Availability of nest hollows and breeding population size of eclectus parrots, *Eclectus roratus*, on Cape York Peninsula, Australia

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Abstract.   The distribution of the Australian mainland endemic subspecies of the eclectus parrot, *Eclectus roratus macgillivrayi*, is currently confined to the lowland rainforests of the Iron–McIlwraith Ranges of eastern Cape York Peninsula. Females breed in large hollows in emergent rainforest trees that are readily visible from above. Aerial surveys were used to sample 58% of the rainforest (454 km^2) of the Iron Range region to estimate the density of these nest trees. Corrections for overcounting bias (not all observed emergent trees were active nest trees) and undercounting bias (not all active nest trees were visible from the air) were made by ground-truthing over 70 trees. The tree count data were treated in two different ways, producing estimates of 417 (s.e. = 25) and 462 (s.e. = 31) nest trees for the Iron Range region. Long-term observational data on the number of eclectus parrots associated with each nest tree were used to estimate the population size of eclectus parrots at Iron Range: 538–596 breeding females, and 1059–1173 males. These results have three implications. First, this relatively low population estimate suggests that the Australian subspecies of eclectus parrots should be considered vulnerable to habitat loss or perturbation, especially in light of their complex social system, male-biased adult sex ratio, low breeding success and high variance in reproductive success among females. Second, the low density of nest trees suggests that eclectus parrots are absent from the rainforests of Lockerbie Scrub and the Jardine dunefields because these areas are too small. Finally, if eclectus parrots persisted in the Iron–McIlwraith region during the rainforest contractions of Pleistocene glacial maxima (e.g. 14000–17000 years ago), the refugium in this region must have been fairly substantial in order to support a viable population – probably larger than previously assumed.

Introduction

The eclectus parrot, *Eclectus roratus*, is large (500–600 g) and colourful, with various subspecies inhabiting the lowland rainforests of Sumba, the Moluccas, New Guinea and its satellite islands, the Bismarck Archipelago, the Solomons, and Cape York Peninsula, Australia (Juniper and Parr 1998). Although it is usually common throughout its range, the eclectus parrot is a favoured cage bird and some island populations are endangered or even extinct as a result of trapping and habitat loss (Juniper and Parr 1998).

The Australian subspecies (*E. r. macgillivrayi*) is confined to a relatively small patch of lowland rainforest in the Iron–McIlwraith Ranges, and is listed as 'Near Threatened' in the Australian Action Plan for Birds (Garnett and Crowley 2000) on the basis of its small population size. Although the Iron–McIlwraith Ranges hold the largest remaining area of lowland rainforest in Australia, the rainforest there is floristically distinct from the more southern tropical forests. It contains a high proportion of Australian endemics (Crisp *et al*. 2001), and is most closely related to the Malesian lowland rainforest of New Guinea, with which it shares a large number of genera (Webb and Tracey 1981; Barlow and Hyland 1987; Crisp *et al*. 2001). Faunistically, the Iron–McIlwraith ranges are also derived largely from New Guinean stocks. For example, all mammal taxa in Cape York rainforests and all bird taxa that, within Australia, are restricted to Cape York rainforests, are shared with New Guinea (Kikkawa *et al*. 1981). The Iron–McIlwraith Ranges are also the major Australian refugium for a diverse, New Guinean insect fauna (Kikkawa *et al*. 1981). The floral and faunal uniqueness of this region make it of extremely high conservation significance (Mackey and Nix 2001).

Within this unique region, the eclectus parrot is an unusual bird. The two sexes have completely different plumages: males are predominantly emerald green whereas females are arguably more colourful with their red and blue plumage. They have a unique and complex social system, where a female mates with several males and then relies on these males to bring food to her and her chicks (Heinsohn and Legge 2003). Cooperative breeding is extremely rare in parrots, being previously reported only for Vasa parrots (Wilkinson 1994). The eclectus parrot's version of polyandry fits neither into the standard 'cooperative polyandry' nor 'sequential polyandry' mating systems (Hartley and Davies 1994). Finally, eclectus parrot females are able to control the sex of the offspring they produce, although the adaptive reason for this remains unclear (Heinsohn *et al.* 1997).

Eclectus parrots are generalist frugivores and seed-eaters (Juniper and Parr 1998). In Cape York they breed between July and February, laying their clutch of two eggs in large hollows in emergent rainforest trees. Females are responsible for all incubation and brooding, and they feed chicks with regurgitated food that males have brought back to the nest. Hollow use is 'traditional', with females occupying the same hole for multiple years (Heinsohn and Legge 2003).

Three observations suggest that hollows are a limiting resource for eclectus parrots. First, the parrots have relatively specific hollow requirements (tree spp., height, orientation, depth, etc: Heinsohn *et al.* 2003). Second, as well as being present at their nest during breeding attempts, females also 'guard' their hollows even when there are no eggs or chicks present, which suggests intense intra- and interspecific competition for nesting hollows (Heinsohn and Legge 2003). Finally, hollows vary in quality, with some being more accessible to predators (e.g. lower), or prone to flooding during rainstorms (causing chicks to drown). These features contribute to high variance in reproductive success among females, where many females routinely fail to produce any young (Heinsohn and Legge 2003). Thus, not only are suitable hollows rare, but high-quality hollows are even rarer.

The complex social system of eclectus parrots may make them susceptible to Allee effects (Courchamp *et al.* 1999) because many males are required to support one female, and breeding success is both low and concentrated among a small proportion of females. Moreover, the Iron–McIlwraith rainforests cover a relatively small area, and like many large and/or wide-ranging animals, eclectus parrots may exist as a relatively small population. Despite its conservation significance, only a small proportion (8.9%) of the 215091-ha Iron–McIlwraith Ranges rainforests lies within national parks. Most of the area exists as freehold, mainly Aboriginal land (49%) and unallocated State land (32.5%), with pastoral leases (6.6%) and resource and other non-conservation reserves (3.0%) making up the remainder.

Within this context, our aim was to estimate the availability of tree hollows and thus the population size of eclectus parrots in the Iron Range region. The trees that eclectus parrots prefer to nest in are highly visible from the air because they tower above the rest of the canopy. We therefore used a combination of aerial surveys and ground-truthing to determine the density of eclectus parrot nest trees in the area. Over the last four years we have monitored breeding attempts at over 40 eclectus parrot nest hollows in the Iron Range National Park. Using these data, we are able to derive the mean number of eclectus parrots attending each nest tree, and thus to estimate the population size in the region.

Methods

Study site

The climate of Cape York Peninsula is monsoonal with most rain falling between December and May. The escarpment and ranges of the Great Dividing Range in the Iron–McIlwraith region are high enough to cause some precipitation during the dry season, thereby sustaining the wetter and more complex types of rainforest that occur there.

The vegetation of the Iron–McIlwraith Ranges is characterised by a complex mosaic of rainforest, sclerophyll woodland and heath. The vegetation of Cape York Peninsula has been surveyed and classified by Neldner and Clarkson (1995), who divided it into 30 broad vegetation groupings, each containing several sub-types, which they called vegetation map units.

Two broad vegetation groupings dominate the Iron Range rainforests. 'Gallery closed-forests and *Melaleuca* spp. dominated open-forests on alluvia' contains two subtypes: semi-deciduous mesophyll vine forest is mainly found on the alluvial floodplains of the Claudie River (the major river in the region), and is the dominant rainforest type at Iron Range (Table 1). In addition, larger streams and rivers are fringed with an 'evergreen notophyll vine forest' (Table 1). The second common broad vegetation grouping is the 'closed-forests of the Iron–McIlwraith Ranges region', with two common subtypes: an 'evergreen to semi-deciduous notophyll vine forest' that is largely confined to the Iron–McIlwraith Ranges, and 'a simple evergreen notophyll vine forest' that, within Cape York, is mainly confined to the Iron–McIlwraith region, but is also found in the Wet Tropics (Table 1). A third broad vegetation grouping ('closed-forests of coastal dunes and dunefields') occurs in a few small patches behind beachfronts, and comprises evergreen notophyll vine forest dominated by *Syzygium* spp., *Terminalia* spp. and *Xanthostemon* spp. (Table 1).

The different rainforest types are characterised by different assemblages of canopy and emergent tree species (see Table 1). Eclectus parrots nest in some tree species much more commonly than others: of 33 eclectus nest trees monitored over four years, 82% were in just four types (milky pines, *Alstonia* spp.; blackbeans, *Castenospermum australe*; green figs, *Ficus albipila*; and paperbarks, *Melaleuca* spp.: Heinsohn and Legge 2003). Conversely, one of the commonest emergents in the area (*Tetrameles nudiflora*) was rarely used for nesting (1 of 33 nest trees), probably because it is far less likely to form suitable hollows compared with milky pines, blackbeans, figs and paperbarks (authors' observations).

The area surveyed lies around the Claudie River, within the rectangular block delineated by map coordinates 07240E by 86170S to 07640E by 85630S (Australian Topographic Survey; Series R631, Sheet 7552, Edition 1-AAS) (Figs 1 and 2).

The nests monitored for four years (Heinsohn and Legge 2003) lie within 292 ha of rainforest near the centre of the area surveyed from the air. The vegetation in this 292-ha study area is dominated by semi-deciduous mesophyll vine forest, but includes patches of

Table 1. Rainforest types in the Iron Range region
Follows the classifications of Neldner and Clarkson (1995)

	Mean basal area (m² ha⁻¹)	Mean emergent height (m) and canopy height (m)	Frequency of emergents favoured as nest trees in sample plots[A]	Frequency of canopy trees favoured as nest trees in sample plots[A]	Probability that at least one favoured nest tree is found in a sample plot[B] Emergent	Canopy	Comment
Gallery closed-forests and Melaleuca dominated open-forests on alluvia (Broad Vegetation Grouping 2)							
Semi-deciduous mesophyll vine forest on alluvia, and metamorphic and granitic foothills and lower hillslopes (Claudie and Normanby Rivers (vegetation map unit 8)	36	38.7, 28.6	*Ficus albipila* (27%), *Alstonia scholaris* (9%)	*Castenospermum australe* (64%), *A. scholaris* (41%)	0.43	0.88	Seasonally flooded alluvial terraces
Evergreen notophyll vine forests on major streams (vegetation map unit 18)	24	24.3, 17	*Melaleuca leucadendra* (17%), *M. argentea* (4%)	*M. leucadendra* (29%), *A. actinophylla* (13%)	0.2	0.58	Banks of major watercourses of Cape York Peninsula
Closed-forests of the Iron–McIlwraith Region (Broad Vegetation Grouping 6)							
Evergreen to semi-deciduous notophyll vine forest (Iron–McIlwraith Ranges), (vegetation map unit 21)	20	32.3, 26.7	*A. actinophylla* (8%), *A. scholaris* (8%)	*A. scholaris* (33%)	0.17	0.45	Slopes with acid volcanic soils
Simple evergreen notophyll vine forest (with *Acacia aulacocarpa*, *Eucalyptus tessellaris*, *Blepharocarya involucrigera* emergents; Iron Range, Wet Tropics) (vegetation map unit 26)	22	27.7, 22.6	*M. dealbata* (11%)	*A. scholaris* (22%)	0.11	0.31	Exposed steep slopes, drier western margins of vine forests
Closed-forests of coastal dunes, dunefields and the Jardine River frontage (Broad Vegetation Grouping 4)							
Evergreen notophyll vine forest dominated by *Syzygium* spp., *Terminalia* spp., *Xanthostemon* spp.; beach rainforest, east coast (vegetation map unit 20)	22	None, 18.9			0	0	Beach ridges and sheltered dunes

[A]From Neldner and Clarkson (1995). Percentage of sample plots where the species was present.
[B]Calculated from the frequencies that each preferred species occurred in the sampling plots of Neldner and Clarkson (1995).
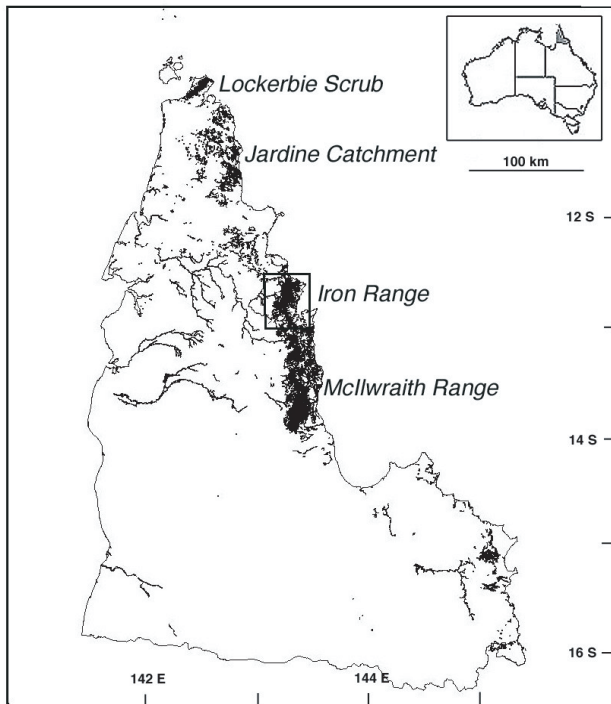
Fig. 1. Cape York Peninsula. Dark shading shows where the rainforest types (vegetation map units) of Table 8 occur (i.e. suitable eclectus parrot habitat). The box shows where the aerial surveys were carried out. The four major rainforested areas on Cape York are labelled.

Fig. 2. The Iron Range region, showing flightpaths (black lines) and observed emergents (black dots). Light grey shading shows areas where rainforest is the dominant vegetation. The five major topographical features are outlined with a grey perimeter line (CC: Claudie river alluvial plain; RB: coastal hills, Roundback and Ogilvie Hills; G: gallery forests on major creeks; UP: upland plateau west of Tozer escarpment; ES: east-facing escarpment of Tozer and Dorriwill Ranges).

evergreen notophyll vine forest along streambanks, and simple evergreen notophyll vine forest.

Survey method

Potential eclectus nest trees were surveyed with a total of 585 km of aerial transects over rainforest. Surveys were carried out over an 11-day period (7–18 December 1999), between 0630 and 1000 hours, and between 1530 and 1800 hours, when the more horizontal light made emergent trees stand out most clearly. We flew a light aircraft (Piper Cherokee) at a fixed speed (80 km) 150 m above the ground. The observer on the right-hand side of the aircraft visually searched a strip of rainforest between the fuselage and a fixed point on the aircraft's wing. Given the plane's height above the ground, this corresponded to a strip of rainforest 500 m wide. Each time a potential nest tree was spotted we noted the tree species whenever possible, marked the position of the plane with a Global Positioning System, and estimated the distance of the tree from the plane. The positions of potential nest trees were overlain onto topographical and vegetation maps using ESRI Arcview version 3.2.

Ground-truthing (corrections for counting biases)

Not all potential nest trees visible from the air contain hollows that are useful for eclectus parrots, and not all eclectus parrot nest trees are visible from the air. Therefore, 71 potential nest trees were ground-truthed in the 292-ha study area. From this, the proportion of potential nest trees observed during aerial surveys that were active nest trees was estimated. To estimate the proportion of active nest trees that were not observed during aerial surveys, we flew over 32 known nest trees in the 292-ha study area in simulated transects to determine whether they were visible from the air or not.
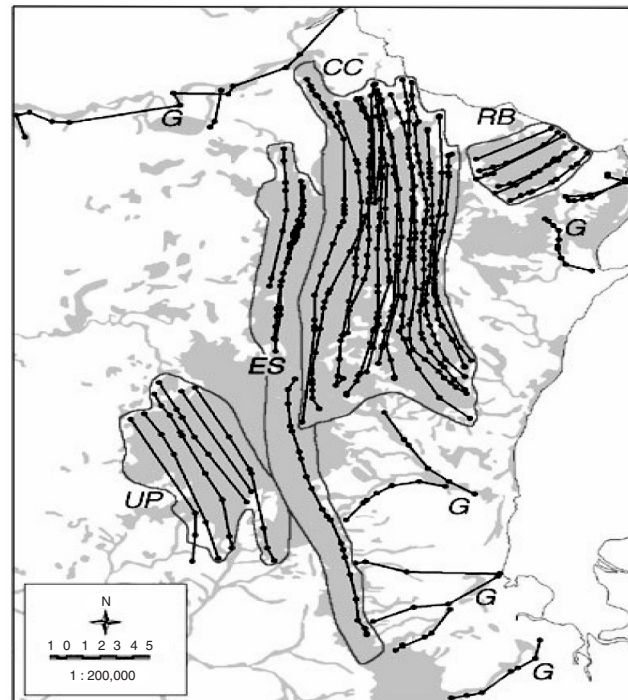
Estimation of nest tree density

Three alternative estimation methods were used to determine the number of nest trees. The first and simplest method was a crude extrapolation of the nest tree density in the 292-ha study area. However, the density of eclectus nest trees is likely to vary with topography and rainforest type, so in the remaining two methods nest tree numbers were estimated using stratified sampling regimes with strata based on topography or vegetation.

Extrapolating from the density of known nest trees

In the 292-ha study site we know the location of most, if not all, active nest trees, and could thus calculate a crude density. This figure was extrapolated to provide an estimate of the number of eclectus parrot nest trees in all the rainforested areas of the Iron Range region. The estimate is probably too high because the 292-ha study area is located on prime eclectus parrot habitat – flat floodplains of the Claudie River covered mainly with semi-deciduous mesophyll vine forest. However, it provided a ball-park check on the alternative estimation methods.

Nest tree density based on topographical strata

There are five distinct topographical areas (strata) in the study region: the Claudie River alluvial plain, the east-facing escarpments of Tozer and Dorriwill Ranges, the coastal hills (Roundback and Ogilvie Hills), the upland plateau west of the Tozer escarpment, and finally the gallery forest on major creeks. Each topographical stratum (except gallery forest) was sampled in more or less straight, parallel, non-overlapping flight paths (Fig. 2). To survey for potential nest trees

Table 2.   Results of ground-truthing

Status of tree	Visible from air?	Number	
Active	No	14	
Active	Yes	18	Visible trees out of those that are active = 56.3%
Inactive	Yes	39	Active trees out of those observed = 31.6%
Total		71	Ratio of active trees to observed trees = 0.561

in gallery forest the course of the river was followed once (Fig. 2). Strips of gallery rainforest averaged 200 m wide and were always less than 500 m wide, so all the potential nest trees visible from the air could be counted. In all, 45 'topographical transects' were flown, with 14 over the Claudie River alluvial plain, 4 over east-facing escarpments, 6 over the coastal hills, 15 over the uplands, and 6 along gallery forest. A single topographical transect could pass over one to several patches of different vegetation type, mainly one of the two major types of rainforest present in the region.

We corrected for counting biases (based on the results of ground-truthing) to convert the number of trees observed in each transect to an estimate of the actual number of active nest trees in that transect. Transects differed in length since strata were of variable and irregular shapes, so the Ratio Method (Krebs 1989; Caughley and Sinclair 1994) was used to estimate the density of nest trees in each stratum, the total number of nest trees in the stratum, the total number of trees across all strata, and their associated standard errors (assuming sampling with replacement) in the following way:

Density of nest trees in stratum = $d = \sum y / \sum a$

$$\text{s.e.}(d) = {}^{n}/_{\sum a} \cdot \sqrt{(1/n(n-1))} \cdot (\sum y^2 + d^2 \sum a^2 - 2d\sum ay).$$

Number of nest trees in stratum = $y = d.A$

$$\text{s.e.}(y) = A[\text{s.e.}(d)].$$

Total number of nest trees across all strata = $Y = \sum y$

$$\text{s.e.}(Y) = \sqrt{\sum [\text{s.e.}(y)^2]},$$

where d = density of nest trees in stratum, y = total number of nest trees counted in all transects in stratum, a = total area sampled in stratum (sum of transect lengths × transect widths, where width = 500 m in all topographical transects except those over gallery forest, which were 200 m wide), n = number of transects in stratum and A = total area of stratum in the Iron Range area (determined from topographical maps)

Nest tree density based on rainforest type strata

In this estimation method, the two major rainforest types in the region ('gallery closed-forests on alluvia' and 'closed-forests of the Iron–McIlwraith region') were defined as strata. Patches of each rainforest type interdigitate over the whole survey region, and are distributed in various sizes and locations. Using vegetation maps of the area (Neldner and Clarkson 1995), a 'rainforest transect' was defined as a section of a flightpath (flown during the topographical transects) that passed over one stretch of a single rainforest type. Rainforest transects within the same flight path were often contiguous, but they were occasionally interrupted by small patches of woodland, grassland, swamp or mangroves. Unlike the topographical transects, rainforest transects were defined *post hoc*, and consequently some were short. Those whose lengths were in the lowest 10% of the distribution of all transect lengths (i.e. less than 0.5 km long) were therefore excluded, leaving 134 transects. Of these, 77 were over 'gallery closed-forests on alluvia', and 53 over 'closed-forests of the Iron–McIlwraith region'. Only one transect of 1.07 km was flown over the rare broad vegetation

grouping 'closed-forests of coastal dunes'. An estimate of density would consequently have been unreliable. Since this was a type of notophyll vine forest, this transect was reclassified into the 'closed-forests of the Iron–McIlwraith region', which also contained notophyll vine forests.

After correcting for counting biases, we calculated the density of nest trees in each rainforest stratum, the total number of potential nest trees in each rainforest stratum and in the whole Iron Range region (with their associated standard errors) in the same way as for Estimation Method 2.

Number of eclectus parrots per nest tree

The mean number of birds observed at nest trees over four years in the 292-ha study area was multiplied by the estimate of the number of eclectus nest trees to derive a population estimate for eclectus parrots in the Iron Range area. Nest trees can have multiple hollows, but each hollow is guarded and used by a single female. In all, 35 nest trees monitored over 107 nest-years contained 45 occupied hollows (i.e. 1.29 hollows (or breeding females) per tree). At 34 of these trees, we observed 67 males (sum of mean of males attending a nest in 104 nest-years), making an average of 1.97 males per nest and 2.54 males per tree (Heinsohn and Legge 2003).

Results

Ground-truthing

The nesting activity and visibility from the air for 71 trees are shown in Table 2. Of 32 active nest trees known in the 292-ha study area, 18 (56.3%) were visible from the air in simulated aerial transects. Ground-truthing showed that 18 of the 57 trees visible from the air (31.6%) were used as nesting trees by eclectus parrots. Therefore, for every tree counted from the air there were 0.561 'real' nest trees (0.316/0.563).

Estimation of nest tree density

Extrapolating from the density of known nest trees

In the 292-ha study area there were 32 nest trees, making a density of 1.096 trees km^{-2}. The whole Iron Range region contains 532 km^2 of rainforest. However, 78 km^2 of this is found scattered as very small fragments away from the main rainforested area – we believe these isolated patches are less useful nesting habitat to eclectus parrots (see Discussion). Nonetheless, the total number of nest trees in the region therefore lies between 498 and 583 using this estimation method.

Nest tree density based on topographical strata

The average length of the 45 topographical transects was 13 ± 9.2 (s.d.) km; they covered an area of 263 km^2, which was 58% of the total area of rainforest in the region (Table 3).

Table 3. Survey results for the topographical strata

Sampling intensity = area surveyed in stratum divided by total area of stratum

Topographical strata	No. of transects	Length of transects (mean ± s.d.)	Area sampled (km²)	Area of rainforest on that topography (km²)	Sampling intensity	No. of potential nest trees counted	Corrected no. of nest trees	Nest tree density (trees per area sampled (km²))	Total no. of nest trees (mean ± s.e.)
Alluvial plain of Claudie River	14	22.9 ± 4.9	160	207	0.78	278	156	0.98 ± 0.05	203 ± 10
East-facing escarpments of Tozer and Dorriwill Ranges	4	15.7 ± 4.9	31.4	111	0.28	59	33	1.05 ± 0.13	117 ± 14
Roundback Hills	6	5.87 ± 0.8	17.6	35	0.50	23	13	0.74 ± 0.2	26 ± 11
Upland plateau west of Tozer escarpment	6	11.3 ± 2.5	34.0	76	0.45	21	12	0.35 ± 0.07	27 ± 15
Gallery forest	15	6.48 ± 8.3	19.5	25	0.77	60	34	1.74 ± 0.32	44 ± 2
Total	45	13.0 ± 9.2	262.5	454	0.58	441	248		417 ± 25

Table 4.   Frequency of different tree types in the topographical strata
'Other tree species' comprised other types such as *Tetrameles nudiflora*, *Melaleuca* spp., or trees we were unable to identify

Topographical strata	Milky pine	Green fig	Blackbean	Other tree species	% of observed trees that were preferred species
Claudie River alluvial plain	70	30	26	152	45.3
East-facing escarpments of Tozer and Dorriwill Ranges	19	4	0	36	39.0
Coastal hills (Roundback and Ogilvie Hills)	2	6	1	14	39.1
Upland plateau west of Tozer escarpment	0	0	0	21	0
Gallery forest	9	17	0	34	43.3

The density of potential nest trees was lowest in the upland plateau west of the escarpment, and highest in gallery forest; the remaining topographical features showed similar tree densities (Table 3). Overall, we observed 441 potential nest trees; after correcting for counting biases this translated to 248 active nests. Combining the total number of trees estimated in each stratum resulted in a final figure of 417 ± 25 (s.e.) eclectus parrot nest trees in the Iron Range area.

About 40% of the counted trees in all the topographical strata except for the uplands were of the three preferred species (milky pines, green figs, blackbeans). Thus, as well as having a lower density of emergents, the emergents in the uplands may be less useful for eclectus parrots. Different tree species predominated in the different topographical features (Table 4): blackbeans were mostly found on the Claudie River alluvial plain. These trees have deep taproots and probably need deep soils to flourish. Green figs were found on the Claudie plain and in gallery forest; their roots are shallow but they prefer wetter sites. Milky pines are able to grow on well drained, relatively dry sites, including steep slopes, which is probably why they were common on the east-facing escarpments as well as on the Claudie River alluvial plain and gallery forest.

Nest tree density based on rainforest strata

The average length of 131 rainforest transects was 4.38 ± 4.5 (s.d.) km; they covered an area of $258\ \mathrm{km}^2$, or 48% of the total area of rainforest. Note that the sampling intensity for rainforest transects is lower than that calculated for the topographical transects. Data from some rainforest transects were discarded because the transects were short (see Methods). More importantly, the total area of rainforest in the region has a higher value in this estimation method than with Method 2 ($532\ \mathrm{km}^2$ *v.* $454\ \mathrm{km}^2$) because it includes isolated small patches lying outside the main topographical strata. The implications of this are outlined in the Discussion.

Overall, 437 potential nest trees were observed. After correcting for counting biases and finding the estimated number of trees in each rainforest stratum, this resulted in an overall estimate of 462 ± 31 (s.e.) active nest trees in the Iron Range region.

The number of potential nest trees, and the proprtion that were of the preferred types for eclectus parrots, was higher in the broad vegetation grouping 'gallery closed-forests on alluvia' than in the 'closed-forests of the Iron–McIlwraith region' (Tables 5, 6).

Population size of eclectus parrots in Iron Range region

Given the number of females per nest tree, the number of breeding females in the region lies between 538 and 596, and the number of males between 1059 and 1173, depending on the estimation method used for the number of nest trees (Table 7).

Discussion

Evaluation of the survey technique

Aerial surveys can be an extremely useful way to estimate animal abundances, particularly when the areas concerned are large or inaccessible from the ground. They are most often used when animals are large and in open habitats (e.g. large herbivores on the African savannah: Grimsdell 1979). They have also been used to count conspicuous animal sign that correlate with the animal's density, such as rabbit warrens in arid areas (Parker and Myers 1974).

A common problem with aerial census is that observers tend to undercount because of sightability problems (e.g. because the aircraft is moving quickly, or targets are concealed from the air by thick cover: Caughley 1974; Krebs 1989). Although there are several ways of correcting for these counting biases such as using sightability curves (Caughley 1974; Seber 1979) and correction factors (e.g. Marsh and Sinclair 1989), the simplest method conceptually is to estimate the bias by using the survey technique in an area where the real number of animals or animal sign is known (Krebs 1989). In the surveys for eclectus parrot nest trees there were two sources of counting bias: undercounting occurred because not all nest trees are visible from the air,

Table 5. Survey results for the rainforest strata

Rainforest strata	No. of transects	Length of transects (mean ± s.d.)	Area sampled (km²)	Area of rainforest on that topography (km²)	Sampling intensity	No. of potential nest trees counted	Corrected no. of nest trees	Nest tree density (trees per area sampled (km²))	Total no. of nest trees (mean ± s.e.)
Gallery closed-forests on alluvia	77	5.13 ± 5.0	173	246	0.70	331	186	1.08 ± 0.05	265 ± 13
Closed-forests of Iron–McIwraith region	54	3.30 ± 3.5	85.4	286	0.30	106	59	0.69 ± 0.10	197 ± 28
Total	131	4.38 ± 4.5	258	532	0.48	437	245		462 ± 31

Table 6.   Frequency of different tree types in the two rainforest strata

Rainforest strata	Milky pine	Green fig	Blackbean	Other	% observed trees that were preferred species
Gallery closed-forests on alluvia	74	48	26	183	44.7
Closed-forests of Iron–McIlwraith region	26	9	1	74	32.7

Table 7.   Projections for population size of eclectus parrots for each estimation method

Estimation method	Estimate of no. of eclectus trees	Projected no. of breeding females	Projected no. of breeding males	Estimate bias?
1	498–583	642–752	1265–1481	Overestimate
2	417	538	1059	Underestimate
3	462	596	1173	Overestimate

but overcounting also took place because not all emergents seen from the air contain suitable hollows for eclectus parrots. However, the extent of each bias was estimated by using the survey technique in the 292-ha study area where we know the location of all nest trees. Over half (56%) of all eclectus parrot nest trees were visible from the air. This lies well within the range of undercounting biases reported by Caughley (1974) (23–89%). However, ground-truthing showed that only one-third of trees seen from the air were active nest trees. The combined effects of the overcounting and undercounting biases meant that in the 292-ha area where 58 potential nest trees were counted from the air, there were actually 32 eclectus parrot nest trees (or 56.1%).

There are few examples of successful aerial surveys over closed forests. Bradford and Harrington (1999) undertook aerial surveys for the yellow-bellied glider, *Petaurus australis reginae*, in north-eastern Queensland. As in the study reported here, they surveyed for 'sign' (in this case sap-trees) rather than the animal itself. However, they found their undercounting bias to be so great (spotting only 9% of all sap-trees) that they concluded that the technique was unreliable. This problem arose mainly because of the difficulty of seeing feeding scars on trunks through thick foliage. Since we were searching for a general growth form (a tree emerging from the canopy), our task was much easier.

Evaluation of different estimation methods

We estimated the number of eclectus parrot nest trees in the Iron Range region in different ways, but they gave broadly similar results. The largest and crudest estimate (of 498–583 nest trees) took the density of eclectus nest trees from the 292-ha study area where we have monitored a population of eclectus parrots for four years, and extrapolated this to the total area of rainforest in the region. This estimate is certain to be inflated: the 292-ha study area is dominated by 'prime' eclectus parrot nesting habitat – semi-deciduous mesophyll vine forest on the alluvial floodplains. All four tree types favoured by eclectus parrots for nesting (*Alstonia* spp.,

Castenospermum australe, *Ficus albipila*, *Melaleuca* spp.) occur with high frequency in this vegetation type (Table 1).

The other two estimation methods used data from the aerial surveys, but the data were treated differently in each case. The first estimation used a stratified sampling regime based on major topographical features that are likely to affect nest tree densities. The estimate of 417 ± 25 trees could be too small, since this method ignored small, isolated rainforest patches lying outside the rainforest blocks on the main topographical features. The alternative estimation method used a stratified sampling regime based on the broad vegetation groupings identified by Neldner and Clarkson (1995), and resulted in an estimate of 462 ± 31 nest trees. This estimation assumed that emergents in each vegetation grouping were equally likely to be useful to eclectus parrots as nest trees. However, emergents in each broad vegetation grouping are made up of different species, and eclectus parrots show strong preferences for certain tree species that are more common in 'gallery closed-forests on alluvia' than 'closed-forests of Iron–McIlwraith region' (Table 6), so the real number of nest trees is probably lower than 462.

Notwithstanding the possible biases of each of the two stratified sampling methods, the number of eclectus parrot nest trees in the Iron Range area probably lies between 367 (lower 95% confidence limit of lowest estimate) and 524 (upper 95% confidence limit of largest estimate).

Population size of eclectus parrots in the Iron Range area

Although we estimate that ~1597–1769 adult eclectus parrots live in the Iron Range region (estimates 2 and 3: Table 7), the number of breeding females is only about one-third of this figure (538–596). Eclectus parrots have a complex social system, where several males mate with a single female then feed her and her chicks (Heinsohn and Legge 2003). Even away from nest trees males are encountered far more frequently than females (Forshaw and Cooper 1989). The sex ratio of fledglings in the population is even (Heinsohn *et al*. 1997; Heinsohn and Legge 2003) so the bias in the adult sex ratio must be caused by

post-fledgling mortality. There are two likely sources: only females incubate eggs and brood chicks, and nest-hole occupation makes them more vulnerable to predation from large pythons (Heinsohn and Legge 2003). In addition, their bright red plumage makes them more conspicuous than males against the green backdrop of the rainforest canopy, and therefore more vulnerable to visually hunting avian predators (Legge *et al.* 2003).

Coupled with knowledge of their breeding biology, the low number of female eclectus parrots is of some concern. The average breeding success of eclectus parrots at Iron Range is low – only 18% of all eggs laid result in a fledgling (Heinsohn and Legge 2003). Coupled to this, variance in reproductive success is highly skewed. Over multiple years, 39% of females always failed to produce any young at all, whereas 29% of females produced 72% of all fledglings. This means that only ~156–173 females in the region are routinely successful at producing young, so the successfully breeding population of eclectus parrots at Iron Range is very small. Although there is no reason to believe that the eclectus parrot population is currently unstable, any habitat loss (due to logging operations), or any other factor that further reduces the already low breeding success of this population (such as climatic changes that increase the incidence of flooding in nest hollows: Heinsohn and Legge 2003) may have serious consequences.

Eclectus parrots in the McIlwraith Range area

Eclectus parrots are also found in the McIlwraith Range, which lies to the south of Iron Range, and the two populations may be connected by thin strips of gallery forest and other topographical rainforest isolates that occur in the intervening 50 km. It is unclear how frequently eclectus parrots move between the two populations; this may be resolved in the future with molecular approaches. However, since eclectus parrots are rarely seen far from substantial rainforest patches (authors' observations), these habitat corridors are probably important for them as well as other rainforest-restricted fauna, since they link two larger rainforest blocks. The loss of these corridors could cause many species to be fractured into two smaller populations, with concomitant long-term conservation concerns.

It is difficult to extrapolate the density estimates for eclectus parrots at Iron Range into McIlwraith Range (and thus generate an estimate for the entire Australian population) because the topography and vegetation types differ. The McIlwraith Range is more mountainous with larger areas at higher altitude, and the rainforest type favoured by eclectus parrots is relatively less common. Whereas nearly half of the available rainforest at Iron Range (46.2%: Table 8) is in the broad vegetation grouping 'gallery closed forests on alluvia', less than a quarter of the rainforest (20.9%) at McIlwraith Range is of this type (Table 8). Further, a sizeable proportion of the rainforest south of Iron

Range (particularly the area north and east of the McIlwraith massif) occurs as small fragments and gallery strips far from larger continuous blocks. These isolated fragments may be of limited use to eclectus parrots. As well as the anecdotal observation that eclectus parrots are rarely seen far from large patches of rainforest, preliminary radio-tracking data has shown that males that are provisioning females and young range widely (up to 100 km^2) without crossing significant non-rainforested areas (unpublished data). Consequently, although the total area of rainforest in the McIlwraith and intervening areas exceeds that of Iron Range (1475 km^2 compared with 523 km^2: see Table 8), it is unlikely that McIlwraith Range holds three times the number of eclectus parrots. Ideally, aerial surveys and ground-truthing should be carried out in the McIlwraith region to estimate nest-tree densities and population sizes.

Distribution of eclectus parrots on Cape York Peninsula

Although the Iron and McIlwraith Ranges contain the largest area of lowland rainforest on Cape York Peninsula (and indeed in Australia), there are other large areas of rainforest on Cape York including Lockerbie Scrub near the Tip of Cape York, and the riverbanks and dunefields of the Upper Jardine River. Table 8 shows the different rainforest types that are known to be suitable for eclectus parrots (because eclectus parrots currently occur in these rainforests), or are potentially suitable because they contain species used as nest trees and food sources. The area of each rainforest type is shown for the four major regions of rainforest on Cape York (Iron Range, McIlwraith Range, Lockerbie Scrub, Jardine catchment) as well as the remaining parts of the cape (Fig. 1).

Of the 325 721 ha of suitable or potentially suitable rainforest in Cape York, the majority (64%) occurs in the Iron–McIlwraith Ranges. However, this still leaves large areas of rainforest elsewhere on the cape, raising the question of why eclectus parrots are found exclusively in the Iron–McIlwraith Ranges. One possibility is that eclectus parrots obligately depend on one or more resources found only in semi-deciduous mesophyll vine forest, a rainforest type within the broad vegetation grouping 'gallery closed-forests on alluvia', which occurs solely in the Iron–McIlwraith Ranges. This seems surprising, since they are generalist fruit- and seed-eaters, and outside Australia they are able to persist even in disturbed forest (Forshaw and Cooper 1989).

Alternatively, eclectus parrots may need relatively large unbroken blocks of rainforest, and even a network of patches that are below a threshold size or shape may not sustain a viable population. For example, the suitable and potentially suitable rainforest found outside the Iron–McIlwraith Ranges is mostly distributed as small isolates associated with topographic features such as river banks, dunefields and fire-protected gullies. The rainforest of the Jardine catchment is dominated by a type of simple evergreen

Table 8. Area (in hectares) of the rainforest types in Cape York
First half of table shows types known to be suitable to eclectus parrots; second half shows types that are potentially suitable

Broad vegetation grouping	Vegetation map unit	Rainforest type (following Neldner and Clarkson 1995)	Iron Range	McIlwraith Range	McIlwraith and Iron Ranges	Lockerbie	Jardine catchment (excluding Lockerbie)	Elsewhere on Peninsula	Cape York Peninsula
6	8	Semi-deciduous mesophyll vine forest (on alluvia, and metamorphic and granitic foothills and lower hillslopes; Claudie and Normanby rivers)	21807	24571	46378	0	0	0	46378
6	18	Evergreen notophyll vine forest (on major streams)	2818	7673	10491	501	2085	45562	58639
2	21	Notophyll vine forest (Iron and McIlwraith Ranges)	12946	63336	76282	0	19	1395	77696
2	26	Simple evergreen notophyll vine forest (with *Acacia aulacocarpa*, *Eucalyptus tessellaris*, *Blepharocarya involucrigera* emergents; Iron Range, Wet Tropics)	14750	51945	66695	0	0	61	66756
		Subtotal	52321	147525	199846	501	2104	47018	249469
6	16	Evergreen mesophyll vine forest (with *Archontophoenix alexandrae*; streams)	0	227	227	0	0	6215	6442
6	19	Evergreen notophyll vine forest (dominated by *Melaleuca leucadendra*, *Xanthostemon crenulatus*, *Lophostemon suaveolens*; swamps)	19	1802	1821	0	24	98	1943
4	20	Evergreen to semi-deciduous notophyll vine forest (dominated by *Syzygium* spp, *Terminalia* spp, *Xanthostemon* spp; beach rainforest, east coast)	921	1911	2832	108	341	922	4203
3	11	Semi-deciduous notophyll vine forest (Lockerbie)	0	0	0	8062	1625	0	9687
3	12	Semi-deciduous notophyll vine forest (small patches on plateaus)	63	0	63	0	5717	9443	15223
3	24	Simple evergreen notophyll vine forest (NE Cape York Peninsula, sometimes with emergent *Callitris intratropica*)	0	88	88	32	14328	17578	32026
3	25	Simple evergreen notophyll vine forest (dominated by *Callitris intratropica* emergents)	0	0	0	0	3681	173	3854
2	9	Semi-deciduous mesophyll/notophyll vine forest (granite slopes, Birthday Mountain)	0	2874	2874	0	0	0	2874
		Subtotal	1003	6902	7905	8202	25716	34429	76252
		Overall total	53324	154427	207751				325721

notophyll vine forest (Neldner and Clarkson 1995) that is floristically related but relatively depauperate compared with Iron Range rainforests (Lavarack and Stanton 1977). In addition, it is distributed as a series of small discrete patches (Neldner and Clarkson 1995). One or both of these features may make the area unsuitable for eclectus parrots. In contrast, the rainforest of Lockerbie Scrub occurs mostly as a single continuous block, and many of its characteristic tree species are shared with the Iron–McIlwraith rainforests. The major difference between Lockerbie Scrub and the Iron–McIlwraith rainforests is their size: Lockerbie Scrub contains only 8703 ha of potentially suitable rainforest. Using our most 'generous' estimation method – the known density of nest trees from prime habitat at Iron Range (1.096 km^{-2}) – this translates to a crude estimate of only 95 nest trees, 241 males and 123 breeding females, of which only a proportion would be successful at producing young. A population of that size could be vulnerable to both genetic and stochastic effects, thus Lockerbie Scrub is probably too small to support eclectus parrots in the long term.

Implications for the biogeographic history of Cape York rainforests

The rainforests of Cape York Peninsula have undergone major expansion and retractions corresponding to the glacial cycles of the Pleistocene (Nix and Kalma 1972; Webb and Tracey 1981). Sea-levels have also fluctuated – being much lower than today in the cooler, arid intervals, and similar or higher than today in warmer, wetter periods. At certain combinations of sea-level and climate, the rainforests of Cape York Peninsula have been joined to those of New Guinea across the Torresian landbridge. The last strong connection was 80 000–120 000 years ago (Kershaw 1978; 1985), but a shorter, weaker connection is postulated for 7000 years ago (Nix and Kalma 1972).

The biogeographic history of the Cape York Peninsula rainforests during the Pleistocene has received less empirical attention than the Wet Tropics rainforests (e.g. Moritz *et al*. 1997). However, authors have suggested that the Peninsula rainforests would have almost disappeared in the interval between these two relatively wet periods, with small refugia persisting around the Iron–McIlwraith Ranges as gallery strips and on topographical features such as rocky outcrops and gullies (Webb and Tracey 1981; Barlow and Hyland 1987). Major replenishment of the Peninsula rainforests from New Guinea would therefore have occurred during the most recent connection (7000 years ago). The high degree of New Guinean–Cape York Peninsula overlaps in the assemblages of rainforest mammals and birds (Kikkawa *et al*. 1981; Winter 1988), and rainforest plants (Webb and Tracey 1981; Barlow and Hyland 1987) are consistent with this.

However, it is possible that much of the strong floral and faunal similarities between Cape York Peninsula and lowland New Guinea rainforest are due to substantial replenishment

80 000–120 000 years ago (rather than 7000 years ago), when the rainforest connection was relatively strong and persistent across the Torresian landbridge (Kershaw 1985). For example, a recent analysis found a high degree of endemism in Cape York Peninsula rainforest plants at the species level (20%: Crisp *et al*. 2001), which suggests that major replenishment of the Peninsula rainforests occurred before 7000 years ago. These differences had gone unacknowledged in earlier distributional analyses that concentrated on differentiation at the generic level (Webb and Tracey 1981; Barlow and Hyland 1987), and suggest that the Iron–McIlwraith refugium was more substantial than previously thought.

Irrespective of the strength of the connection 7000 years ago, rainforest would have been more extensive during this period; if eclectus parrots recolonised Cape York Peninsula from New Guinea at this time, they were presumably initially present at Lockerbie, but have since become extinct there as the rainforest contracted. Alternatively, if eclectus parrots colonised Cape York Peninsula from New Guinea 80 000–120 000 years ago, they must have survived throughout the intervening arid period, which reached its height 14 000–17 000 years ago (Nix and Kalma 1972). Our data on the density of eclectus parrot nest trees coupled with the fact that eclectus parrots are currently absent from Lockerbie again suggest that the Iron–McIlwraith Ranges refugium during arid periods may have been larger (i.e. >90 km^2) than previously assumed. Moreover, given that eclectus parrots are not found in the extensive system of gallery forest of Cape York Peninsula, nor in the fragmented rainforests of the Jardine dunefields, the refugium must have existed as a fairly continuous patch, and not simply confined to disjunct and isolated topographical features. Phylogeographic analyses of eclectus parrots and other rainforest fauna that currently inhabit Cape York Peninsula and New Guinea would help shed light on the size and importance of the Iron–McIlwraith refugium during the Pleistocene.

Acknowledgments

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