produce a second clutch after successfully fledging a first clutch for five breeding *Eclectus roratus* females

Female	Year attempted	Success?	Stage failed at
Lofas	1998	No	Chick
	1999	Yes	–
	2000	Yes	–
Smugglers Bat Hole	1999	No	Egg
	2000	Yes	–
Catfish	1998	No	Chick
	1999	No	Chick
Mamas	1999	No	Eggs
	2000	No	Eggs
Safis	1998	No	Chicks

mating by males. Further, there are large and consistent differences in reproductive success between breeding females. Here we discuss how these observations provide an essential foundation for studying the evolutionary forces responsible for the unusual reverse dichromatism and sociality seen in eclectus parrots.

Nesting requirements and seasonality

Most parrots nest in tree hollows, and some have specific nesting requirements which render them vulnerable to habitat disturbance (e.g. Forshaw & Cooper, 1989; Mawson & Long, 1994; Nelson & Morris, 1994). However, few data exist for the hollow requirements of tropical rainforest parrots (e.g. Marsden & Jones, 1997). Eclectus parrots used high and deep hollows with small entrances in a limited number of species of canopy-emergent trees. These attributes probably provide the best protection from terrestrial predators. For example, pythons and monitor lizards *Varanus* spp. may have difficulty climbing large trees when nests are high and there is no surrounding vegetation to assist in climbing. Height, good visibility, and a small entrance may also help the female guard the nest from aerial predators. Given that the female is brightly coloured and advertises her presence to other eclectus parrots by calling frequently, there seems to be little chance for the strategy of concealment. The small, sideways-facing entrance to the hollow also limits flooding from heavy rain. However, most hollows flood to some extent, and one further variable that determines the quality of a hollow is how quickly it drains. This is more difficult to measure but probably relates to whether there are holes in the nest floor, and the porosity (e.g. state of decay) of the wood.

Most of the hollows were found in four tree genera, *Alstonia* sp., *Castanospermum* sp., *Ficus* sp., and *Melaleuca* sp. Of these, *Castanospermum australe*, is endemic to Australia. A strong preference for particular tree types was also reported for eclectus parrots on the island of Sumba where 83% of nests were in two species of *Tetrameles* (Marsden & Jones, 1997). This preference probably reflects the tree species that produce the best

hollows. For example, *Tetrameles nudiflora* is one of the commonest canopy emergents in Cape York rainforest but rarely forms hollows. Although it is well established that breeding densities of many hole-nesting birds can be limited by a shortage of sites (Newton, 1994), only one study to date has shown that nest hollow availability can limit the size of a parrot breeding population (Beissinger & Bucher, 1992). Data from aerial surveys show that trees of the required height and species are relatively rare; there may be as few as 250 nest trees in the 500 km² of rainforest found in and around Iron Range National Park (0.5 trees/km²) (S. Legge & R. Heinsohn, pers. obs.). The extreme hollow guarding behaviour of female eclectus parrots (discussed below), and documented competition for nest hollows between eclectus parrots and sulphur-crested cockatoos *Cacatua galerita*, also suggests a shortage of suitable trees (Heinsohn, Murphy & Legge, in press).

Most anecdotal reports suggest that breeding by eclectus parrots in most parts of their range is relatively aseasonal (Juniper & Parr, 1998). In this respect, the population at Iron Range differs because breeding is strongly seasonal, with most clutches being laid from August to December. Although some tree species bear fruit during the dry season, eclectus parrots do not time their breeding to coincide with the peak fruiting period which is usually in the wet season in Australia's tropical rainforests (Nix & Kalma, 1972). The seasonality of breeding in eclectus parrots is similar to that reported for medium to large parrot species in temperate Australia (e.g. Saunders, 1982, 1986; Smith & Saunders, 1986; Krebs & Magrath, 1998) and other seasonal climates such as Pacific Ocean islands (e.g. red-shining parrot *Prosoeia tabuensis*; Rinke, 1989).

The threat of hollow flooding suggests that eclectus parrots should initiate their clutches as early as possible in the dry season. They none the less showed considerable variation in the initiation of breeding between years. The earliest clutches in 1997 were in September, whereas in 2000 and 2001 many clutches were initiated in June and July (Fig. 1a). Although the sample size of 5 years is too low for statistical analysis, timing of egg-laying may be correlated to rainfall at the start of the dry season, with females more likely to initiate clutches early when rainfall from May to July is low (Fig. 2). Two possible reasons for this pattern are: (1) because their hollows dry out and become available more quickly when rainfall is low; (2) that fruit availability depends on the extent of rainfall during the 'dry' season. Longer term data are required to resolve these issues.

Breeding behaviour

Sex roles, sex ratios, and co-operative breeding

Most parrots are socially monogamous and seem to have long-term pair bonds (Forshaw & Cooper, 1989). Both sexes usually contribute to parental care but females perform all incubation, and are fed by the male during

this period. Usually, females begin to leave the nest to forage when their nestlings become thermally self-sufficient (Juniper & Parr, 1998). Female eclectus parrots are highly unusual as most seem never to leave the vicinity of the hollow from the time they occupy the breeding site (July or earlier) until the breeding season ends as late as March the next year. During this period they call many times each day, and are aggressive towards other females and males. When not incubating or brooding, they spend most of their time sitting at the hollow entrance, with their bright red heads showing.

Females thus receive all (or most) of their food from between one and five attending males who regurgitate it to them at the entrance of the hollow or on a nearby branch. Nestlings also get all of their food from the males, but indirectly via their mothers. Females prevent males from entering the hollow, despite their repeated attempts to enter or to look inside. Parental roles change when the young fledge; from this time on the fledglings stay with the males who feed them directly. Usually females remain at the hollow for days or weeks after the young fledge, and continue to visit the hollow (frequency unknown) throughout the non-breeding season. The extreme protection of hollows by females seems to be the principal cause of the departure of eclectus parrots from the usual parental roles seen in parrots.

Our observations of the number of males attending females at the nest are based on simple counts of males present, and how many were observed to be feeding the females together. Thus, although we can be sure that multiple males were both present and feeding, our estimates of group size are probably conservative. Two sets of data are presented, the maximum number of males ever observed at a nest during a breeding episode, and the mean number of males observed over repeated nest visits. It is important to present the data in both ways as it suggests that some males visit only occasionally, perhaps to monitor the female's reproductive status, whereas a smaller number seem to be involved in regular feeding. Preliminary evidence from recent radio-tracking of adult males (pers. obs.) suggests that males feed one female primarily but occasionally visit other nest trees.

None of 24 banded male fledglings remained in their natal groups. Combined with the male-male aggression commonly observed at the nest, and our observation of multiple mating, this suggests that male attendants are probably unrelated to the breeding female and compete for mating access. Thus co-operative breeding in eclectus parrots could take one of two forms. First, it may entail co-operative polyandry in which males share paternity and provide care at the nest (e.g. Davies, 1992; Whittingham, Dunn & Magrath, 1997), although the number of males present is unusually large for such a system (Hartley & Davies, 1994). The opportunities for sharing paternity in one clutch of two eggs are small, but sequential polyandry is also possible. Second, unrelated males may also help at the nest as an attempt to gain future reproductive favour with the female, or female chicks. Such a system is believed to occur in rifleman *Acanthisitta chloris* (Sherley,

1989), and pied kingfishers *Ceryle rudis*, in which unrelated males help without any immediate reproductive reward (Reyer, 1990).

Naturalists have commented that the adult sex ratio of eclectus parrots is skewed towards males (e.g. Forshaw & Cooper, 1989). This study provides the first estimate of the extent of the skew (between 1.47 and 2.87 males for every female) although it should be noted that these ratios were measured at nest trees. It is possible that uncompetitive males and females that cannot find nest hollows live elsewhere. However, we have very rarely encountered female eclectus parrots in our surveys of rainforest away from nest trees whereas males are commonly seen foraging in fruiting trees. Consequently we believe that the sex ratios observed around nest trees are representative of the entire population.

Since the overall sex ratio at fledging is approximately even (47% males, $n=51$, this study; 46% males, Heinsohn, Legge *et al.*, 1997), the skewed adult sex ratio suggests that female eclectus parrots suffer higher mortality than males after fledging. This could result from their relatively gaudy plumage which renders them more vulnerable to attack from visually hunting predators such as raptors. Both rufous owls *Ninox rufa*, and peregrine falcons *Falco peregrinus*, are known predators of female eclectus parrots (Legge *et al.*, in press). Although the skewed sex ratio suggests higher mortality for females, our observations show that breeding females have low mortality. Since breeding females spend so much time at their nest hollow, they may be relatively safe because of the protection the hollow affords, and also because they are spared potentially dangerous foraging journeys.

A low number of nest hollows and high female mortality suggest that breeding females are a limiting resource for males. This may in turn further necessitate a system of 'co-operative' breeding by males (e.g. Pruett-Jones & Lewis, 1990) in which males compete for access to the females. At present, it is not clear whether males gain access through intra-sexual competition or whether females choose the best males, or whether both processes take place (Andersson, 1994). That males are larger than females (Forshaw & Cooper, 1989), and fight each other at the nest, certainly suggests a role for intra-sexual competition.

Female turnover and fidelity to nest sites

Our data for colour-banded breeding females suggest complete nest site fidelity between years. Surviving banded females returned to the same nest hollow in all 18 subsequent years in which it was possible. In 107 female breeding-years, five known deaths (two predation, three mysterious) of breeding females and two disappearances were documented, all during the breeding season. The mean annual survival rate for breeding females was 93.7% (90.5%, 100%, 90.9%, and 93.3% from 1997 to 2000). Inter-annual survival in tropical birds is generally high compared to temperate species (Johnstone *et al.*, 1997), and has been linked to low rates of territory

turnover in many species (e.g. Greenberg & Dradwohl, 1997; Stutchbury & Morton, 2001). Survival amongst breeding female eclectus parrots seems especially high, and stands in contrast to their apparently low survival between fledging and breeding.

Data for nest site fidelity and female mortality are rare for large parrots. Some of the best information comes from studies of white-tailed black cockatoos *Calyptorhynchus funereus*. Saunders (1982) found that only one-third of nesting attempts in this species were made in the same hollow that had been used previously, and concluded that hollows were not a limiting resource. Using survival data from tagged birds, he also concluded that mean annual survival was 61% and 66% (at two sites) for adult females and 69% (at both sites) for adult males. In contrast to white-tailed black cockatoos, the complete nest site fidelity of breeding female eclectus parrots suggests that appropriate hollows are limited. Our observations of intense intra-sexual nest defence by females, and deaths from apparent fighting, further support this contention. However, it is intriguing that two hollows remained unoccupied in the following season, as this suggests that there were not always 'floating' females ready to take over, possibly because of the differential mortality on females discussed above.

In our study to date, there were three young females, all banded as nestlings, that attempted to breed for the first time. All disappeared for lengthy periods (2–3.5 years), before reappearing to attempt nesting. Two dispersed (1.8 and 6.9 km) to distant trees, and one returned to its natal nest tree, so it is not possible to state from this limited sample whether dispersal is the normal strategy, as it is for most female birds (Greenwood & Harvey, 1982). However, two of these young females settled in the same tree as established females, and one was within 80 m of another female. Young females may attempt to maximize attention from males by settling in an area already frequented by them. This may explain why two hollows remained vacant as both were > 300 m from another established hollow. Both young females used hollows that seemed to be of low quality (e.g. shallow or facing skywards and therefore prone to flooding). Our observations also establish a minimum breeding age for females in the wild of 2 years.

Reproductive success

Eighty-four per cent of clutches in this study had two eggs and the remainder had one. Parrots lay between one (e.g. macaws *Ara* sp.) and 10 eggs (e.g. green-rumped parrotlets *Forpus passerinus*; Waltman & Beissinger, 1992), but the preferred clutch size of two in eclectus parrots is similar to other large parrots (e.g. some black cockatoos *Funereus* spp.; Saunders, 1982). Only 18% of eclectus eggs laid in 146 clutches produced a fledgling, but at least one chick was produced from 26.7% of clutches. Another way to express overall success is that 51 fledglings were produced, representing 39 successful attempts from 146 clutches in 107 female breeding-years.

Nest predation in eclectus parrots is unusually high for hole-nesting birds, which are usually less vulnerable than open-cup nesters (Martin & Li, 1992). Whereas brood reduction caused by starvation of nestlings was rare (6% of eggs), presumed predation of eggs and nestlings accounted for 45% of all eggs laid. That is, 30% of eggs disappeared suddenly with no trace of remains, and a further 15% were lost in a similar manner at the nestling stage. Known predators were large (3–4 m) amethystine pythons, and monitor lizards. There was no evidence of any loss of young to avian predators, but likely candidates are black butcherbirds *Cracticus quoyi*, grey goshawks *Accipiter novaehollandiae*, and rufous owls. These owls are known to prey on adult female eclectus parrots (Legge *et al.*, in press), and may also pose a threat to nestlings.

Breeding success for tropical hole-nesting birds is usually higher than that reported here for eclectus parrots, e.g. 78% in New Guinea (Bell, 1982), 67% in the neotropics (Skutch, 1985), and 66% in a study of buff-breasted paradise kingfishers *Tanysiptera sylvia*, also conducted in the Iron Range area (Legge & Heinsohn, 2001). Breeding success in eclectus parrots is also low compared to other parrots. Examples of fledging success ranked from smaller to larger species include 82% of eggs in green-rumped parrotlets (Waltman & Beissinger, 1992), 50% in crimson rosellas *Platycercus elegans* (Krebs & Magrath, 1998), 63% in Hispaniolan parrots *Amazona ventralis* (Snyder, Wiley & Kepler, 1987), and 65% in white-tailed black cockatoos (Saunders, 1982). One reason for high nest predation in eclectus parrots might be that they are very noisy around the hollow entrance, and do not conceal their presence. Males can also be conspicuous when they return to feed the female, especially when they squabble with other males near the entrance. Eclectus parrots may pay a high nest predation cost for their noisy interactions and for the conspicuous coloration of females.

Thirteen per cent of eggs or young were lost as a result of flooding of the nest hollow. Most of the flooding occurred because of sudden storms from October to December, which varied between years. Other parrot species have reproductive success that depends on rainfall patterns but this is manifested in different ways. For some, higher rainfall leads to better food supplies and an increase in reproductive success (e.g. western rosellas *Platycercus icterotis*, regent parrots *Polytelis anthopeplus*, and Port Lincoln parrots *Barnardius zonarius*; Long, 1990), and in others high rainfall leads to hollow damage and exposure of nestlings (e.g. galahs *Cacatua roseicapilla*; Rowley, 1990; long-billed corellas, *Cacatua tenuirostris*, Smith, 1991). The large losses of young in eclectus parrots highlight the advantages of having a dry hollow, or of breeding early enough so that young fledge before the commencement of heavy rains.

Twelve per cent of eggs failed to hatch for no apparent reason; about half of these had obvious embryos at various stages of development. There are three possible explanations for high rates of hatching failure. First, hatching failure has been reported to be higher in birds in lower latitudes (Koenig, 1982; but see Skutch, 1985), and may result from greater exposure to inappropriate

temperatures (Stoleson & Beissinger, 1999). Second, inbreeding depression because of high levels of philopatry may cause hatching failure in some co-operatively breeding birds (e.g. green woodhoopoes *Pheonichulus purpureus*; Ligon & Ligon, 1990). However, this seems unlikely in eclectus parrots as young disperse from their natal areas. A third explanation concerns the potential for decreased heterozygosity and inbreeding depression resulting from the small size of the Iron Range population, and the probable bottlenecks experienced in the last glacial period (Nix & Kalma, 1972). Based on surveys, there are currently estimated to be 250 breeding females in the population (S. Legge & R. Heinsohn, pers. obs.). Since over one-third of these females have never been observed to breed successfully (see below) the effective population size is even smaller. These data have strong conservation implications and will be used for population viability analyses.

A further 6% of eggs were damaged such that the contents spilled out, or so that the embryo became desiccated. Other eclectus parrots were probably responsible for these losses, especially as some eggs had been shattered with force but with no attempt made to remove the contents. The real figure could be even higher, because destroyed eggs were not left in the nest, and may have been counted as whole clutch or brood losses in Tables 5 & 6. Although various bird species are known to destroy the eggs of conspecifics (e.g. acorn woodpeckers *Melanerpes formicivorus*; Koenig *et al.*, 1995), definitive evidence for parrots has only been presented for the crimson rosella *Platycercus elegans*. In an aviary experiment, Vogels (reported in Krebs & Magrath, 1998) found that dominant crimson rosellas destroyed the eggs of subordinate females. Krebs (1998) also found that egg destruction was common amongst wild crimson rosellas, and twice observed males perpetrating the destruction. The aggression shown by female eclectus parrots towards males suggests that the latter pose a threat to eggs and nestlings. Egg destruction may reflect competition between males for mating access to the female, or if carried out by females may reflect competition for nest hollows. For example, female crimson rosellas abandoned their nest boxes if their clutch had been destroyed (Krebs & Magrath, 1998). Together with a possible shortage of nesting hollows, the threat of egg destruction and infanticide suggests an alternative reason for the extreme protection of hollows by females. If females can rely on sufficient food from males, they may be best served by continuous protection of their eggs and chicks.

Super-females, high reproductive variance for both sexes

Female reproductive success is marked by high skew between individuals; 39% of individual females observed over at least three seasons were never successful, and only 29% produced more than one fledgling per year on average. Although many females may have failed by chance, it is also possible that the successful females were

of higher quality (e.g. colour, size, age or experience) or owned better (i.e. drier, safer) hollows. These two variables may also be correlated such that higher quality females gain ownership of better resources (e.g. Bleiweiss, 1985; Stutchbury & Morton, 2001). However, limited hollow availability, high mortality of immature females, and high skew in reproductive success between the small number of females that do breed has clearly led to high reproductive variance amongst females. The consequent shortage of breeding females could in turn be the driving force behind competition and enforced co-operative breeding amongst males. This would create strong sexual selection in both sexes. Further, intense hollow guarding by females has led to a complete separation of sex roles which, in combination with strong sexual selection on each sex, may explain the unique sexual dichromatism seen in eclectus parrots. The function of colour, combined with molecular analyses of the mating system, will be the subject of future research.

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REFERENCES

- Andersson, M. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- Beissinger, S. R. & Bucher, E. H. (1992). Sustainable harvesting of parrots for conservation. In *New World parrots in crisis*: 73–115. Beissinger, S. R. & Snyder, N. F. R. (Eds). Washington, DC: Smithsonian Institution Press.
- Bell, H. L. (1982). A bird community of lowland rain forest in New Guinea. 2. Seasonality. *Emu* **82**: 65–74.
- Best, H. & Powlesland, R. (1985). *Kakapo*. Dunedin: John McIndoe and New Zealand Wildlife Service.
- Bleiweiss, R. (1985). Iridescent polychromatism in a female hummingbird: is it related to feeding strategies? *Auk* **102**: 701–713.
- Cockburn, A., Legge, S. & Double, M. (2002). Sex allocation in birds and mammals: disentangling the hypotheses. In *Sex ratios: concepts and research methods*: 266–286. Hardy, I. C. W. (Ed.). Cambridge: Cambridge University Press.
- Davies, N. B. (1992). *Dunnoek behaviour and social evolution*. Oxford, Oxford University Press.
- Forshaw, J. M. & Cooper, W. D. (1989). *Parrots of the World*. Willoughby: Lansdowne Press.
- Grafen, A. (2000). W. D. Hamilton. *Guardian* 9 March: 23.
- Greenberg, R. & Dradwohl, J. (1997). Territoriality, adult survival, and dispersal in the checker-throated antwren in Panama. *J. Avian Biol.* **28**: 103–110.
- Greenwood, P. J. & Harvey, P. H. (1982). The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* **13**: 1–21.
- Hartley, I. R. & Davies, N. B. (1994). Limits to cooperative polyandry in birds. *Proc. R. Soc. Lond. B Biol. Sci.* **257**: 67–73.
- Heinsohn, R., Legge, S. & Barry, S. (1997). Extreme bias in sex allocation in eclectus parrots. *Proc. R. Soc. Lond. B Biol. Sci.* **264**: 1325–1329.

- Heinsohn, R., Murphy, S. & Legge, S. (In press). Overlap and competition for nest holes among eclectus parrots, palm cockatoos and sulphur-crested cockatoos. *Aust. J. Zool.*
- Higgins, P. J. (Ed.) (1999). *Handbook of the Australian, New Zealand, and Antarctic birds*. Melbourne: Oxford University Press.
- Johnstone, J. P., Peach, W. J., Gregory, R. D. & White, S. A. (1997). Survival rates of temperate and tropical passerines: a Trinidadian perspective. *Am. Nat.* **150**: 771–789.
- Juniper, T. & Parr, M. (1998). *Parrots: a guide to parrots of the World*. Sussex: Pica Press.
- Koenig, W. D. (1982). Ecological and social factors affecting hatchability of eggs. *Auk* **99**: 526–536.
- Koenig, W. D., Mumme, R. L., Stanback, M. T. & Pitelka, F. A. (1995). Patterns and consequences of egg destruction among joint-nesting acorn woodpeckers. *Anim. Behav.* **50**: 607–621.
- Komdeur, J., Daan, S., Tinbergen, J. & Mateman, C. (1997). Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature (Lond.)* **385**: 522–525.
- Krebs, E. A. & Magrath, R. D. (1998). Breeding biology of crimson rosellas *Platycercus elegans* on Black Mountain, Australian Capital Territory. *Aust. J. Zool.* **46**: 119–136.
- Legge, S. & Heinsohn, R. (2001). Kingfishers in paradise: the breeding biology of *Tanysiptera sylvia* at the Iron Range National Park, Cape York. *Aust. J. Zool.* **49**: 85–98.
- Legge, S., Heinsohn, R., Blackman, C. & Murphy, S. (In press). Predation by rufous owls on eclectus parrots and other animals at Iron Range National Park, Cape York. *Corella*.
- Ligon, J. D. & Ligon, S. H. (1990). Green woodhoopoes: life history traits and sociality. In *Cooperative breeding in birds*: 33–65. Stacey, P. B. & Koenig, W. D. (Eds). Cambridge: Cambridge University Press.
- Long, J. J. (1990). *The breeding biology of four species of parrots in the south of Western Australia. Technical Series No. 6*. Perth: Agriculture Protection Board.
- Marsden, S. J. (1992). The distribution, abundance and habitat preferences of the salmon-crested cockatoo *Cacatua moluccensis* on Seram, Indonesia. *Bird Conserv. Int.* **2**: 7–14.
- Marsden, S. J. & Jones, M. J. (1997). The nesting requirements of the parrots and hornbill of Sumba, Indonesia. *Biol. Conserv.* **82**: 279–287.
- Martin, T. E. & Li, P. (1992). Life history traits of open- vs cavity-nesting birds. *Ecology* **73**: 579–592.
- Mawson, P. R. & Long, J. L. (1994). Size and age parameters of nest trees used by four species of parrot and one species of cockatoo in south-west Australia. *Emu* **94**: 149–155.
- Nelson, J. L. & Morris, B. J. (1994). Nesting requirements of the yellow-tailed black-cockatoo, *Calyptorhynchus funereus*, in *Eucalyptus regnans* forest, and implications for forest management. *Wildl. Res.* 267–278.
- Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biol. Conserv.* **70**: 265–276.
- Nix, H. A. & Kalma, J. D. (1972). *Climate as a dominant control in the biogeography of northern Australia and New Guinea: bridge and barrier: the natural and cultural history of Torres Strait*. Canberra.
- Oren, D. C. & Novaes, F. C. (1986). Observations on the golden parakeet *Aratinga guarouba* in northern Brazil. *Biol. Conserv.* **36**: 329–337.
- Pruett-Jones, S. G. & Lewis, M. J. (1990). Sex ratio and habitat limitation promote delayed dispersal in superb fairy-wrens. *Nature (Lond.)* **348**: 541–542.
- Reyer, H.-U. (1990). Pied kingfishers: ecological causes and reproductive consequences of cooperative breeding. In *Cooperative breeding in birds*: 529–557. Stacey, P. B. & Koenig, W. D. (Eds). Cambridge: Cambridge University Press.
- Rinke, D. (1989). The reproductive biology of the red shining parrot *Prosopelia tabuensis* on the island of 'Eua, Kingdom of Tonga. *Ibis* **131**: 238–249.
- Rowley, I. (1990). *Behavioural ecology of the galah Eolophus roseicapillus in the wheatbelt of Western Australia*. Sydney: Surrey Beatty.
- Saunders, D. A. (1982). The breeding behaviour and biology of the short-billed form of the white-tailed black cockatoo *Calyptorhynchus funereus*. *Ibis* **124**: 422–455.
- Saunders, D. A. (1986). Breeding season, nesting success, and nestling growth in Carnaby's cockatoo, *Calyptorhynchus funereus latirostris*, over 16 years at Coomallo Creek, and a method for assessing the viability of populations in other areas. *Aust. Wildl. Res.* **13**: 261–273.
- Saunders, D. A., Smith, G. T. & Rowley, I. (1982). The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia. *Aust. Wildl. Res.* **9**: 541–556.
- Sherley, G. H. (1989). Benefits of courtship-feeding for rifleman (*Acanthisitta chloris*) parents. *Behaviour* **109**: 309–318.
- Skutch, A. F. (1985). Clutch size, nesting success, and predation on nests of neotropical birds, revisited. *Ornithol. Monogr.* **36**: 575–594.
- Smith, G. T. (1991). Breeding ecology of the western long-billed corella, *Cacatua pastinator pastinator*. *Wildl. Res.* **18**: 91–110.
- Smith, G. T. & Saunders, D. A. (1986). Clutch size and productivity in three sympatric species of cockatoo (Psittaciformes) in the south-west of Western Australia. *Aust. Wildl. Res.* **13**: 275–285.
- Snyder, N. F. R., Wiley, J. W. & Kepler, C. B. (1987). *The parrots of Luquillo: natural history and conservation of the Puerto Rican parrot*. Los Angeles: Western Foundation of Vertebrate Zoology.
- Stoleson, S. H. & Beissinger, S. R. (1999). Hatching asynchrony, brood reduction, and food limitation in a neotropical parrot. *Ecol. Monogr.* **67**: 131–154.
- Stutchbury, B. J. M. & Morton, E. S. (2001). *Behavioral ecology of tropical birds*. San Diego: Academic Press.
- Waltman, J. R. & Beissinger, S. R. (1992). Breeding biology of green-rumped parrotlet. *Wilson Bull.* **104**: 65–84.
- Whittingham, L. A., Dunn, P. O. & Magrath, R. D. (1997). Relatedness, polyandry, and extra-group paternity in the cooperatively-breeding white-browed scrubwren. *Behav. Ecol. Sociobiol.* **40**: 261–270.
- Wilkinson, R. (1994). Vasa parrot's fascinating breeding behaviour. *Psittascene* **6**: 9.
- Wyndam, E. (1981). Breeding and mortality of budgerigars (*Melopsittacus undulatus*). *Emu* **81**: 240–243.