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Overlap and competition for nest holes among eclectus parrots, palm cockatoos and sulphur-crested cockatoos

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Abstract

We examined the extent of overlap in the characteristics of nest holes used by eclectus parrots (*Eclectus roratus*), palm cockatoos (*Probosciger aterrimus*) and sulphur-crested cockatoos (*Cacatua galerita*) in patches of rainforest and woodland in and around Iron Range National Park, Cape York Peninsula, Australia. Eclectus parrots nested only in rainforest and palm cockatoos nested mostly in eucalypt woodland adjacent to rainforest. Sulphur-crested cockatoos nested in both habitats. Nest holes of eclectus parrots and rainforest sulphur-crested cockatoos were in trees of larger DBH (diameter at breast height) and higher off the ground than those of palm cockatoos and sulphur-crested cockatoos in woodland. Palm cockatoos differed from the other parrots in their use of deeper holes with entrances that faced skywards rather than sideways. Both palm cockatoos and woodland sulphur-crested cockatoos used nests with smaller entrances than eclectus parrots and rainforest sulphur-crested cockatoos. All species showed intraspecific competition for nest holes. Behavioural conflict was also common between sulphur-crested cockatoos and the other two species. Each year 9.7–25.8% of eclectus parrot nests were taken over either permanently or temporarily by sulphur-crested cockatoos. Only one palm cockatoo nest was taken over by sulphur-crested cockatoos. Nest-holes were destroyed by natural causes at similar rates in rainforest (3.8% per annum over 174 nest-years) and woodland (5.4% per annum over 93 nest-years). Four nest trees fell over, and the floor of the nest collapsed at a further four holes. Three woodland nest trees burnt down during dry-season fires (August–October). New eclectus parrot and rainforest sulphur-crested cockatoo holes originated from incipient hollows on the tree that were modified by the parrots. We discuss the intense competition between these large parrots in light of the apparent shortage of appropriate nest holes in Cape York rainforest and eucalypt woodland.

Introduction

Many bird species rely on holes in trees (also called cavities or hollows) for breeding. Although some (e.g. woodpeckers) dig their own holes, most are ‘secondary hole-nesters’ that rely on pre-existing holes formed through the action of insects or fungi, or those that are dug by other species (Newton 1994). Nests in tree holes provide security from predation compared with open nests in other locations such as branches, the canopy or ground, and may support microclimatic conditions that aid thermoregulation and help control water loss (reviewed by Gibbons and Lindenmayer 2002). Limited availability of holes creates intra- and interspecific competition for nest sites and limits the population size of many hole-nesting birds (Newton 1994). Entrance size and the internal dimensions of the hole, especially depth, are the primary determinants of occupancy by birds of different sizes. Deep holes with small entrances are probably preferable because they hinder access by both predators and larger competitors (Newton 1994; Gibbons and Lindenmayer 2002).

Worldwide, obligate hole-nesting is concentrated in seven orders of birds, the Passeriformes (songbirds), Piciformes (woodpeckers), Apodiformes (swifts), Coracii-

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formes (rollers and kingfishers), Strigiformes (owls), Psittaciformes (parrots), and Anseriformes (waterfowl) (Newton 1994). Saunders *et al.* (1982) and Newton (1994) noted that Australia has a higher proportion of hole-nesting birds than other continents, possibly due to the larger number of holes found in Australian forests and woodlands. In total, 11% of Australia's birds are obligate hole-nesters compared with 5% in Europe, 4% in North America, and 6% in Africa (Gibbons and Lindenmayer 2002). Australian hole-nesters are not evenly distributed across the seven orders mentioned above, as there are no woodpeckers, only one species of roller, and none of Australia's swifts nest in tree holes (Pizzey 1997). However, Australia does have approximately one-fifth of the world's parrot species and the greatest taxonomic diversity of that group (Forshaw and Cooper 1989). Parrots account for a high proportion (almost 40%) of the 119 Australian hole-nesting bird species compiled by Gibbons and Lindenmayer (2002).

Our research is aimed at determining the ecology and population viability of two large parrot species, eclectus parrots (*Eclectus roratus*) and palm cockatoos (*Probosciger aterrimus*), found in patches of rainforest and woodland on eastern Cape York Peninsula. Rainforest within the study area comprises a semi-deciduous mesophyll vine forest, up to 35 m high and dominated by the canopy tree species *Castenospermum australe*, *Beilschmedia obtusifolia*, *Nauclea orientalis*, *Syzgium bamagense* and *Terminalia sericocarpa*. Woodland, on the other hand, is a more open and lower (up to 20 m) forest type dominated by the sclerophyllous species *Eucalyptus tetradonta*, *Corymbia nesophila* and *C. clarksoniana*. Woodland in the region is also characterised by a grassy understory dominated by *Imperata cylindrica*.

In contrast to the growing number of studies from temperate Australia (e.g. Saunders 1982; Rowley and Chapman 1991; Krebs 1998), information on the ecology of parrots (and indeed most hole-nesting birds) in tropical Australasia is lacking (for rare examples see Marsden 1992; Marsden and Jones 1997). On Cape York, such knowledge is essential because many species have limited ranges and are threatened by changing land tenure and management practices. For example, changed fire regimes may affect the availability of nest holes in eucalypt woodland (Gibbons and Lindenmayer 2002), and logging of rainforest could remove key hole-bearing tree species (Heinsohn and Legge 2003).

The specific aim of this paper is to outline the nesting requirements and degree of competition for nest holes between eclectus parrots, palm cockatoos, and sulphur-crested cockatoos (*Cacatua galerita*). These parrots all actively defend their nest holes, and engage in aggressive intra- and inter-specific encounters that suggest competition for limited nesting resources. Female eclectus parrots have high between-year nest-site fidelity and reoccupy their holes up to eight weeks before laying their clutches. They rarely leave the nest tree for the entire 8–9-month breeding period (Heinsohn and Legge 2003). Unpublished aerial survey data confirms the scarcity of trees of the required height and species: two different extrapolation methods from the surveys show that there are only approximately 400 eclectus parrot nest trees in the 500 km^2 of rainforest found in and around Iron Range National Park (Legge and Heinsohn, unpublished data). Nest holes of sulphur-crested cockatoos are also constantly guarded by at least one member of each pair during breeding, but palm cockatoos have a different form of nest-site defense. Males defend holes and advertise their presence most mornings and afternoons with displays that include loud calling and whistling, bowing, crest erection, and drumming on the nest tree with a stick held in the foot. Aggressive interactions between male palm cockatoos, with growling, full body contact during flight and major loss of feathers are common (S. Murphy, personal observation).

The similar size of these species, overlapping breeding seasons, and observations of behavioural conflict all suggest that they compete for large tree holes. Here we outline the physical characteristics of the nest holes of each species, and compile behavioural observations of nest usurpation and delays in breeding due to such competition. We also compare the rate at which nest holes were both created and lost in rainforest and woodland due to natural causes.

Methods

Study species

In Australia, eclectus parrots are restricted to a narrow strip of coastal rainforest from the McIlwraith Range to the Iron Range (Forshaw and Cooper 1989; Juniper and Parr 1998). They weigh 550–650 g, lay a clutch of two eggs, and breed from July to February. They exhibit a unique form of reversed sexual dichromatism, in which the females are spectacular red and blue whereas the males are shiny green. Their social system is also unusual amongst parrots. In Australia, they breed cooperatively, with multiple males providing all food to the female and her chicks (Heinsohn and Legge 2003). The female incubates and broods alone but, unlike other parrots, remains guarding the hole throughout the entire nesting period. She also has strong control over the sex of her offspring (Heinsohn *et al.* 1997). Incubation takes 30 days, and the nestling phase takes 72–97 days (Heinsohn and Legge 2003).

Palm cockatoos in Australia are found in woodlands and rainforest on northern Cape York Peninsula (Forshaw and Cooper 1989; Juniper and Parr 1998). They weigh 650–1000 g and lay a single egg in a hole in a tree or in the upward-facing end of a tree-stump. In New Guinea they are primarily a rainforest species, but most nests in Australia have been found in eucalypt woodlands close to rainforest patches. Like eclectus parrots, they breed from August to February but some nest holes are not used every year (S. Murphy, unpublished data). A stick platform up to 2 m deep is constructed above the bottom of the hole; its function is believed to be to keep eggs and chicks dry during heavy rain and to allow excreta to wash away. Incubation takes about 30 days, and chicks take 60–70 days to fledge (S. Murphy, unpublished data).

Sulphur-crested cockatoos occur in a variety of habitats in lowland New Guinea and Australia roughly along the eastern half of Australia to Tasmania (Forshaw and Cooper 1989; Juniper and Parr 1998). On Cape York, they nest in both rainforest and woodland, and most breeding occurs between August and December. They weigh 600–700 g and lay a clutch of two eggs. Although larger than eclectus parrots, their chicks fledge more quickly (62–72 days) (Heinsohn and Legge, unpublished data).

Study site

Our ongoing studies of parrots are being conducted at Iron Range National Park on Cape York Peninsula, in far north Queensland, Australia (12°45′S, 143°17′E) (Fig. 1). The national park includes the coastal plain and low ranges of hills east of the Tozer and Janet Ranges and comprises patches of rainforest, eucalypt woodland and heath in a complex mosaic. The mean annual rainfall for the national park is 2780 mm (M. Blackman, personal communication), with most rain falling during a distinct ‘wet’ season from December to April.

Two of the authors (RH and SL) began studying eclectus parrots in July 1997 and the third (SM) began work on palm cockatoos in June 1999. Both projects have included opportunistic observations of tree hole use and nesting habits of sulphur-crested cockatoos. To find eclectus parrot nest trees, RH and SL walked along tracks and creek beds listening for eclectus parrot vocalisations. Females call very loudly at the beginning of the breeding season, apparently to advertise their presence at the nest hole. Colour banding shows that nest trees are re-used by the same individuals each year (Heinsohn and Legge 2003). Breeding efforts at 34 trees with 46 nest holes have been monitored throughout the study. Sixteen of the eclectus parrot nests had at some stage also been used by sulphur-crested cockatoos for breeding (see Results), and a further eight nest holes used only by sulphur-crested cockatoos were also located in rainforest. Single-rope techniques were used to gain access to each nest once every two weeks to monitor breeding activity, and breeding behaviour and competition were observed from permanent hides built in neighbouring trees (Heinsohn and Legge 2003).

SM located 24 active palm cockatoo nests using similar search methods in the eucalypt woodlands. Search effort was initially concentrated in areas where the birds were seen displaying in the late afternoon, and in patches of woodland close to rainforest. Later surveys, which were aimed at determining habitat requirements, extended searches into areas of low palm cockatoo density (S. Murphy, unpublished data).

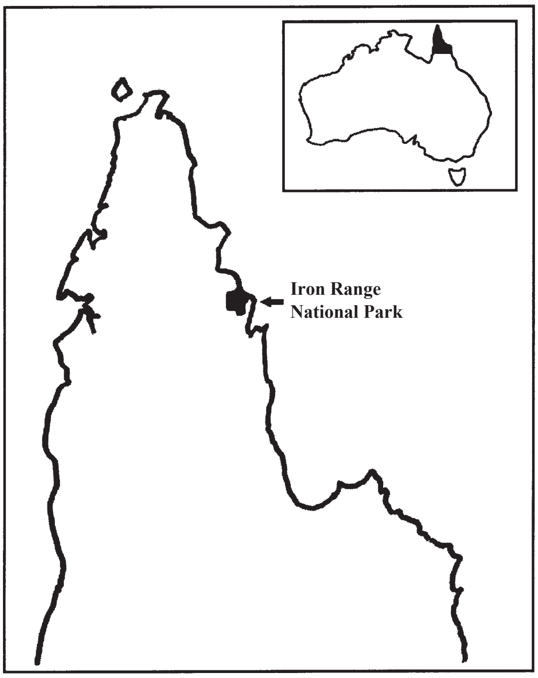

Fig. 1. Location of the study area at Iron Range National Park (12°45′S, 143°17′E).

SM mounted a small video camera on an extendable pole and attached it with light cables to a monitor to look into all potential nest holes up to 12 m high. This system allowed nests to be checked for eggs, chicks, and the broken sticks that palm cockatoos place in holes to build nesting platforms. Single-rope techniques and extendable ladders were used to climb to higher holes. Palm cockatoos build platforms in many more holes than they use for nesting; the data used in this paper refer only to those holes known to be used for breeding. SM also located and monitored breeding activity at seven sulphur-crested cockatoo nest holes.

We recorded/measured the following characteristics of each nest hole for all three parrot species: (1) tree species, (2) whether the tree was dead or alive, (3) diameter at breast height (DBH, m) (4) height of hole entrance above the ground (m), (5) depth of hole (entrance to floor, cm), (6) entrance angle (from facing horizontal = 0° to facing skywards = 90°), (7) angle of hole (from vertical chamber = 0° to horizontal chamber = 90°), (8) shortest entrance dimension (cm), (9) longest entrance dimension (cm), and (10) the number of entrances to the hole (the main entrance was used for the measures outlined above). We recorded the annual rate of hole loss and its causes (e.g. fire damage, tree fall), and in the case of eclectus parrots and rainforest sulphur-crested cockatoos we also recorded the rate and cause of new nest hole formation. During our regular nest checks we also noted opportunistically the incidences of behavioural competition (e.g. fighting) and actual displacement (e.g. hole occupation) between species at nest holes.

Results

Tree species

Eclectus parrots nested in 11 tree species, with 36 out of 46 holes occurring in only five species (Table 1). Rainforest sulphur-crested cockatoos used five of the same species with one additional species, *Palaquium galactoxylum* (Table 1). Many of the palm cockatoo nest trees were dead and could only be identified to genus level. Palm cockatoos nested in at least eight tree species, with 17 out of 24 nests occurring in either *Eucalyptus tetradonta* or *Corymbia* sp. Sulphur-crested cockatoos in woodland nested in species that were a subset of those used by palm cockatoos. Overlap in tree species between eclectus parrots and palm cockatoos was small and included only one species commonly used by eclectus parrots

Table 1. Tree species used by eclectus parrots, sulphur-crested cockatoos and palm cockatoos for nest holes
Numbers in parentheses indicate the number of times that nest-tree species was used

Parrot species	Tree species
Eclectus roratus	*Alstonia scholaris* (10), *Castenospermum australe* (7), *Ficus albipila* (9), *Alstonia actinophylla* (4), *Melaleuca dealbata* (6), *Ficus* sp. (dead) (1), *Tetrameles nudiflora* (2), *Endospermum myrmecophilum* (1), *Lophostemon* sp. (3), *Syzigium* sp. (2), *Eucalyptus tessellaris* (1)
Cacatua galerita (rainforest)	*Alstonia scholaris* (2), *Melaleuca dealbata* (2), *Tetrameles nudiflora* (1), *Castenospermum australe* (1), *Palaquium galactoxylum* (1), *Lophostemon* sp. (1)
Cacatua galerita (woodland)	*Melaleuca leucadendra* (4), *Melaleuca dealbata* (3), *Eucalyptus tetradonta* (1)
Probosciger aterrimus	*Eucalyptus tetradonta* (10), *Corymbia* sp. (7), *Blepharocarya involucrigera* (1), *Eucalyptus brassiana* (1), *Eucalyptus tessellaris* (1), *Lophostemon sauveolens* (1), *Melaleuca dealbata* (1), *Melaleuca* sp. (1), *Alstonia scholaris* (1)

(*Melaleuca dealbata*) and one species rarely used by both (*Eucalyptus tessellaris*). There was one nest hole in an *Alstonia scholaris* that was used by all three parrot species in succession, first by eclectus parrots, followed by sulphur-crested cockatoos, and then by palm cockatoos.

Physical characteristics of nest holes

Statistical tests of single characteristics of nest trees and holes indicated some differences between the physical characteristics used by the three parrot species. Most eclectus parrots and sulphur-crested cockatoos nested in live trees whereas 7 of 24 palm cockatoo nests were in dead trees. Eclectus parrots and rainforest sulphur-crested cockatoos nested in trees with significantly greater DBH, and in holes that were significantly higher from the ground than palm cockatoos (Table 2). Palm cockatoos used holes that were, on average, more skyward-facing than those used by sulphur-crested cockatoos, and both palm cockatoos and woodland sulphur-crested cockatoos used nests with smaller shortest-entrance dimensions than those of eclectus parrots. The longest entrance dimension, hole angle, and number of entrances did not differ between the species (Table 2).

Overlap in nest-hole dimensions

We used a principal components analysis (JMP Statistical Package) to determine the overall similarity of the physical characteristics of nest holes used by the three parrot species. We included six measures of nest holes that could vary similarly in rainforest and woodland trees, but excluded the height of the hole and DBH as these strongly reflect the different tree types available in the two habitats. The first three principal components accounted for 29.1%, 21.9%, and 19.9% of the variation. The eigenvalues and eigenvectors for these are shown in Table 3.

Plots of PC1 versus PC3 and PC2 versus PC3 suggested that palm cockatoos differed in their values of PC3 (Fig. 2). Kruskal–Wallis tests (single-factor analysis of variance by ranks) confirmed significant differences between palm cockatoos, eclectus parrots and rainforest and woodland sulphur-crested cockatoos in values of PC3 ($\chi^2_3 = 20.1$, $P = 0.002$) but not PC1 ($\chi^2_3 = 2.6$, $P = 0.455$) or PC2 ($\chi^2_3 = 4.2$, $P = 0.239$). The eigenvectors indicated

Table 2. The physical characteristics of nest holes, with comparison of these characteristics for the three parrot species

Numbers denote means ± standard errors

Character	*Eclectus roratus*	*Cacatua galerita* (rainforest)	*Cacatua galerita* (woodland)	*Probisciger aterrimus*	ANOVA
No. of nests	46	24	7	24	–
No. of nests in live trees	44	23	7	17	–
DBH (m)	1.5 ± 0.1	1.3 ± 0.1	0.9 ± 0.2	0.6 ± 0.1	$F_{3,97} = 29.1$, $P < 0.001$
Hole height (m)	22.2 ± 0.7	21.7 ± 0.9	13.5 ± 1.7	9.1 ± 0.9	$F_{3,97} = 50.6$, $P < 0.001$
Hole depth (cm)	84.8 ± 4.9	66.5 ± 6.8	58.7 ± 12.7	99.2 ± 6.7	$F_{3,97} = 5.1$, $P = 0.003$
Entrance angle	15.4 ± 4.4	18.9 ± 6.1	18.6 ± 11.3	51.9 ± 6.1	$F_{3,97} = 8.4$, $P < 0.001$
Shortest entrance dimension (cm)	30.4 ± 1.2	31.7 ± 1.6	22.3 ± 3.0	25.2 ± 1.6	$F_{3,97} = 4.9$, $P = 0.004$
Longest entrance dimension (cm)	34.3 ± 1.4	35.8 ± 2.0	37.3 ± 3.7	33.3 ± 2.0	$F_{3,97} = 0.5$, $P = 0.718$
Hole angle	23.6 ± 4.9	24.6 ± 6.7	10.0 ± 12.5	16.3 ± 6.7	$F_{3,97} = 0.6$, $P = 0.608$
No. of entrances	1.2 ± 0.1	1.1 ± 0.1	1.3 ± 0.1	1.1 ± 0.1	$F_{3,97} = 0.5$, $P = 0.674$

Table 3. Results of a principal components analysis describing the physical characteristics of nest holes of eclectus parrots, sulphur-crested cockatoos, and palm cockatoos to the first three principal components

	PC1	PC2	PC3
Eigenvalue	1.75	1.32	1.19
Percentage variation	29.20	21.94	19.91
Eigenvectors			
Hole depth (cm)	0.21	0.36	0.58
Entrance angle	0.03	–0.24	0.76
Shortest entrance diameter (cm)	0.65	–0.21	–0.19
Longest entrance diameter (cm)	0.65	–0.24	–0.06
Hole angle	0.09	0.69	–0.18
No. of entrances	0.32	0.49	0.09

that hole-entrance dimensions had the greatest influence in PC1, hollow angle had the greatest influence in PC2, and that entrance angle and hole depth were the greatest contributors to PC3. Thus, entrance angle and hole depth were the chief factors separating palm cockatoos from the other parrots. Specifically, palm cockatoos nested in deeper holes than the other two parrots, and in holes that faced skywards rather than side-ways.

Behavioural conflict at nest sites

Behavioural conflict between eclectus parrots and sulphur-crested cockatoos at nest holes was common in each year of the study. Female eclectus parrots and sulphur-crested cockatoos (unsexed) were observed to attack and chase each other, and in some instances hole 'ownership' changed between and even within breeding seasons. Table 4 shows the number of eclectus parrot nests where some form of competition between the two species was observed, and the number of nests where take-overs by sulphur-crested cockatoos prevented the eclectus parrots from breeding there that year or potentially caused them to delay breeding. This was based on instances where sulphur-crested cockatoos physically occupied holes that had been previously used by eclectus parrots, while the latter species milled around waiting for the cockatoos to complete breeding. In all, 9.7–25.8% of eclectus parrot nests were affected in this manner each year (Table 4). A further three of the 16 holes used by both sulphur-crested cockatoos and eclectus parrots were used by the former at the start of our study but were later taken over by the latter. One nest hole that was used by eclectus parrots for three years was taken over in 2000 by rufous owls (*Ninox rufa*) and later by European bees (*Apis mellifera*).

Direct behavioural conflict between palm cockatoos and sulphur-crested cockatoos was observed at six nests. In three cases, palm cockatoos were known to drop sticks and splinters inside nests used previously by sulphur-crested cockatoos, which promptly removed them. In one case, palm cockatoos and sulphur-crested cockatoos both regularly visited the same nest hole. The palm cockatoos dropped sticks inside the hole and the sulphur-crested cockatoos removed them, but neither species used the hole for breeding. Sulphur-crested cockatoos were only once known to take over a hole previously used for breeding by palm cockatoos. Sulphur-crested cockatoos appeared regularly at two other palm cockatoo nests but were chased away each time. One of these nest holes had previously been used by eclectus parrots before being used by sulphur-crested cockatoos and ultimately by palm cockatoos (Table 5).

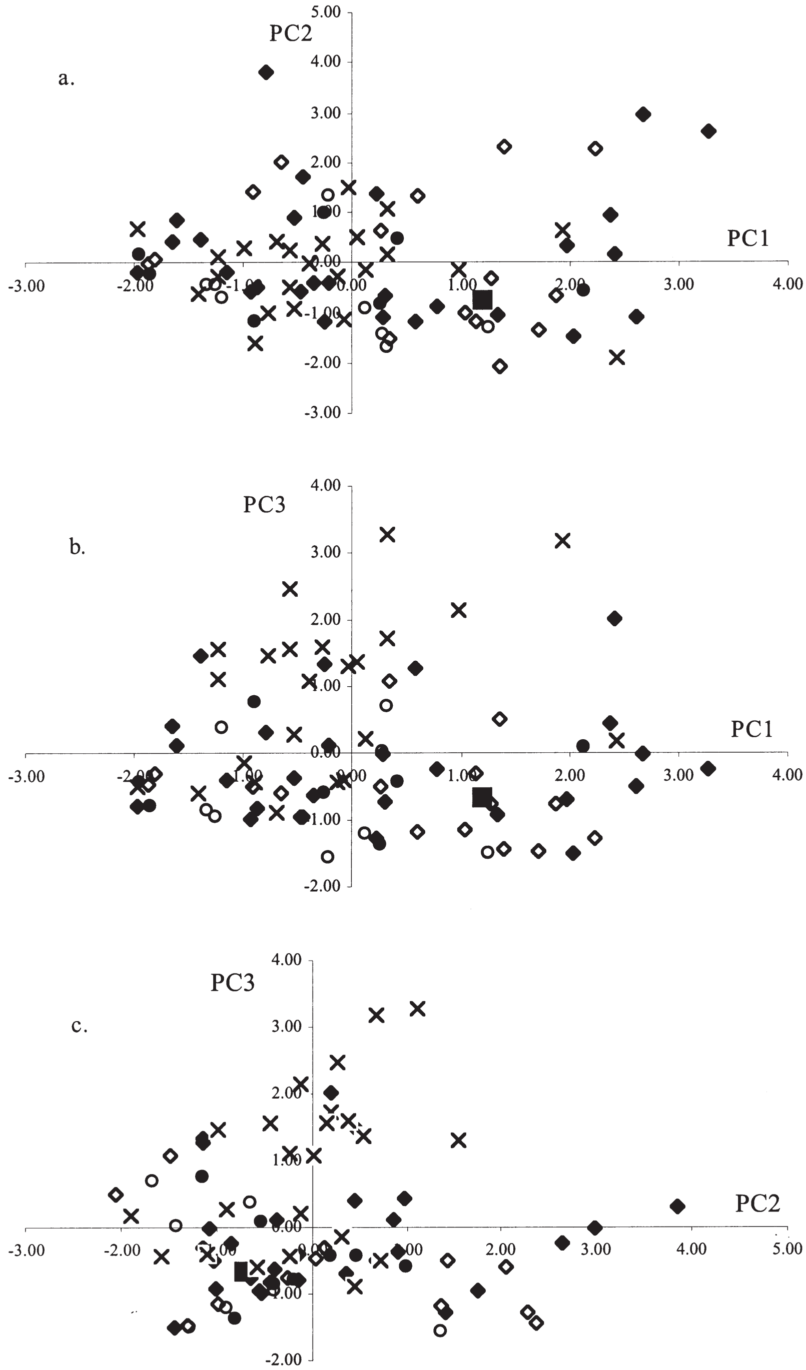

Fig. 2. Pair-wise plots of first three principal components of physical characteristics of nest holes. (*a*) First principal component (PC1) versus PC2, (*b*) PC1 versus PC3, and (*c*) PC2 versus PC3. Symbols refer to nest holes used by: palm cockatoos (crosses), eclectus parrots (filled diamonds), eclectus parrots and sulphur-crested cockatoos (open diamonds), sulphur-crested cockatoos in rainforest (open circles), sulphur-crested cockatoos in woodland (closed circles), all three species (closed squares).

Table 4. Instances of behavioural competition (fighting and opposing bird in hole), and the number of breeding attempts by eclectus parrots that were potentially delayed because of nest take-overs by sulphur-crested cockatoos over five years of the study

Year	Total no. of nests	No. of nests at which competition detected	No. of nests at which breeding lost/delayed	Percentage of nests at which breeding lost/delayed
1997	16	8	3	18.8
1998	31	9	3	9.7
1999	31	12	8	25.8
2000	31	7	3	9.7
2001	25	4	3	12.0

Table 5. Behavioural interactions between parrot species at six tree holes
PCs, palm cockatoos; SCCs, sulphur-crested cockatoos; EPs, eclectus parrots

Nest	Nest used by:	Form of competition
1	SCCs 1999–2001	PCs irregularly add sticks, SCCs remove them
2	SCCs 1999	PCs add sticks in 2000–01, SCCs remove them
3	PCs and SCCs visit hole 1999–2001	PCs add sticks, SCCs remove them
4	PCs 1999–2000	SCCs take over nest in 2001
5	PCs 1999–2001	SCCs regularly at hole
6	EPs 1997–98	SCCs chased away
	SCCs 1999, PCs 2001	SCCs chased away

None of us have ever observed any form of aggression or competition at nest holes between eclectus parrots and palm cockatoos.

Creation, destruction, and turnover of nest holes

We documented the destruction of existing holes and the creation of new holes for both eclectus parrots and rainforest sulphur-crested cockatoos, but only the destruction of nest holes for palm cockatoos and woodland sulphur-crested cockatoos. Three eclectus parrot nest trees fell over, and the floor of the nest collapsed at a further three eclectus parrot nests and one sulphur-crested cockatoo hole. One sulphur-crested cockatoo nest tree fell over. In the eucalypt woodland, two palm cockatoo nest trees and one sulphur-crested cockatoo nest tree burnt down during dry-season fires (August–October). All three of these trees were already dead (Table 6). One further palm cockatoo nest hole was lost when it was taken over and altered dramatically by extensive gouging and chewing by sulphur-crested cockatoos.

All new eclectus parrot and rainforest sulphur-crested cockatoo holes originated from existing holes in the tree, mostly where branches had broken off. We observed the parrots actively enlarging these holes by gouging out and removing the inner wood in six out of seven cases (Table 6). Palm cockatoos were never observed enlarging or manipulating the hole by chewing or gouging. Holes were lost at approximately the same rate they were gained for the rainforest parrots (i.e. eight lost, seven gained over five years) (Table 6).

In 174 nest-years for rainforest and 93 nest-years for woodland, the mean annual rate of hole loss for each species was 4.0% for eclectus parrots, 2.5% and 9.8% for sulphur-crested cockatoos in rainforest and woodland, respectively, and 5.3% for palm cockatoos. Despite the different causes, the overall rates of loss for rainforest (3.8%) and woodland (5.4%) were similar (Table 7).

Table 6. Tree holes lost and gained, including causes, by eclectus parrots, sulphur-crested cockatoos, and palm cockatoos

Parrot species	Cause of hole loss and tree species involved	Cause of hole gain and tree species involved
Eclectus roratus	Tree fell over (1 × *Castanospermum australe*, 1 × *Melaleuca dealbata*, 1 × *Ficus* sp. – dead)	Rot at small hole (1 × *M. dealbata*, 1 × *Tetrameles nudiflora*)
	Nest floor collapsed (1 × *C. australe*, 1 × *Syzigium* sp., 1 × *Ficus albipila*)	Rot at small hole, enlarged by parrot (1 × *Alstonia scholaris*, 1 × *F. albipila*, 1 × *M. dealbata*, 1 × *C. australis*)
Cacatua galerita (rainforest)	Tree fell over (1 × *Melaleuca dealbata*)	Rot at small hole, enlarged by parrot (1 × *Endospermum myrmecophilum*, 1 × *Lophostemon* sp.)
	Nest floor collapsed (1 × *C. australe*)	
Cacatua galerita (woodland)	Tree burnt (1 × *Melaleuca* sp. – dead)	None recorded
Probosciger aterimmus	Tree burnt (1 × *Corymbia clarksoniana*, 1 × *Eucalyptus tetradonta*), both trees already dead	None recorded
	Nest hole lost to take-over/modification by sulphur-crested cockatoos (1 × *Melaleuca dealbata*)	

Table 7. Annual loss of nest holes for eclectus parrots and sulphur-crested cockatoos in rainforest, and for palm cockatoos and sulphur-crested cockatoos in woodland

Year	Eclectus parrots	Sulphur-crested cockatoos (rainforest)	Total rainforest	Sulphur-crested cockatoos (woodland)	Palm cockatoos	Total woodland
1997	0/16 (0%)	0/8 (0%)	0/24 (0%)	–	–	–
1998	2/31 (6.5%)	0/8 (0%)	2/39 (5.1%)	–	–	–
1999	1/31 (3.2%)	0/8 (0%)	1/39 (2.6%)	0/7 (0%)	0/24 (0%)	0/31 (0%)
2000	2/31 (6.5%)	0/8 (0%)	2/39 (5.1%)	1/7 (14.3%)	1/24 (3.2%)	2/31 (6.5%)
2001	1/25 (4.0%)	1/8 (12.5%)	2/33 (6.1%)	1/7 (14.3%)	2/24 (12.8%)	3/31 (9.7%)
Mean	4.0%	2.5%	3.8%	9.5%	5.3%	5.4%

Discussion

On northern Cape York, the major ecological separation in nest-hole use by the three largest parrot species was whether they bred in rainforest or woodland, rainforest being a tall (25+ m), closed forest community with a high diversity of mesophyllic species, and woodland having low diversity of mainly sclerophylous species that are more widely spaced and have a low canopy height (10–20 m). Although palm cockatoos nest primarily in rainforest in New Guinea (Paul Igag, personal communication), only two active palm cockatoo nests have been recorded inside rainforest in our study. Unpublished survey results of habitat use confirms that the highest breeding densities of palm cockatoos are in woodland (S. Murphy, unpublished data). Thus, most potential for overlap in nest sites between the three parrots in this study is between eclectus parrots and sulphur-crested cockatoos in rainforest, and between palm cockatoos and sulphur-crested cockatoos in woodland. Consequently, eclectus parrots and palm cockatoos used few of the same nest-tree species. Eclectus parrots used tall rainforest trees, especially of the genera *Alstonia*, *Castenospermum* and *Ficus* whereas palm cockatoos mainly used *Eucalyptus* and *Corymbia*. *Melaleuca* was used frequently by eclectus parrots but only occasionally by palm cockatoos; for both species these were usually found in creek-beds or swamps.

In contrast, sulphur-crested cockatoos in each habitat used a subset (with one exception) of the tree species used by the other two parrots. In woodland, a higher proportion of sulphur-crested cockatoo nests were in *Melaleuca* than for palm cockatoos. Sulphur-crested cockatoos and eclectus parrots also used more live trees (only 4% were in dead trees) whereas 29% of palm cockatoo nests were in dead trees.

Comparisons of the physical attributes of nest holes indicated some differences between parrot species. For example, palm cockatoos used deeper holes with entrances that faced skywards. Both eclectus parrots and sulphur-crested cockatoos used entrances that opened sideways. This accords with the observation that only palm cockatoos actively build platforms inside the holes to overcome flooding. Losses of young due to flooding are a major determinant of reproductive success in eclectus parrots (Heinsohn and Legge 2003). Sulphur-crested cockatoos were less choosy in this regard and had shallower holes, on average, in both environments. Flooding may be less of a problem for them because their breeding season is shorter and overlaps less with the wet season.

Rainforest nest holes were higher from the ground and in trees with larger DBH than those in woodland, which reflects the size of available nest trees in each habitat. High holes are safer from some predators than low holes (e.g. Nilsson 1984; Marsden and Jones 1997) and it is noteworthy that sulphur-crested cockatoos nested much higher in rainforest (i.e.

when taller trees were available). Palm cockatoos had the lowest nest heights, mostly due to their habit of nesting in holes in broken stumps. The shortest entrance dimension was also smaller for the woodland parrots such that entrances were usually ‘slits’ rather than round openings. Entrance size is important for exclusion of both competitors and predators, and most species choose the smallest entrance they can fit through (Newton 1994; Gibbons and Lindenmayer 2002). The narrower entrances in woodland probably reflect the larger number of available holes in that habitat (Gibbons and Lindenmayer 2002), and therefore the greater choice available for hole nesters.

Our principal components analysis of the physical attributes of the nest holes (i.e. PC1 *v.* PC3 and PC2 *v.* PC3) indicated a high degree of overlap between the three parrots. This analysis excluded DBH and hole height as these features relate almost exclusively to the type of trees available in rainforest and woodland, whereas the other physical attributes (e.g. entrance size) are more independent of habitat. Palm cockatoos showed the most separation. They differed significantly from the other parrots in values of the third principal component, which reflected their preference for deeper holes and holes that faced skywards. Hole depth is clearly important for palm cockatoos and was probably underestimated owing to the birds’ habit of building stick platforms inside the hole, which makes accurate estimates of depth difficult. Eclectus parrots and sulphur-crested cockatoos in both habitats overlapped considerably in the physical characteristics of their nest holes (Fig. 2).

Behavioural conflict was observed most frequently between eclectus parrots and sulphur-crested cockatoos. These species showed a high convergence in nest-site characteristics in rainforest, and indeed actively competed for the same hole in many instances. Temporary or permanent take-overs by sulphur-crested cockatoos led to delays in breeding at 9.7–25.8% of eclectus nests each year. Such delays often led to reproductive failure for the eclectus parrots, especially when the hole was prone to flooding, because the breeding effort was extended further into the wet season (Heinsohn and Legge 2003).

Behavioural conflict was also regularly observed between woodland sulphur-crested cockatoos and palm cockatoos, even though only one palm cockatoo nest was ever taken over by sulphur-crested cockatoos. Most interactions took the form of sticks being added to the hole by the palm cockatoos and removed by the sulphur-crested cockatoos, or with the former chasing the latter.

No behavioural conflict was recorded between eclectus parrots and palm cockatoos. This is unsurprising since they use different habitats and the physical dimensions of their nest holes are relatively divergent. It is nonetheless interesting that palm cockatoos in New Guinea nest primarily in rainforest, whereas those on Cape York seem to prefer to breed in the woodlands adjacent to rainforest. Two possible and non-mutually exclusive reasons for this are (1) that palm cockatoos face stiff competition for rare nest hollows inside the rainforest, and (2) that they have gained access to the more abundant source of hollows in woodlands that are near enough to rainforest for them to retain access to the food and shelter it provides.

The rate of loss of nest holes was similar in rainforest and woodland, but losses occurred for different reasons. In rainforest, all losses were either from the entire tree falling over or from the floor of the hole collapsing; in most cases the wood was damp, decayed and attacked by insects and fungi. In contrast, the greatest cause of hole loss in the woodlands was from nest trees burning down during dry-season fires. In rainforest, eight new nests were created over five years compared with the seven that were lost, supporting the expectation of an equilibrium in undisturbed forest (e.g. Sedgwick and Knopf 1992;

Newton 1994). The same agents responsible for hole demise (insect and fungal pests) were also responsible for hole creation, although in most cases existing holes in the tree were further enlarged by the parrots. It is important to note that while eclectus parrots and sulphur-crested cockatoos do enlarge existing holes, thereby making otherwise unsuitable holes usable, this behaviour does not abate the problem of hollow limitation as it does for true 'primary' hole-nesting species. Thus, eclectus parrots and sulphur-crested cockatoos are midway between 'primary' (e.g. woodpeckers) and 'secondary' hole-nesters (most hole-nesting species), whereas palm cockatoos are clearly in the latter category.

In conclusion, our data demonstrate a high degree of overlap and competition between eclectus parrots and sulphur-crested cockatoos in rainforest, and a smaller degree of overlap between palm cockatoos and sulphur-crested cockatoos in woodland. Together with our observations of conflict, this supports the hypothesis that nest holes are a limiting factor for these large birds (e.g. Newton 1994; Gibbons and Lindenmayer 2002). This is despite the fact that both eclectus parrots and sulphur-crested cockatoos can modify existing holes to create cavities suitable for breeding.

There are many accounts of competition and usurpation of holes between parrots and other species (e.g. galahs, *Eolophus roseicapillus*: Rowley 1990) but our results provide a rare demonstration that competition can also be intense between large hole-nesting species in mature tropical rainforest. Studies from temperate Australia and elsewhere in the world (e.g. Mannan *et al.* 1980) show that the abundance and diversity of hole-nesting birds increases as the forest ages. Indeed, eucalypts with holes appropriate for large parrots in Western Australia and southern Australia have been shown to be over 100 and 200 years old respectively (Saunders 1979; Nelson and Morris 1994). The rarity of hole-bearing trees of the required DBH and height in the Iron Range rainforest (approximately 0.8 km^{-2}: Legge and Heinsohn, unpublished data) is suggestive of a small and geographically limited breeding population of eclectus parrots, and our unpublished surveys for palm cockatoos suggest that they are also highly concentrated in just a few areas. Our future research is aimed at determining what affects the spatial distribution of palm cockatoo density, as well as conducting population viability analyses for both palm cockatoos and eclectus parrots. At this stage we caution against any management practice that might cause the destruction of old hole-bearing trees in this region. In rainforest, this includes logging for important nest-tree species such as *Castenospermum*, and in woodland any fire practice that increases the likelihood of loss of hole-bearing *Eucalyptus*, *Corymbia*, or *Melaleuca* species.

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