

The breeding biology of palm cockatoos (*Probosciger aterrimus*): a case of a slow life history

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Abstract

The breeding of palm cockatoos *Probosciger aterrimus* was studied for 3 years from July 1999 to February 2002 in and around Iron Range National Park, Cape York Peninsula, Australia. Palm cockatoos were weakly seasonal breeders, with the peak of egg-laying occurring in September; 41 breeding attempts were monitored at 28 nesting hollows. Nearly all (27/28) nests were in tropical savanna woodland and an average distance of 320 m to rainforest. Males defended about four nest sites, only a subset of which were used for breeding. The typical active nest tree was in a near-vertical hollow with an opening that faced skywards; 62.1% of active nests were in living trees and the most common species of nest tree was *Eucalyptus tetradonta* (48.3%). DNA fingerprinting revealed that some pairs reused the same nest hollow even when breeding attempts were separated by 1 or more years of no breeding activity, but that changes in hollow ownership also occurred. Nest usurpation, male territorial displays at the nest and evidence of interference competition by conspecifics suggest strong competition for nest sites, which is probably driven by variation in hollow quality and high investment in the nesting platform. Of active nests, 81% failed to produce a fledgling, thereby ranking the breeding success of palm cockatoos among the lowest reported for any species of parrot. They also invariably laid a single egg and seemed to breed infrequently, and thus they use an extremely slow life-history strategy. We suggest that this slow life history makes palm cockatoos on Cape York Peninsula sensitive to environmental perturbations, with fire being the most probable threatening process.

Key words: *Probosciger aterrimus*, palm cockatoo, Cacatuidae, hollow nesting, slow life history, nest competition

INTRODUCTION

Cockatoos (Cacatuidae) are a well-known but highly threatened family of birds. Over half of all species face extinction in the wild in the short- to medium-term (Juniper & Parr, 1998), and most species are well-represented in aviaries throughout the world. However, despite their high profile, there have been few detailed studies on their ecology in the wild. Of the 21 or so species of cockatoo, the most detailed studies have concentrated on just seven species, all of which are entirely or mostly temperate in distribution (e.g. Saunders, 1976, 1979, 1982, 1986; Saunders, Smith & Rowley, 1982; Smith & Saunders, 1986; Rowley & Chapman, 1991; Nelson & Morris, 1994). Most tropical species live in relatively inaccessible regions at low densities, and often nest in trees that are difficult to find and access, which makes detailed studies difficult.

Palm cockatoos *Probosciger aterrimus* are one such tropical-dwelling species of which little is known. Their distribution covers lowland New Guinea to 1300 m, the Aru Islands, the islands of Geelvink Bay, West Papua, and far northern Cape York Peninsula, Australia (Juniper & Parr, 1998). In New Guinea, palm cockatoos are found in areas of pure rainforest and tropical savanna, whereas in Australia they are thought to inhabit savanna adjacent to rainforest (Juniper & Parr, 1998).

In a molecular study examining the systematics of the cockatoos, Brown & Toft (1999) identified palm cockatoos as the most distantly related species in the group, being the first extant taxon to split from the other cockatoos. Morphologically they resemble the typical cockatoos, although there are several features that attest to their evolutionary distinctiveness. For example, they are the only cockatoo to possess a naked cheek patch that they use in signalling to conspecifics, and they are the only black cockatoo not to have a coloured band in their tail. Perhaps the most striking feature that sets them apart from most birds in general is their habit of 'drumming' with a stick or hard fruit on nest trees during display (Wood,

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1984). Despite these charismatic peculiarities, there has been no comprehensive study of their ecology. Most of the references to palm cockatoos in the literature are based on opportunistic encounters or observations made over short periods (e.g. MacGillivray, 1914; Forshaw, 1964; Bell, 1967; Forshaw & Muller, 1978; Wood, 1984; Frith & Frith, 1993; Storch, 1996; Diamond, Bishop & Gilardi, 1999).

Palm cockatoos are a CITES Appendix 1 listed species (Collar, Crosby & Stattersfield, 1994). Outside Australia, adults and chicks are taken as food by local hunters (Beehler, 1991; Igag, 2002) and adults are occasionally seen for sale in village markets (Mackay, 1970). In Australia it has been suggested that nestlings have been taken for the live bird trade (Garnett in Marchant & Higgins, 1999a). Sport shooting has been blamed for some local declines early last century (Barnard, 1911), and it has been suggested that land clearing on the west coast of Cape York has caused a contraction in range in this region (Forshaw, 1964). However, the most serious threat to palm cockatoos in Australia may be from changes in fire regimes. Some cases of fires destroying nests containing eggs or chicks have been reported (e.g. Frith & Frith, 1993), but they may also be threatened by widespread landscape changes caused by inappropriate fire regimes.

In Australia, palm cockatoos are classified as Near Threatened, meaning that they are close to qualifying for vulnerable with a restricted range and suspected small population size (Garnett & Crowley, 2000). The aim of this study was to collect information on the breeding biology of palm cockatoos, so that we can understand the implications of their life history for conservation. Specifically, we were interested in identifying the breeding season, breeding habitat, nest hollow characteristics, breeding success, breeding regularity and nest site fidelity, and causes of nest site destruction. In addition, observational data were also collected on adult behaviour at the nest pre-, during and post-breeding, incubation and nestling periods, and the post-fledging period.

METHODS

Study area

The study was undertaken between July 1999 and February 2002 in and around Iron Range National Park, Cape York Peninsula, Australia ($12^{\circ}47'S$, $143^{\circ}18'E$; Fig. 1). The region contains a diverse mosaic of semi-deciduous mesophyll vine forest interspersed by various types of savanna (see Tables 1a & 1b; Neldner & Clarkson, 1995). The average annual rainfall is 2130 mm, most of which falls between December and April during the monsoon season (Bureau of Meteorology). The late dry season (August–November) is characterized by frequent savanna fires, mostly purposefully lit by land managers and traditional Aboriginal landowners. Our fieldwork was carried out in *c.* 25 km² of non-contiguous areas within this region.

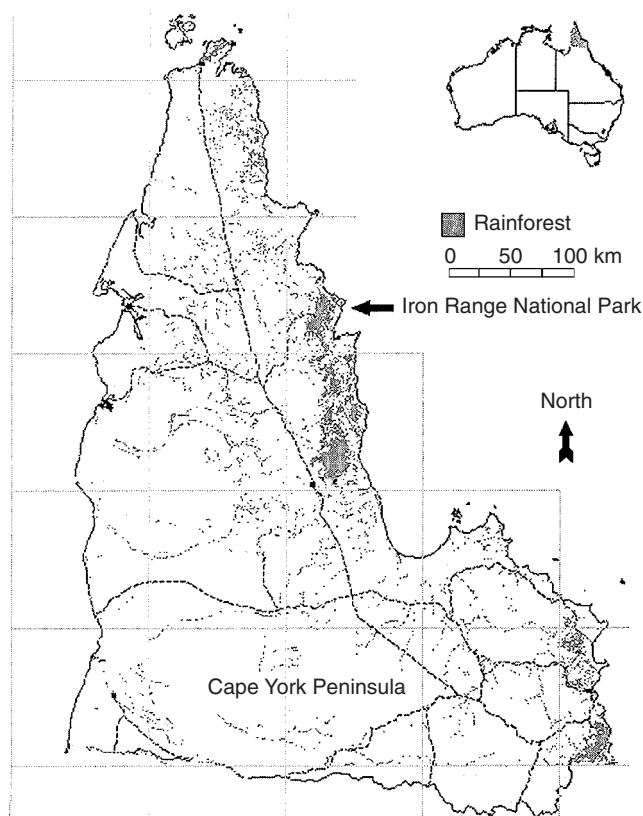


Fig. 1. Location of study area ($12^{\circ}45'S$, $143^{\circ}17'E$).

Nest finding

Nest sites were located by listening for palm cockatoo activity and inspecting nearby hollows. Hollows lower than 12 m were inspected with a small infrared video-camera mounted on a telescopic pole, and hollows higher than 12 m using single-rope techniques. It was possible to determine if a hollow was being maintained by palm cockatoos because of their characteristic nesting platform of splintered sticks. Palm cockatoos visited and maintained more nest hollows than they actually used for breeding. To distinguish between nest hollows that were used for breeding and those that were not, only nests containing eggs and chicks are referred to as active nests. Nests that contained breeding platforms only, which were often incomplete and unsuitable for breeding, and were never known to be used for a breeding attempt (i.e. never known to contain an egg or a chick) were defined as inactive nests. Because structural differences were found between active and inactive nests (see Results), only active nests were used in the analysis of preferred breeding habitat.

Breeding habitat

The position of each palm cockatoo nest was marked using a global positioning system (GPS). To determine where nests occurred in the landscape, the GPS coordinates of each nest were overlaid onto vegetation maps of the area (Neldner & Clarkson, 1995) using GARtrip version

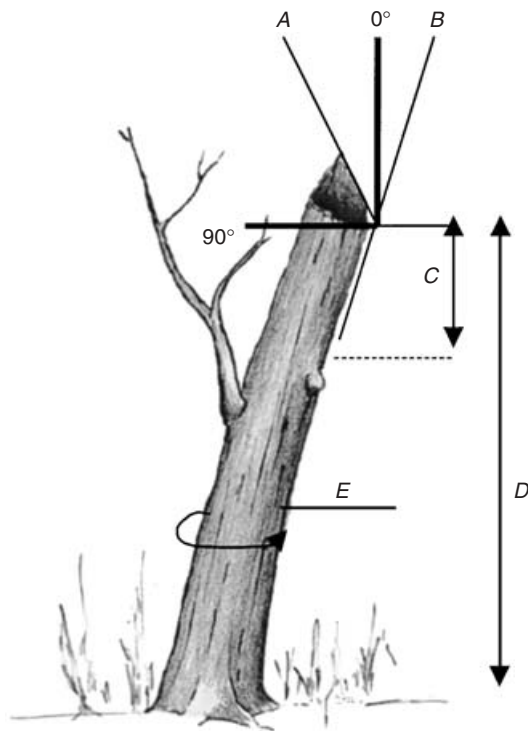


Fig. 2. Measurements taken for each palm cockatoo *Probosciger aterrimus* nest tree: A, entrance angle; B, hollow angle; C, depth to nesting platform; D, height from lowest part of entrance to ground; E, diameter at breast height.

204c© software (Pfeifer, 2001). The vegetation maps prepared by Neldner & Clarkson (1995) are based on 201 'map units' that identify different plant associations for all of Cape York Peninsula. The map units present in the study area were used as the basis for describing the various habitats used by palm cockatoos.

Nest hollow characteristics

For each active and inactive nest tree, the following attributes (see Fig. 2) were measured: species; status (dead or alive); diameter at breast height (DBH); entrance origin (either trunk shear or branch drop); entrance angle (i.e. 90° for skyward facing to 0° for sideways facing); hollow angle (0° for vertical to 90° for horizontal); longest and shortest dimensions at the entrance; longest and shortest internal dimensions at the platform; depth from the bottom of the entrance to the top of the breeding platform. These characteristics were compared between active and inactive nests to determine if palm cockatoos only bred in a subset of all the nests they maintained.

Breeding season

To define the breeding season, all hollows containing nesting platforms were visited *c.* every 2 months throughout the year to check for breeding activity. Most breeding activity was detected at the egg stage and the laying date

was established (± 3 days) by 'candling' the egg using a small light. Some breeding attempts were further defined as a second attempt if they occurred within 30 days after an initial attempt failed. For chicks of unknown age that were discovered in nests, the hatching date was established retrospectively using weight-by-age data (unpublished) from known-aged chicks.

Nest site fidelity

Adult birds were not captured or banded, making direct observation of nest site fidelity difficult. However, in a few nests, small blood samples (10–50 μ l) were collected from chicks from 2 or more breeding attempts. DNA fingerprinting techniques were used to determine whether these chicks were related, which would show that breeding adults re-used the same nest site. This included 3 nests for which there were samples for 2 chicks each, and a fourth nest for which samples were obtained from 3 chicks. A further 2 samples from chicks from 2 other nests were used to calculate the band-sharing of non-relatives (see below). The number of samples from subsequent breeding attempts at the same nest is small because about half of the breeding attempts failed at the egg stage (see Results), which precluded genetic sampling.

Standard DNA fingerprinting techniques were carried out using the minisatellite DNA probes 33.15 and per (Jeffreys, Wilson & Thein, 1985; Shin *et al.*, 1985). Refer to Legge & Cockburn (2000) and Bruford *et al.* (1992) for laboratory protocols. The principle of DNA fingerprinting is that each individual is characterized by a unique profile of bands (alleles) of different size, which are inherited roughly equally from the mother and father. Consequently, individuals that share one or both parents will share more bands on average than unrelated individuals. The degree of relatedness is estimated by the band-sharing coefficient, which is twice the number of shared bands divided by the sum of all bands scored in both individuals (Lynch, 1990).

It was assumed that chicks from different nests (which were an average of 10.5 km apart) were unrelated, and the distribution of band-sharing values between all possible dyads ($n = 49$) were plotted. Band-sharing values greater than the upper 95th percentile limit of this distribution share significantly more bands than expected for non-relatives. The band-sharing values between chicks from the same nest were then calculated, and a pair of chicks considered to share at least 1 parent if their band-sharing value was greater than this upper 95th percentile of the band-sharing distribution of non-relatives. The theoretical band-sharing expected between 2 full siblings was also calculated using the formula:

$$BS_{\text{exp}} = \frac{(4 + 5q - 6q^2 + q^3)}{4(2 - q)}$$

where q (mean allele frequency) is derived from the formula $x = 2q - q^2$, and x = the observed mean band-sharing value between non-relatives (Jeffreys *et al.*, 1985).

Table 1a. Number of active palm cockatoo *Probosciger aterrimus* nests found in each vegetation community (based on Neldner & Clarkson, 1995). Floristic, structural and landform descriptions of each map unit are shown in Table 1b

| No. of nests (%) | Vegetation community | Map unit (%) |
|------------------|----------------------|------------------------------|
| 12 (48) | A | 101 (70); 116 (30) |
| 6 (24) | B | 101 (60); 116 (30); 146 (10) |
| 6 (24) | C | 94 (70); 108 (2); 44 (10) |
| 1 (4) | D | 94 (50); 108 (20); 144 (10) |

Breeding success and general breeding biology

To keep disturbance to a minimum while monitoring breeding success, nests were checked only at hatching (c. 30 days) once they became active, and then when the chick was 30 days old and 60 days old (just before fledging). For 3 nests where exact hatching dates were known, nests were checked every second day when fledging was imminent to determine the nestling period accurately. To record incubation behaviour and possible predation events, a small infrared video camera was installed at 3 nests into a hole cut into the nest wall, and this was linked to a 24-h time-lapse video recorder.

To gain an estimate of the number of nest trees defended by individual males, the average number of displaying palm cockatoos (from unpublished survey data) were compared to the number of nest trees within a 1 km² area. The area used for this analysis was thoroughly searched to find all nest trees.

Incidental behavioural observations were noted whenever possible, and contributed general information about the pre-breeding, incubation, nestling and post-fledging periods.

RESULTS

Breeding habitat

Our nest-finding method (which involved following displaying birds) qualitatively showed that savanna was

preferred over rainforest as a breeding habitat. Unpublished quantitative survey results also support this preference (S. Murphy, S. Legge & R. Heinsohn, pers. obs.). Twenty-seven out of 28 active palm cockatoo nests were found in savanna adjacent to rainforest (mean distance to rainforest, 0.32 km; range 0.01–1.04 km), and one in rainforest. Of the 27 active nests monitored in savanna sites, 12 (48%) were located on erosional plains in vegetation community A, which comprised 70% *Eucalyptus tetrodonta* and *Corymbia nesophila* woodland (map unit 101; Neldner & Clarkson, 1995) and 30% *E. leptophloeaba* and *C. clarksoniana* woodland (map unit 116; Neldner & Clarkson, 1995). Six (24%) nests were found in vegetation community B and six in vegetation community C, and only one nest (4%) was found in vegetation community D. Table 1a shows the number of nests in each vegetation community and the map units which define each community (based on Neldner & Clarkson, 1995). Table 1b shows the floristic and structural characteristics, and the dominant landforms that characterize each map unit.

Nest hollow characteristics

Differences between active and inactive nests

The measurements of 37 inactive and 27 active nest hollows were compared to determine if palm cockatoos only breed in a subset of the nest hollows they maintained. Of 12 measurements analysed, only hollow angle was significantly different, with inactive nest hollows being significantly more vertical than active nest hollows (Table 2). Most of the inactive nest hollows had coarse, incomplete breeding platforms unsuitable for breeding, whereas active nest hollows had complete platforms of fine splintered sticks (see also Nest preparation and maintenance below).

Active nest characteristics

Active palm cockatoo nests were in existing tree hollows in eight species of savanna tree and one species of rainforest tree (*Blepharocarya involucrigera*). Two species of

Table 1b. Floristic, structural and landform descriptions of each map unit used in Table 1a

| Map unit ^a | Dominant canopy species | Average canopy height (m) | Project foliage cover (%) | Dominant landform |
|-----------------------|---|---------------------------|---------------------------|---------------------------------------|
| 44 | <i>Eucalyptus tessellaris</i> , <i>Corymbia clarksoniana</i> | 17.7 | 32.0 | Alluvial plains |
| 94 | <i>E. tetrodonta</i> , <i>C. clarksoniana</i> , <i>E. tessellaris</i> , <i>Lophostemon sauveolens</i> | 19.8 | 27.1 | Erosional and alluvial plains |
| 101 | <i>E. tetrodonta</i> , <i>C. nesophila</i> | 21.2 | 25.0 | Gently undulating rises and low hills |
| 108 | <i>Melaleuca viridiflora</i> , <i>E. tetrodonta</i> , <i>Acacia crassicarpa</i> , <i>Asteromyrtus brassii</i> , <i>M. stenostachya</i> | 14.0 | 20.0 | Erosional plains |
| 116 | <i>E. leptophloeaba</i> , <i>C. clarksoniana</i> , <i>E. papuana</i> ^b | 17.5 | 12.5 | Erosional plains |
| 146 | <i>M. viridiflora</i> , <i>Neofabrica myrtifolia</i> , <i>Allocasuarina littoralis</i> , <i>Asteromyrtus brassii</i> , <i>A. crassicarpa</i> | 11.8 | 26.5 | Erosional plains and low hills |

^a Based on the vegetation classification system of Cape York Peninsula by Neldner & Clarkson (1995). ^b Species not present in study area.

Table 2. Comparisons of 12 measurements between active and inactive palm cockatoo *Probosciger aterrimus* nests

| Measurement | Active nests | Inactive nests | Statistic ^a | P-value | |
|-------------------------------|--|---|------------------------|---------|----|
| Species | <i>Eucalyptus tetrodonta</i> = 14; <i>Corymbia clarksoniana</i> = 8 | <i>E. tetrodonta</i> = 19; <i>C. clarksoniana</i> = 12 | $\chi^2_1 = 0.03$ | 0.86 | NS |
| Tree state | Living = 18; dead = 9 | Living = 24; dead = 13 | $\chi^2_1 = 0.02$ | 0.88 | NS |
| DBH (cm) | 52.6 ± SE (4.4) | 46.2 ± SE (3.9) | $F_{1,51} = 1.14$ | 0.29 | NS |
| Entrance origin | Branch drop = 11; Trunk shear = 15 | Branch drop = 16; Trunk shear = 21 | $\chi^2_1 = 0.01$ | 0.94 | NS |
| Entrance angle | 57.8° ± SE (7.3) | 47.0° ± SE (6.2) | $F_{1,46} = 1.27$ | 0.27 | NS |
| Hollow angle | 17.7° ± SE (2.9) | 8.4° ± SE (2.4) | $F_{1,51} = 6.19$ | 0.016 | * |
| Hollow height (m) | 7.7 ± SE (5.9) | 7.4 ± SE (5.3) | $F_{1,50} = 0.11$ | 0.74 | NS |
| Entrance long dimension (cm) | 33.9 ± SE (3.0) | 34.1 ± SE (2.6) | $F_{1,50} = 0.002$ | 0.97 | NS |
| Entrance short dimension (cm) | 25.3 ± SE (1.6) | 24.7 ± SE (1.5) | $F_{1,50} = 0.07$ | 0.80 | NS |
| Internal long dimension (cm) | 33.6 ± SE (2.1) | 28.6 ± SE (1.8) | $F_{1,49} = 3.31$ | 0.083 | NS |
| Internal short dimension (cm) | 27.4 ± SE (1.3) | 24.6 ± SE (1.2) | $F_{1,49} = 2.52$ | 0.12 | NS |
| Nest depth (cm) | 99.9 ± SE (13.1) | 89.9 ± SE (11.3) | $F_{1,45} = 0.33$ | 0.57 | NS |

^a Statistical comparisons between count data were made using contingency tests, and between means of data using ANOVA.

Table 3. Tree species used by palm cockatoos *Probosciger aterrimus* for nesting

| Tree species | n | % |
|------------------------------------|----|------|
| <i>Blepharocarya involucrigera</i> | 1 | 3.4 |
| <i>Corymbia clarksoniana</i> | 6 | 20.7 |
| <i>C. nesophila</i> | 2 | 6.9 |
| <i>Eucalyptus brassiana</i> | 1 | 3.4 |
| <i>E. tessellaris</i> | 1 | 3.4 |
| <i>E. tetrodonta</i> | 14 | 48.3 |
| <i>Lophostemon</i> sp. | 2 | 6.9 |
| <i>Melaleuca dealbata</i> | 1 | 3.4 |
| <i>M. leucadendra</i> | 1 | 3.4 |

savanna tree accounted for over two-thirds of all active nests (*E. tetrodonta* 48.3% and *C. clarksoniana* 20.7%). A further six tree species roughly shared the remaining 27.6% of active nests (Table 3).

The majority of active nests were located in living trees (62.1%). Access to most (62.1%) hollows was gained via the trunk shearing (as opposed to branch dropping) and the average entrance angle was 59.4° (SD = 33.4). The average hollow angle was 15.0° (SD = 17.0). Thus, the typical palm cockatoo active nest was found to be in a slightly off-vertical hollow with an opening that faced skywards in a living tree. The internal dimensions of the active nests were most surprising in that some nests were very small given the large size of the bird (range 18.5 × 20.5 cm to 35.0 × 80.0 cm). These and other parameters are shown in Table 2.

Nest destruction

The two agents of nest destruction observed were fire and wind. The percentage of savanna nest trees (inactive and active) destroyed by fire in each year of the study was 0% ($n = 28$ nest sites), 6.7% ($n = 45$) and 5.2% ($n = 57$) in the 3 years, respectively. During these 3 years, one nest fell

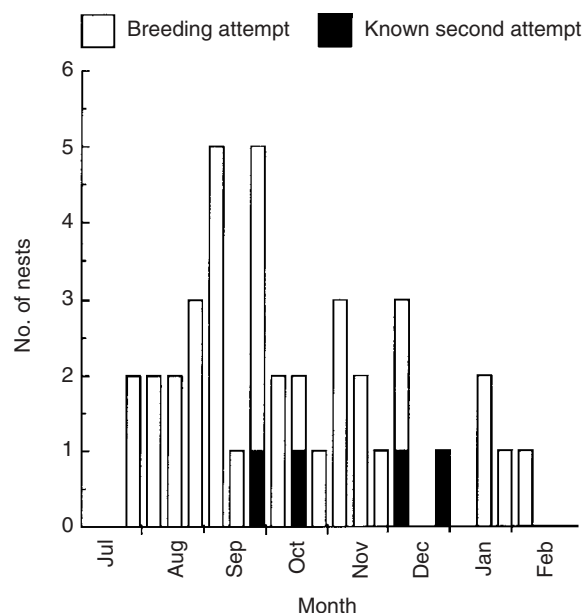


Fig. 3. The breeding season of palm cockatoos *Probosciger aterrimus* based on the laying dates (assigned to 10-day intervals) of 41 breeding attempts at 28 active nests in the study. A 'breeding attempt' occurred when an egg or chick was detected in a nest.

over in a wind storm. No data are available for the rate of nest hollow creation, but hollows apparently arise from a process involving fire-induced tree weakening followed by termite attack and sculpturing (Perry, Lenz & Watson, 1985).

Breeding season

Palm cockatoos on Cape York Peninsula seem to have a protracted breeding season. Of the 41 breeding attempts monitored at 28 active nests between 1999 and 2002, eggs were laid in 8 months of the year (Fig. 3). The fairly

protracted laying season translates into an even longer breeding season given that incubation and chick rearing takes *c.* 90–100 days (see below). Thus, palm cockatoos can be involved in breeding at almost any time of the year from late July to early May. However, there seemed to be more egg laying in September (Fig. 3). Pairs were detected to re-lay after a failed first attempt on four occasions, but re-laying in the same breeding season was never observed after a successful attempt. Breeding attempts, including second attempts, may be more frequent than we observed if our bimonthly nest site checks missed some breeding attempts that failed quickly.

Nest site fidelity

An average of 22 minisatellite bands were scored for each individual. The mean DNA fingerprinting band-sharing value between unrelated individuals was 0.23 ± 0.11 SD; 95% of the values were lower than 0.43 (or alternatively, band-sharing values higher than 0.43 strongly indicate that the two individuals are related). The mean band-sharing expected for full siblings, based on the allele frequency and mean band-sharing value for non-relatives, was 0.63.

In the three nests where we had sampled chicks from two breeding attempts, the chicks from two shared at least one parent since their band-sharing values were well above 0.43 (the chicks from nest 1 shared 0.56 of their bands, the chicks from nest 2 shared 0.50 of their bands). In the third nest (nest 3) the two chicks shared 0.41 of their bands, just below the 95th percentile for non-relatives. However, one of the chicks had a much lower number of bands than the other, which will artificially depress their band-sharing value. Therefore, it is highly possible that these chicks shared at least one parent. In the fourth nest (nest 4), where chicks from three breeding attempts were sampled, the chicks from seasons 1997–98 and 2000–01 shared at least one, but probably both parents (band-sharing = 0.60). However, the chick from the third breeding attempt in 2001–02 was unrelated to both of the earlier chicks (band-sharing of 0.31 and 0.36), suggesting that nest ownership changed between the 2000–01 and 2001–02 seasons.

These results show that adult palm cockatoos do reuse the same nest between breeding attempts, even when they are 3 years apart (nest 4). However, the results also show that nest ownership can change between years (also nest 4). In addition, given that the band-sharing values of two dyads (nest 1 = 0.56 and nest 4 = 0.60) were close to that expected for full siblings (0.63), it seems that adults can remain paired for more than one breeding attempt.

Breeding success

Forty-one breeding attempts at 28 active nests were recorded. Of these, nine (22.0%) successfully produced a fledgling, 29 (70.7%) were unsuccessful, and for three the outcome was unknown; 15 out of 38 (39%) breeding attempts failed at the incubation period, and 14 (61%) of the 23 eggs that actually hatched failed. Thus,

Table 4. Cause of nest failure in 41 palm cockatoo *Probosciger aterrimus* breeding attempts

| Cause of failure | <i>n</i> (%) |
|-----------------------------------|--------------|
| Egg infertile | 5 (12.2) |
| Egg abandoned | 1 (3.4) |
| Egg preyed upon | 7 (24.1) |
| Egg crushed, but uneaten | 2 (6.9) |
| Chick preyed upon | 11 (37.9) |
| Young chick died in hole | 2 (6.9) |
| Platform collapsed, killing chick | 1 (3.4) |

overall, more breeding attempts failed during the nestling period compared to the incubation period. However, the incubation period is about only half as long as the nestling period. Taking the length of each period into account (by dividing the observed failure rate by the average time spent in each period of 31 and 72 days, respectively), the daily risk of failure during the egg period is 1.3%, whilst during the nestling period it was 0.85%. Thus, eggs were actually more likely to fail on a per-day basis.

The main causes of nest failure were chicks and eggs disappearing, presumably owing to predation (11 and 7 cases, respectively), and hatching failure (5 cases). These and the minor causes of breeding failure are shown in Table 4. It is possible that some breeding attempts went undetected if eggs were lost quickly, so the success rate of breeding attempts could be even lower than that reported here.

At four nests where the egg disappeared, a major proportion of the egg shell remained intact while the contents were missing, suggesting predation by smaller predators such as small varanids *Varanus* spp., large rodents, e.g. *Uromys caudimaculatus*, and black butcherbirds *Cracticus quoyii*. Each of these predators are common in the study area and were observed in or near nest trees on several occasions. Four chicks older than 30 days disappeared, suggesting large predators such as amethystine pythons *Morelia amethystina* or large varanids, e.g. *Varanus panoptes*, both of which are also common in the study area. Amethystine pythons are known predators of adult and nestling eclectus parrots *Eclectus roratus* (Heinsohn & Legge, 2003), and adult and nestling sulphur-crested cockatoos *Cacatua galerita*. In the 2001–02 breeding season, large varanid tracks were left in sand at the base of an active nest tree from which a chick disappeared.

Breeding frequency

It is difficult for us to estimate the breeding frequency of pairs because marked birds were not monitored. However, our observations suggest that palm cockatoo pairs do not breed annually. Of all the nest hollows that became active during the study, 11 were monitored for the full 3 years. During this period, breeding efforts were initiated just once at seven nest sites, and twice at the remaining four nest sites. This suggests that nest sites are used between one

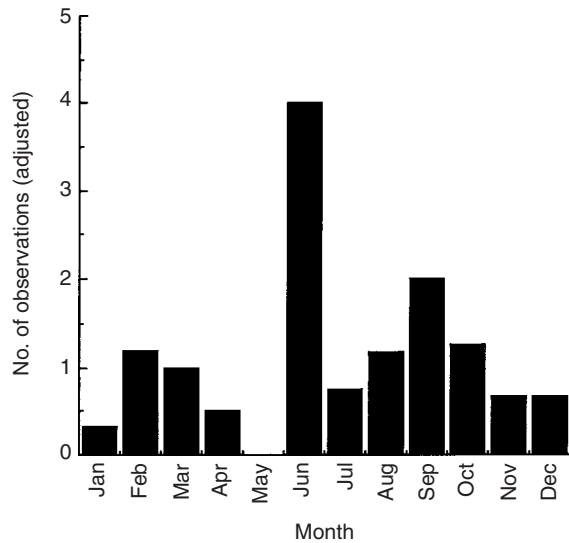


Fig. 4. The number of territorial displays by palm cockatoos *Probosciger aterrimus* at nests by month, adjusted for observer effort by dividing the number of observations in the month by the total number of fortnights spent in the field for that month over the 3 years of the study.

and two times every 3 years, or at an average frequency of once every 2.2 years.

General breeding behaviour

Nest site defence

Displays at nests were observed in all months of the year (except May, when limited time was spent in the field), although there was a concentration of activity in the months leading up to the breeding season (Fig. 4). Most displays were observed during the early morning and late afternoon (Fig. 5). Those displays that were observed later in the day usually occurred on overcast or wet days. Displays involved much calling (with disyllabic whistle, harsh ‘crac’ call, and ‘hello’ call), wing-spreading, blushing (complete exposure and darkening of red cheek patch), crest erection, upside-down swinging, pirouetting, foot stamping and drumming. Displays were performed mainly by males. Of 46 displays at nests where the sex of the bird(s) could be identified, 31 (67%) involved a single male, seven (15%) involved a male and a female, one (2%) involved two pairs, and one (2%) involved two males.

In one thoroughly searched area of *c.* 1 km², there were 15 active and inactive nest trees. Unpublished survey data of displaying palm cockatoos revealed an average 4.4 cockatoos for the same area, suggesting that each male defends and maintains between three and four nest sites.

Courtship behaviour

On three occasions where pairs were observed courting at the nest, the males positioned themselves at the entrance of the hollow. The males were usually observed

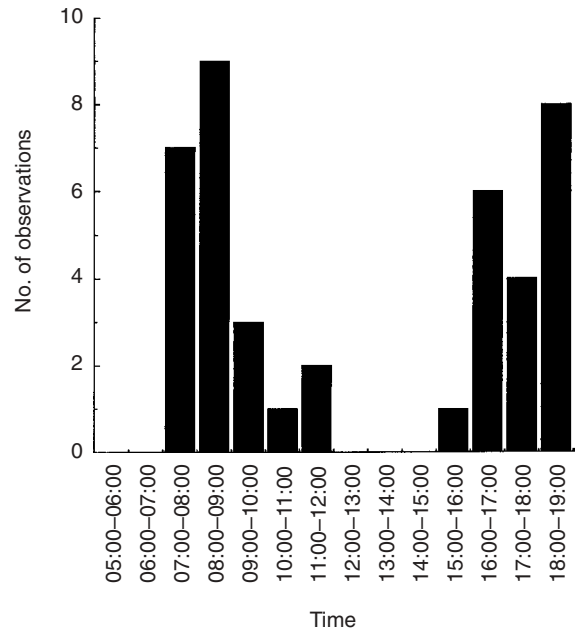


Fig. 5. The number of territorial displays by palm cockatoos *Probosciger aterrimus* at nests by time of day.

wing-spreading, stamping and drumming without making any calls other than soft clicks. Males invariably had their cheeks blushed during this period, and would often chew the rim of the entrance and overtly ‘act out’ dropping the splinters into the hollow. Male palm cockatoos also bobbed their heads into the hollow as if they were feeding, even though nothing was in their beaks. Sometimes males were observed adopting a static posture whereby they sat at the entrance, and held their body in a rigid position roughly parallel to the hollow (see also Frith & Frith, 1993). The reaction of the female during these displays presumably depended on her level of interest in breeding at the time. If ‘uninterested’, the female sat nearby with her cheek patches concealed by her lower cheek feathers, and would often preen. If ‘interested’, the female blushed and brought sticks to the nest to be added to the nesting platform.

Nest preparation and maintenance

Unlike most parrots, palm cockatoos construct a platform of sticks inside the tree hollow. The cockatoos started the platforms by adding large whole or splintered sticks to the hollow. In some nest trees small fissures in the trunk below the platform revealed that the platforms were suspended inside the trunk with a gap between the underside of the platform and the ground or internal ‘mud-gut’ of the tree. At one tree that was recently gutted by fire, a pair of cockatoos were observed dropping in large (20–30 cm long and > 10 mm diameter) sticks, suggesting that the process of platform construction relies on some of these large sticks becoming lodged inside the hollow and acting as foundations for the rest of the structure. Other platforms had no gap underneath and rested directly on the

mud-gut inside the tree. The top layer of splinters added immediately before egg laying were invariably very fine and resembled long match-sticks, and represents much investment by the breeding pair.

Males added sticks to the platform during displays at all times of the year, and therefore they do the majority of the nest preparation and maintenance. Females only assisted when the platforms were nearly complete during the start of the breeding season or before re-laying. Pairs were observed preparing nests on 10 occasions, between August and November (i.e. synchronous with the peak of breeding activity). Video footage from within nests showed that the male or the female, or sometimes both, entered the hollow to splinter twigs and rake the platform. Often one partner dropped in sticks from above while the other bird remained inside. Raking was only ever observed once the splinters were very fine, and it was assumed that raking serves to maintain adequate drainage and to lessen compaction of the platform.

Incubation and nestling period

Of the eggs that were candled and hatched ($n=20$) the incubation time was estimated to be between 30 and 32 days. Both males and females incubated the single white egg in long shifts. Approximately 115 h of video footage and nest watches at four different nests show that males relieved females on average at 08:25 in the morning ($n=6$ changeovers), and that females relieved males at 16:12 in the afternoon ($n=4$). Fourteen random spot checks at 12 different nests showed that males invariably incubated between 10:00 and 15:00. Eight nights of video footage showed that females invariably incubated during the night. Incubating birds often raked the platform while incubating and added fresh splinters at changeovers.

Rival males were observed landing on active nests that contained incubating resident males at two nests. Both times the resident male emerged from within the hollow with cheeks blushed and chased away the intruder. On one other occasion, aggressive calling was heard from at least three birds near an active nest on the day that the egg was due to hatch. The eggshell and hatchling were found crushed but uneaten 2 days later.

At three nests where accurate hatching and fledging dates were known, fledging occurred 65–79 days after hatching. Limited data are available on the roles of each sex during brooding, and on feeding rates. On six occasions both males and females were flushed from nests containing young chicks under 30 days old; and after this time adults were normally flushed from vegetation near the nest tree ($n=7$). At two nests, when the chick approached fledging age the adults became more vocal and started to display on and near the nest tree.

Post-fledging period

Fledgling palm cockatoos were observed on three occasions. On two separate occasions, the young birds were

discovered sitting alone in thin strips of riparian vegetation during the day. In the late afternoon, the same fledglings gave a croaky, rattling call, to which an adult would respond by flying up to the young bird and delivering food. Fledglings gave a rasping begging call while being fed. Both males and females were observed feeding fledglings. For one fledgling, this pattern of summoning, begging and feeding was observed on five occasions in the same location for over 3 weeks in July. On another occasion, a fledgling was observed begging from an adult female who had procured a cluster of *E. tetradonta* fruits. The juvenile adopted a flattened posture, stretched out its wings and extended its throat. On this occasion, no food was delivered. The female chased away the juvenile to a nearby branch where it sat with its red cheek patch concealed by its lower cheek feathers.

DISCUSSION

Despite their evolutionary distinctiveness and charismatic behaviour, ecological information about wild palm cockatoos to date has been based on opportunistic, short-term and often largely anecdotal encounters. This study is the first systematically collected information from a wild population. The three main findings in this study are that: (1) palm cockatoos have a slow life history, being weakly seasonal breeders with infrequent, and usually unsuccessful breeding attempts; (2) palm cockatoos prefer to breed in savanna adjacent to rainforest and that nest site availability and habitat maintenance is therefore affected by fire, which is an annual feature of the savanna environment; (3) nest usurpation, conspicuous male territorial displays at the nest and evidence of interference competition by conspecifics suggest strong competition for nest hollows, which is probably driven by variation in hollow quality and high investment in the nesting platform. Each of these main findings and their conservation implications are discussed below.

Slow life history: protracted and infrequent breeding with low reproductive success

Until this study, it has not been clear exactly when or how often palm cockatoos breed. Some authors have suggested specific breeding seasons, but these were often contradictory and based on small numbers of observations made over short periods (MacGillivray, 1914; Forshaw, 1964; Forshaw & Muller, 1978; Wood, 1988; Frith & Frith, 1993; Storch, 1996). The current study monitored breeding activity every 2 months for 3 years and has shown that the breeding season is very protracted (July–May), with a slight increase in egg-laying in September.

Although the timing of this protracted breeding season means that most attempts occur over the wettest period of the year, palm cockatoos are well suited to an environment that has monsoons. Other species of parrots in the region have their breeding seasons cut short because of nest hollow flooding (e.g. sulphur-crested cockatoos; eclectus parrots, Heinsohn & Legge, 2003). By contrast, palm

Table 5. Aspects of the breeding biology and success for other parrot species, ranked according to overall breeding success

| Species | Clutch size | Incubation period (days) | Nestling period (days) | Hatching success (%) | Overall breeding success* (%) |
|---|-------------|--------------------------|------------------------|----------------------|-------------------------------|
| Western corella ^{a,b} | 1–4 | 22–25 | 53–67 | 67.2 | 75.7 |
| Little corella ^a | 2–4 | – | 59–64 | 82.6 | 65.2 |
| Red shining parrot ^c | 2–3 | 24 | 49 | – | 50.0 |
| Crimson rosella ^d | 3–8 | 16–28 | – | 66.3 | 50.0 |
| Galah ^e | 2–8 | 22–26 | 50–52 | 62.0 | 48.0 |
| Major mitchell's cockatoo ^{f,g} | 3–4 | 23–24 | 53–66 | 75.0 | 47.0 |
| Glossy black cockatoo ^{h,i} | 1(2) | 28–33 | 90 (60–105) | – | 42.0 |
| Short-billed black cockatoo ^{j,k} | 1–2 | 28–29 | 70–77 | 76.5 | 35.0 |
| Sulphur-crested cockatoo ^{f,l,m} | 1–4 | 30 | 66–73 | 60.0 | 35.0 |
| Red-tailed black cockatoo ^{n,a} | 1(2) | 28–32 | 87 (71–100) | 64.4 | 28.8 |
| Palm cockatoo ^o | 1 | 30–32 | 66–79 | 63.4 | 22.0 |
| Eclectus parrot ^p | 2–3 | 30 | 79–86 | 88.0 | 18.0 |
| Yellow-tailed black cockatoo ^{q,r} | 2(3) | 28–31 | 90 | – | – |
| Gang-gang cockatoo ^{s,t,u} | 1–4 | 24–30 | 49–56 | – | – |
| Long-billed corella ^{v,w} | 2–4 | 24 | 42–56 | – | – |

* Number of chicks to fledge as a proportion of number of eggs laid.

^a Smith & Saunders, 1986; ^b Smith, 1991; ^c Rinke, 1989; ^d Krebs, 1998; ^e Rowley, 1990; ^f North, 1901–14; ^g Rowley & Chapman, 1991;

^h Courtney, 1986; ⁱ Sindel & Lynn, 1989; ^j Saunders, 1982; ^k Saunders, 1986; ^l Noske, 1980; ^m Forshaw & Cooper, 1981; ⁿ Saunders, 1977; ^o This study; ^p Heinsohn & Legge, 2003; ^q Saunders, 1979; ^r Mayo & Mayo, 1992; ^s Howe, 1924; ^t Cayley, 1938; ^u Chambers, 1995;

^v Lendon, 1970; ^w Shephard, 1989.

cockatoos are relatively immune to flooding because their unique nesting platform allows rain, as well as excreta and feather sheaths, to be drained from the breeding chamber.

Palm cockatoos are unique among cockatoos in that they invariably lay a single egg. All other large cockatoo species are known to at least sometimes lay two eggs, and some smaller species lay up to eight eggs (e.g. galahs *Cacatua roseicapilla*, Rowley, 1990; Juniper & Parr, 1998; Table 5); 63.4% of all palm cockatoo eggs laid in this study hatched, which is similar to several other cockatoo species (e.g. red-tailed black cockatoos *Calyptorhynchus banksii*, and western corellas *C. pastinator*, Smith & Saunders, 1986). Despite having a similar hatch rate to common species such as galahs (Rowley, 1990), palm cockatoos have one of the lowest breeding success rates reported for any parrot (Table 5). Moreover, as most nest sites were checked bimonthly, it is possible that some breeding attempts were missed altogether, and therefore the breeding success of palm cockatoos in this study has probably been overestimated.

Egg and chick disappearance accounted for 62% of failed breeding attempts in palm cockatoos, with predation being the most probable cause. A study on eclectus parrots in the same region identified predation by amethystine pythons and varanids as the probable cause of nest failure in 34% of cases (Heinsohn & Legge, 2003). Although eclectus parrots are rainforest-dwelling species, amethystine pythons also inhabit savanna adjacent to rainforest, and different species of varanids (e.g. *Varanus panoptes*), equally capable of palm cockatoo predation, also occupy the savanna. *Varanus panoptes* is frequently encountered in the study area, and tracks imprinted in sand at the base of an active nest from which a chick disappeared provide support for their suspected role in nest failure. However, there is no evidence, anecdotal or otherwise, to suggest that the predation rate (the single

factor that is suspected to have caused most egg and chick losses in this study) was unusually high, and therefore palm cockatoos do have a naturally slow rate of reproduction.

The limited DNA fingerprinting results and the low frequency of nest site reuse (less than once every 2 years) suggest that palm cockatoo pairs stay together for consecutive breeding attempts that may be separated by 1 or more years of no breeding activity. Although it is possible that nest hollows remain unused for 2 or more years because the attending adults bred elsewhere in that time, we think this is highly unlikely. The number of displaying birds in any given area exceeds the number of breeding attempts in that area. Thus, palm cockatoos seem to have an extremely slow life-history strategy, laying a single egg in infrequent and mostly unsuccessful breeding attempts. In keeping with these characteristics, palm cockatoos have a long lifespan. Although no data exists on the longevity of wild palm cockatoos, parrots in general, and cockatoos specifically, are renowned for long lifespans compared with other birds (Brouwer *et al.*, 2000). The only longevity data available for palm cockatoos is from captive birds; the oldest authenticated captive palm cockatoo is a 56-year-old female housed at London Zoo (Brouwer *et al.*, 2000). A male palm cockatoo in captivity in an Australian zoo is reputedly 80–90 years old (P. Digney, pers. comm.). Although speculative, palm cockatoos in the wild probably live for 40–60 years and most importantly, they are probably reproductively active for much of their lives. King (1993) reports that a male palm cockatoo bred at a minimum age of 29 years, and four palm cockatoos at Taronga Zoo in Sydney carried on breeding until they were over 30 years old (Muller, 1975). No data exists on what age wild palm cockatoos start breeding. Captive individuals seem to vary greatly in their age of first breeding. A captive female palm cockatoo laid

Table 6. Comparison of some nest tree characteristics of palm cockatoos with four other cockatoo species

| | Tree species (dominant) | % dead | DBH (cm) | Height (m) | Entrance dimensions (cm) | Internal dimensions (cm) | Depth (cm) |
|---|--|--------|----------|------------|-----------------------------|-----------------------------|------------|
| Palm cockatoo | <i>Eucalyptus</i> spp. <i>Corymbia</i> spp. | 37.9 | 54.4 | 8.36 | 25.3 × 33.8 | 27.2 × 32.8 | 99 |
| Red-tailed black cockatoo ^{b,c} | <i>Eucalyptus</i> spp. | 40.5 | 50 | 7.3 | 25.0 × 27.2 | 40 | 171.8 |
| Yellow-tailed black cockatoo ^{d,e,f} | <i>Eucalyptus</i> spp. | 5.6 | 246 | 36.7 | 46 | 30 | 60–240 |
| Corellas ^{b,g} | <i>Eucalyptus</i> spp. | 17.9 | 56.4 | 9.63 | 18.5 × 19.7 | – | 146 |
| Galah ^b | <i>Eucalyptus</i> spp. | 10.4 | 51.1 | 8.86 | 15.7 × 15.9 | – | 107 |

^a This study; ^b Saunders *et al.*, 1982; ^c Saunders, 1976; ^d Nelson & Morris, 1994; ^e Whatmough, 1984; ^f Marchant & Higgins, 1999b.
^g Data from *C. pastinator* and *C. sanguinea*.

her first egg at London Zoo when she was at least 40 years old (Brouwer *et al.*, 2000). A captive female in aviaries at Florida reached sexual maturity at between 7 and 8 years of age (Swigert, 1998).

Nest site preferences

Like all cockatoos and most parrots, palm cockatoos are secondary cavity nesters, breeding in naturally formed tree hollows. It is not surprising that 48.3% of all active palm cockatoo nest sites were in *Eucalyptus tetradonta*, because this species is widespread in the study area (Neldner & Clarkson, 1995) and also seems to be particularly prone to hollow formation. In the Northern Territory, Braithwaite *et al.* (1985) showed that 70% of *E. tetradonta* trees at 54 sites were 'piped' (i.e. hollowed out right through the trunk) by termites, which is a prerequisite for suitable hollow formation. Other nest site parameters presented here for palm cockatoos are similar in most respects to most other cockatoo species (Table 6). One notable difference is the relatively high proportion of dead trees used for nesting, which is a characteristic they share with red-tailed black cockatoos (Saunders, 1976; Saunders *et al.*, 1982).

The results presented here show that palm cockatoos prefer to breed in various types of savanna. Throughout the world tropical savannas are characterized by fire, and particular areas of savanna differ in terms of fire frequency, intensity and timing (Andersen *et al.*, 1998). Even within the study area there was much variation in the frequency and intensity of fires, with some areas burnt every year of the study and others that were not burnt for many years. Generally speaking, this variation in fire history means that the savanna is a dynamic environment that can change with respect to broad vegetation type, structure and floristics. There are concerns that many areas within Cape York are being burnt too often, too intensely or not often enough (Stanton, 1998; M. Blackman, pers. comm.), which could affect the rates of nest site destruction, the pattern of tree (i.e. potential nest site) recruitment and the extent of rainforest encroachment. As the savanna is important breeding habitat, inappropriate burning could detrimentally affect palm cockatoos. Indeed, Garnett & Crowley (2000) suggest that the most serious threat to palm cockatoos in Australia is probably from fires.

Nest hollow competition

During this study, instances of nest usurpation, interference competition and other behavioural observations suggested strong competition for nest sites. Despite few focal watches at active nests, on two occasions rival male palm cockatoos were observed visiting nests containing incubating resident males. Each time, the resident chased away the intruder and quickly returned to continue incubating. These observations suggest that palm cockatoos compete for nest sites. Also, because males are the larger sex (with larger mandibles), nest defence may also be the reason why male palm cockatoos invariably incubate during the day when rival males are most likely to be active. Sex roles in nest defence has been used to explain sexual size dimorphism in several species (Wiklund & Stigh, 1983; Andersson & Wiklund, 1987; Sproat & Ritchison, 1993; Galeotti, Tavecchia & Bonetti, 2000) although the theory does not hold in others (Guerra & Drummond, 1995; Catry, Phillips & Furness, 1999).

Interference competition between palm cockatoos also suggests strong competition for nest sites: 13.8% of unsuccessful breeding attempts failed because either the chick or egg was killed but uneaten, apparently by other palm cockatoos. On one occasion four palm cockatoos were observed chasing one another around a nest in which the egg was crushed but left uneaten. Other hollow users are unlikely to be responsible for this interference behaviour, since Heinsohn, Murphy & Legge (2003) show that the orientation, dimensions and site of hollows used by palm cockatoos differ significantly from those used by the other two large hollow-dependent parrots in the study area (eclectus parrots and sulphur-crested cockatoos). Intraspecific interference competition of this nature has been observed in other bird species. For example, egg destruction and the subsequent usurpation of nest hollows by house wrens *Troglodytes aedon* has been linked to nest hollow limitation (Pribil & Picman, 1991).

Male palm cockatoos defend their nest sites year-round, and this is characteristic of other birds with limited nesting resources. For example, Tengmalm's owls *Aegolius funereus* breed in standing pipe-like trees that are scarce (Lundberg, 1979). To defend nest trees, male owls maintain year-round territories centred around the nest tree despite winter food shortages that cause female owls and other sympatric owl species to migrate (Lundberg,

1979; Korpimäki, 1987). Similarly, Brawn (1984) showed that when nest sites are limiting, western bluebirds *Siala mexicana* defended nest-boxes outside the normal breeding period.

There are two factors that may be driving nest hollow competition in palm cockatoos. First, although hollows seem to be abundant in the savanna (only 43.1% of monitored nest sites were used for breeding), high-quality hollows may none the less be limiting. Inactive nest hollows differed significantly in hollow angle compared to active nest hollows, suggesting that hollows vary in a feature that is important to the birds. Off-vertical hollows may be less exposed to rain, although the nesting platform should abate any flooding problems. More importantly, a hollow that is off-vertical probably provides easier access for adults climbing in and out of the nest. This could be very important if high predation risks means adults need to be able to exit the nest quickly.

The second factor driving hollow competition may be substantial investment in the nesting platform, which can be > 2 m thick. Across species, nest defence often increases as parental investment in the breeding attempt increases. This usually entails increased defence against predators for older broods (Galeotti *et al.*, 2000), for larger clutches (Wiklund, 1990), or for broods dominated by the more valuable sex (Radford & Blakey, 2000). However, nest defence can also vary with investment or 'value' that is not directly related to the offspring (such as the nest itself), although this has been shown more rarely. For example, male warbling vireos *Vireo gilvus* guard and defend against conspecifics stealing nesting materials (Howes-Jones, 1985).

Conservation implications

Our study has shown that palm cockatoos on Cape York have a slow life history. These long-lived birds have a long breeding season, breed infrequently, lay a single egg and have one of the lowest rates of breeding success reported for any parrot. Although they are confined to rain-forest areas of Cape York Peninsula, they mainly breed in adjacent patches of savanna, which is a dynamic, fire-dominated habitat. These results have important conservation implications.

Their extremely poor breeding success may be of special concern because the long lifespan of palm cockatoos means that low recruitment would be masked for many years by a persistent, but ageing adult population. Their slow life history also means that the population would only be capable of a slow recovery following any detrimental environmental perturbations. Consequently, a greater understanding of the actual or potential threatening processes is required for successful management of this species. We have shown that palm cockatoos are dependent on nest hollows that are probably limiting and prone to destruction by fire. Inappropriate burning regimes could threaten the long-term survival of palm cockatoos on Cape York Peninsula, through destruction of existing nest sites, and by restricting the recruitment of future nest

sites by demographic effects on vegetation structure and floristics. Further research on the conservation biology of palm cockatoos should focus on the effects of fire on their habitat and nest sites.

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