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IS THE SUPERB PARROT *Polytelis swainsonii* POPULATION IN CUBA STATE FOREST LIMITED BY HOLLOW OR FOOD AVAILABILITY?

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The Superb Parrot *Polytelis swainsonii* is listed in threatened species legislation at State and National levels. As it is an obligate hollow nester, harvesting of River Red Gum *Eucalyptus camaldulensis* in south-eastern Australia has led to concern over the maintenance of their nest trees. While the availability of hollows is undoubtedly a critical factor in the conservation biology of the Superb Parrot, it is not known whether their recovery is limited by the hollow resource. Timber harvesting is shown to be capable of removing a variable proportion of Superb Parrot nest trees in Cuba State Forest, but the risk to nest trees is minimized by applying harvest plan prescriptions that aim to perpetuate the hollow resource. Consideration of the spatial organization of Superb Parrot nest trees in relation to the hollow resource and extant woodland vegetation indicates that food availability during the breeding season is likely to be a factor regulating population size. Research is required to test the relationship between the reproductive success of Superb Parrots and the area, quality and connectivity of woodland vegetation within their foraging range.

INTRODUCTION

Much of the dispute about use of Australia's native forests stems from uncertainty about the impact of timber harvesting on the abundance and distribution of forest-dependent species, especially fauna that use hollows (Gibbons and Lindenmayer 2002).

The Superb Parrot *Polytelis swainsonii* is endemic to woodlands in south-eastern Australia. Its range has contracted in Victoria, but in New South Wales they have a widespread distribution west of the Great Dividing Range, and can be locally common in the Riverina and South-west Slopes regions (Higgins 1999). As they are obligate hollow nesters, harvesting of River Red Gum *Eucalyptus camaldulensis* on the floodplains of the Murray and Murrumbidgee rivers has led to concern over the maintenance of their nest trees (Webster 1988; NPWS 2000). Given that the Superb Parrot is listed in threatened species legislation at State (Victoria, endangered; New South Wales, vulnerable) and National levels (vulnerable), this concern must be addressed through a legal process.

The pivotal question is whether the recovery of Superb Parrots is constrained by previous or potential future timber harvest practices. For this to be the case, the number of hollows would need to be depleted to the extent that hollow availability limited the abundance and distribution of Superb Parrots. Other factors have undoubtedly influenced the population viability of Superb Parrots, including clearing and degradation of habitats that provide adult and juvenile birds with food (NPWS 2000). However, little information is available to place different threats in context or to prioritize recovery actions. This dearth of information is surprising given their iconic status.

In this paper, physical and spatial characteristics of Superb Parrot nest trees located in Cuba State Forest are used to: (i) assess the threat to nest trees imposed by three timber harvest systems; (ii) identify factors likely to be affecting Superb Parrot population size, and; (iii) identify future research priorities.

BACKGROUND INFORMATION

Superb Parrots

Breeding by Superb Parrots in the Riverina Region is generally associated with three habitat elements: (i) stands of River Red Gum containing suitable nest hollows (Webster 1988); (ii) box woodland within nine kilometres of nests, where parents feed (Webster 1988), and; (iii) corridors of trees between nests and foraging patches, which parents follow during commuting flight (NPWS 2000).

Superb Parrots lay their eggs on a bed of decayed wood in branch and trunk cavities of mature eucalypt trees. They are capable of laying 4–6 eggs and fledging 1–5 young. The male feeds the female 2–3 times per day during the incubation period (*c.* 20 days), and for the first week after hatching. Thereafter, young are fed at the nest by both parents for a further 3–4 weeks. Parental care continues until juvenile birds become independent some 2–4 weeks after fledging (Higgins 1999).

Superb Parrots forage in small flocks, mostly on the ground, on the seeds of native grasses and introduced cereal grains. They also feed in the canopies of trees and shrubs where they consume flowers, fruits and seeds, and glean lerps from leaves. In the Riverina Region, foraging habitats include Boree *Acacia pendula* shrubland, and woodlands containing Black Box *E. largiflorens*, Western Grey Box *E. microcarpa*, Yellow Box *E. melliodora* or White Cypress Pine *Callitris glaucophylla* (Webster 1988; Higgins 1999; NPWS 2000).

Flocks commuting between nest sites and foraging patches develop as a result of parents announcing their presence or responding to in-flight vocalizations sometime after feeding their young. Adults have a loud penetrating contact call to co-ordinate these movements. At other times they are wary, well camouflaged and quiet near their nest, and are subsequently very difficult to detect (pers. obs., R. Webster, pers. comm.). These periods of inactivity may reflect the high energy costs of foraging, as birds foraging in expensive ways require longer subsequent pauses for physiological recovery (e.g. Kacelnik and Cuthill 1987).

Parents are reluctant to fly over large open spaces to reach foraging patches during the breeding season, possibly because they have insufficient energy reserves to avoid aerial predators (NPWS 2000). As the risks involved in exceeding thresholds of exertion are known to constrain parental responses (Moreno *et al.* 1997), the maximum distance they have been observed to fly to obtain food of around nine kilometres (Webster 1988) may indicate the distance at which further parental effort in nestling provisioning cannot be energetically sustained.

Harvesting practices in River Red Gum

River Red Gum attains its best development adjacent to watercourses and areas of floodplain that receive regular flooding (Bacon *et al.* 1993). This increases the potential for conflict between timber harvesting and Superb Parrot conservation because the areas with the highest timber production capability often coincide with the location of Superb Parrot nest trees.

Consequently, a number of harvesting prescriptions currently practiced in NSW State forests aim to minimize the likelihood of Superb Parrot nest trees being felled during harvest operations. It has not been possible to confidently assess the efficacy of these or novel prescriptions, as the physical and spatial characteristics of nest trees derived from distribution surveys (e.g. Webster 1988, 1993, 1997, 1999) may not be representative of the breeding population.

A timber harvest system is defined through the application of one or more silvicultural systems and associated prescriptions. Two silvicultural systems — Single Tree Selection (STS) and Australian Group Selection (AGS) — are used to regenerate River Red Gum stands. Numerous prescriptions are applied to mitigate, for example, potential impacts on threatened species habitat, including hollow-bearing trees.

SILVICULTURAL SYSTEMS

Single Tree Selection is suited to shade tolerant species capable of regenerating successfully in relatively small canopy openings created by the removal of single or small groups of commercially mature trees. However, as the River Red Gum is a shade intolerant species, seedlings are unable to achieve their full growth potential in such small openings (SFNSW 2000). As a result, River Red Gum stands subject to STS over long time frames can become dominated by moribund trees with relatively small dimensions. The capacity of these stands to recruit large trees containing either sawlogs or hollows can, therefore, be compromised.

Australian Group Selection involves creating larger canopy openings by removing groups of trees, including those with no commercial value. To allow regeneration to develop without experiencing excessive competition from surrounding trees, canopy openings ranging in size from 0.3–0.8 hectares are required, depending on the productive capacity of the stand (A. Stirling, pers. comm.). However, if AGS is practiced too regularly or extensively, late mature and senescent trees may be poorly represented in the age-class structure.

HARVESTING PRESCRIPTIONS

The potential impact of native forest silviculture on hollow-using fauna can be mitigated by prescriptions that: (i) exclude harvesting from landscape elements such as formal reserves and riparian zones; (ii) place an upper diameter limit on trees able to be felled for timber production; (iii) retain standing dead trees (stags); (iv) relate to merchantability, whereby trees with no value for timber production (but with high value for wildlife due to the presence of hollows) may be retained, and; (v) require *habitat* and *recruit* trees to be retained within areas available for harvesting.

A habitat tree is a senescing tree with good crown development that appears to contain at least one hollow suitable for occupancy by fauna. A recruit tree is a mature or late mature tree that appears to have good potential for hollow development and long-term survival. As a minimum wildlife requirement, the current practice is to mark two habitat and two recruit trees per hectare for retention in the harvestable area. Many more trees meeting these descriptions are generally retained but, owing to other silvicultural considerations, are not marked. Higher formal retention rates are applied in *habitat corridors*. A habitat corridor consists of a 20 metre-wide exclusion zone commencing from the first tree line adjacent to watercourses and water bodies, and an adjoining 30 metre-wide zone in which five habitat trees and five recruitment habitat trees are retained per hectare.

METHODS

Study area

In the Riverina Region, a large Superb Parrot breeding population occurs between Wagga Wagga and Carrathool contiguous with the Murrumbidgee River (e.g. Webster 1988, 1993, 1997, 1999). Cuba State Forest (1 660 ha) is located near the centre of this breeding range (Fig. 1).

A census of the Superb Parrot breeding population in Cuba State Forest was undertaken in 2001 to establish a baseline against which subsequent measurements can be compared (Webster 2002). Surveys within potential nesting habitat, involving almost 120 hours of auditory and visual searches, identified 98 nests in 81 trees (Webster 2002). As nest tree information for the vast majority of the breeding population was acquired, the ability of existing and novel timber harvest prescriptions to retain the hollow resource used by Superb Parrots can be confidently assessed. The spatial organization of nest trees in relation to the total hollow resource and proximity of woodland vegetation also allows other potential constraints on the breeding population to be investigated.

The distances between active Superb Parrot nests in Cuba State Forest (Fig. 2) show that nests are generally clustered, rather than solitary or continuous, indicating colonial nest dispersion. The term *colony* is used here to indicate a group of nests where adults interact by commuting along the same flight routes to common foraging patches; separate colonies have different flight paths that are regularly used by parents (R. Webster, pers. comm., pers. obs.). The spatial coverage of a colony can therefore be defined by social organization rather than an arbitrary separation distance between nest trees.

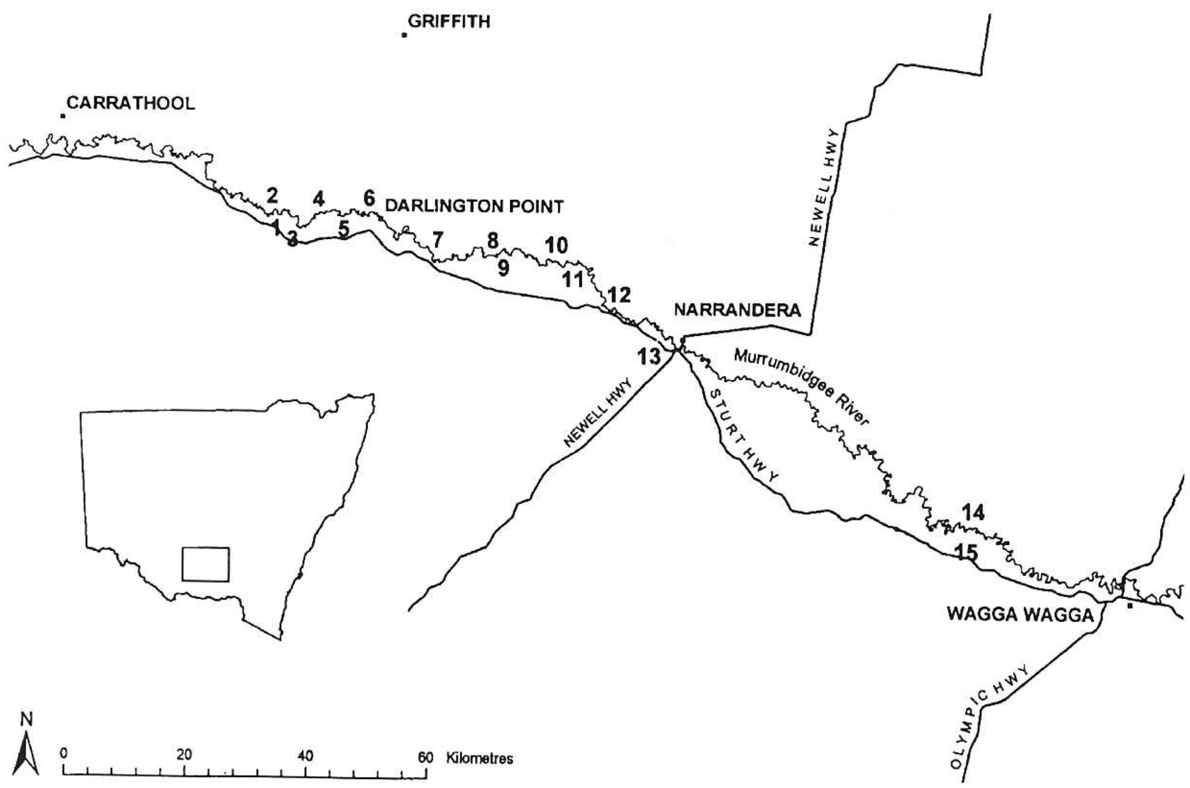

Figure 1. *The Murrumbidgee breeding area for Superb Parrots, showing the location of State forests: 1, Yarrada. 2, Benerembah. 3, Carabury. 4, Dunnoon Lagoon. 5, Uri. 6, Willbriggie. 7, Cuba. 8, MIA III. 9, Jerambla. 10, MIA II. 11, Euroley. 12, MIA I. 13, Narrandera. 14, Currawananna. 15, Berry Jerry.*

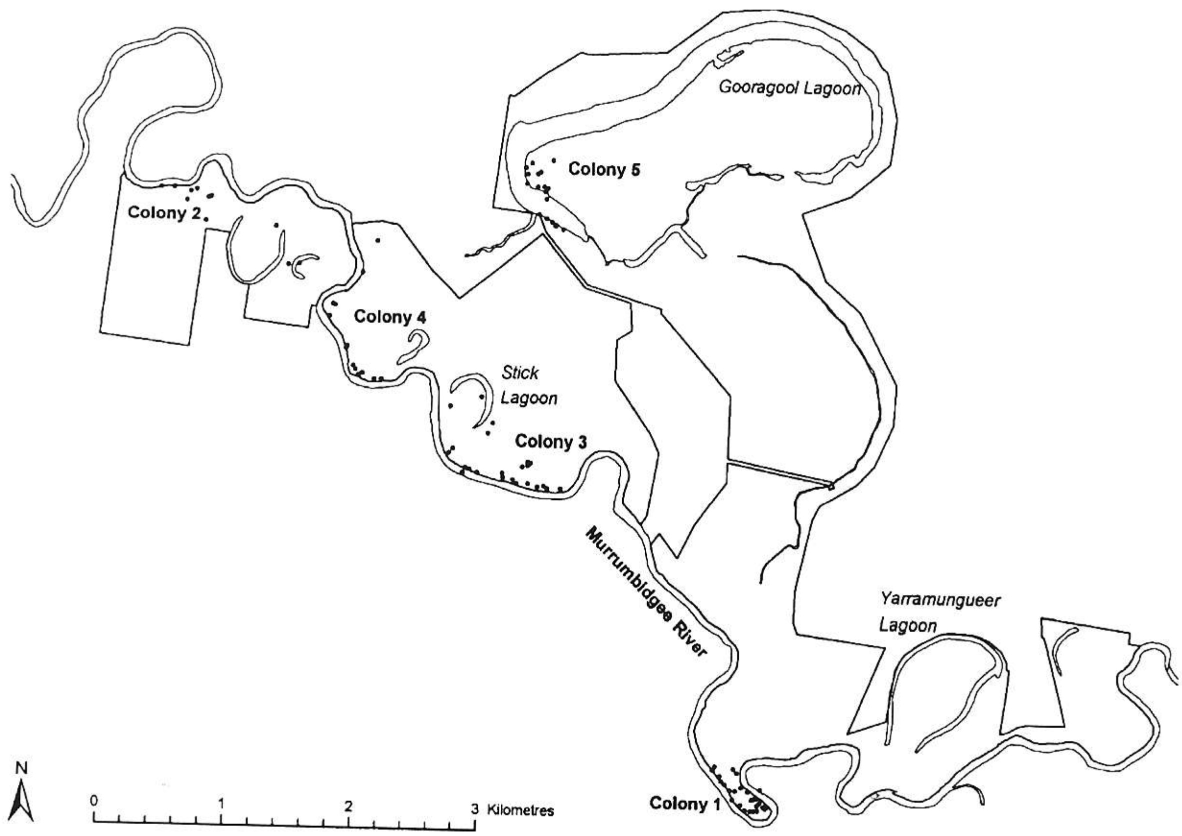

Figure 2. *Superb Parrot colonies in Cuba State Forest. Individual nest trees shown as solid circles.*

Risk to nest trees imposed by different harvest systems

Characteristics of the 81 Superb Parrot nest trees identified by Webster (2002) were analysed to determine the level of protection afforded to known Superb Parrot nest trees using three timber harvest systems (Table 1). Nest trees were considered to be 'at risk' of being felled if they were located within the harvestable area and were not protected by one or more prescriptions. Harvest System #1 was based solely on STS silviculture. Harvest Systems #2 and #3, which included both AGS and STS silviculture, were mainly distinguished by spatial differences in the application of AGS silviculture on the 20–50 metre zone of habitat corridors.

Decisions to select trees for wildlife, as well as the placement of AGS openings, could not be reproduced in the field without introducing observer bias because Superb Parrot nest trees were identifiable by numbered aluminium tags. Accordingly, the number of nest trees retained through application of habitat tree retention prescriptions was not calculated for any of the three harvest systems. Similarly, the risk to nest trees greater than 150 centimetres diameter at breast height over bark (dbhob), or containing no merchantable timber, was also not quantified for Harvest System #2. Given these limitations, the actual risk to Superb Parrot nest trees imposed by each of the harvest systems is expected to be less than the 'risk' calculated here.

Factors affecting the population size of Superb Parrots

HOLLOW AVAILABILITY

The hypothesis that the population size of Superb Parrots in Cuba State Forest is limited by hollow availability was assessed by comparing three measures of Superb Parrot occupation within colonies 1, 2 and 3 (Fig. 2): (i) number of Superb Parrot nests per hectare; (ii) proportion of hollow-bearing trees containing nests, and; (iii) proportion of hollows containing nests.

The following data were captured within the bounds of each colony using a Trimble Pro XRS GPS receiver: grid co-ordinates in AGD66 datum of all hollow-bearing trees; number of visible hollows suitable for occupancy by Superb Parrots; actual number of Superb Parrot nests, and; whether the tree was living or dead. A cavity was considered to be a hollow suitable for occupancy if, during a one-minute per tree search, it was visible to the naked eye, had an external entrance diameter greater than five centimetres and was likely to be at least ten centimetres deep. Given that the internal morphology of cavities cannot be readily predicted from ground surveys (Gibbons and Lindenmayer 2002), the intention here was simply to exclude hollows that were obviously not suitable for occupation. No effort was made to adjust hollow numbers for interpretation errors or for unobserved hollows.

Data were incorporated into a Geographic Information System (GIS). A total area of 63.3 hectares was initially surveyed, containing 807 hollow-bearing trees, 1 996 hollows and 67 Superb Parrot nests. Segments of each colony of equal size (6.5 ha) and distance from the

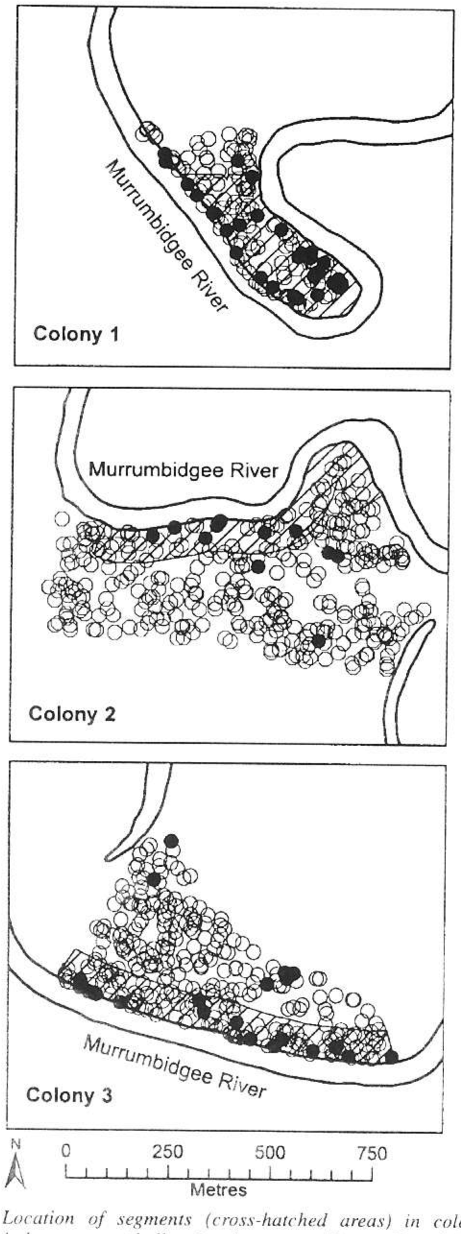

Figure 3. *Location of segments (cross-hatched areas) in colonies 1–3. Hollow circles represent hollow-bearing trees without a Superb Parrot nest. Solid circles represent hollow-bearing trees containing one or more Superb Parrot nests.*

TABLE 1
Harvest system details.

Prescription	Harvest system #1	Harvest system #2	Harvest system #3
1. Habitat corridor	Felling of trees within the 0–20 m zone is not permitted. STS silviculture only is permitted in the 20–50 zone.	Felling of trees wihin the 0–20 m zone is not permitted. AGS silviculture is permitted in the 20–50 m zone.	Felling of trees within the 0–20 m zone is not permitted. AGS silviculture is not permitted in the 20–50 m zone.
2. Upper diameter felling limit	Felling of trees larger than 150 cm dbhob[1] is not permitted.	Felling of trees larger than 150 cm dbhob is not permitted except in AGS openings.	Felling of trees larger than 150 cm dbhob is not permitted.
3. Stag retention	Felling of standing dead trees is not permitted.	Felling of standing dead trees is not permitted.	Felling of standing dead trees is not permitted.
4. Merchantability[2]	Only trees containing sawlog quality timber may be felled.	Outside AGS openings, only trees containing sawlog quality timber may be felled.	Outside AGS openings, only trees containing sawlog quality timber may be felled.

[1]Diameter at breast height over bark.
[2]As the standard Superb Parrot nest tree data did not provide information relating to the merchantability of living trees, all nest trees identified by Webster (2002) were relocated. To make this assessment repeatable, only trees that did not obviously contain sawlog quality timber were designated as unmerchantable: all other trees were designated as merchantable.

Murrumbidgee River (80 m) were used for comparative purposes (Fig. 3). Spatial analysis was performed using ArcView™ software to generate measures of Superb Parrot occupation within each segment, and to assess whether the distribution of Superb Parrot nests within segments was related to the abundance of hollow-bearing trees and/or hollows using 10 metre intervals commencing from the riverbank.

No statistical analysis was conducted in view of the fact that the investigation was one of observational study rather than experimental design. From a management perspective, relative and absolute differences are also generally of greater importance that subtle statistical differences.

As a low occupancy rate may indicate that the hollow resource was in excess, or that only a small proportion of hollows was suitable for occupancy (Gibbons 1999), the developmental history of these stands was considered as part of the methodology. The year 1911 has been identified as the origin of extensive regeneration in riverine forests along the Murrumbidgee River, including Cuba State Forest (FCNSW 1986). However, the hollow resource was mostly contained within older cohorts whose original structure, as judged by the presence, size and age of stumps and the form of existing large trees, was more of an open woodland (pers. obs.). While forest management practices and wildfire have undoubtedly altered the abundance of these older trees, the real issue is whether they have persisted or not. Where they have persisted, age-related influences on the development of tree cavities (Gibbons and Lindenmayer 2002) can be viewed as a physiological constant. A main site variable (i.e. distance to the river edge) has also been controlled for in the spatial analysis. Hollow characteristics that may influence occupancy by Superb Parrots, such as depth, and minimum entrance and internal widths, are therefore likely to exist in similar proportions to the total hollow resource within each segment.

It follows that a case may be established to support the hypothesis that the population size of Superb Parrots in Cuba State Forest is limited by hollow availability if, relative to the total hollow resource, occupancy rates within different segments were consistently high, or at least relatively constant. An underlying assumption is that inter-specific competition for the hollow resource was uniform across similar parts of the State forest landscape.

FOOD AVAILABILITY

The hypothesis that food availability is a factor regulating the population size of Superb Parrots in Cuba State Forest was investigated by comparing measures of Superb Parrot occupation against the area of woodland vegetation adjacent to colonies 1, 2 and 3. A case to support this hypothesis may be established if a correlative relationship exists between measures of occupation and *extant* areas of woodland vegetation within the foraging range of Superb Parrots. A vegetation surrogate was used, as it is difficult to measure food availability directly. It was assumed that areas of high quality foraging habitat were patchily distributed and existed in proportion to the total area of woodland adjacent to each colony.

The hypothesis that colonies 1, 2 and 3 are located centrally relative to foraging areas, to minimize foraging travel distance and as a mechanism to partition resources between different breeding groups, was investigated by comparing the area of woodland vegetation adjacent to each colony. Given that Superb Parrots have traditional nest sites (NPWS 2000), a case to support this hypothesis may be established if the areas of woodland vegetation within the foraging range of Superb Parrots were similar *prior* to clearing.

Predicted (i.e. pre-clearing) and current distribution of woody vegetation in the vicinity of Cuba State Forest was incorporated into a GIS. Metadata was provided by the (then) NSW National Parks and Wildlife Service (Pre-1750 Forest Ecosystem, Western Subregion; Plains-wander Habitat Mapping) and condensed based on broad vegetation types classified by the (then) NSW Department of Land and Water Conservation.

ArcView™ software was used to determine the area and connectivity of woodland vegetation from the centre point of each colony segment to a distance of nine kilometres. A foraging range of five kilometres was also used to consider both hypotheses as it represents approximately half of the maximum distance that Superb Parrots have been observed to travel between their nests and foraging patches. Use of a central reference point recognizes that avian foraging distance is often correlated with food abundance and reproductive success (e.g. Bryant and Turner 1982; Kacelnick 1984; Smith and Bruun 2002). In particular, Stauss *et al.* (2005) found that the total foraging flight distance per breeding pair of Blue Tits *Parus caeruleus* in a good quality foraging habitat was about half of the distance observed in low quality foraging habitat.

Woodland patches included in the area calculation were separated by open spaces less than 500 metres wide, and contained one or more of the following species: Boree, Black Box, Western Grey Box, Yellow Box and White Cypress Pine. River Red Gum woodland was excluded as Superb Parrots rarely forage in this habitat type during the breeding season (pers. obs.).

RESULTS

Efficacy of harvest prescriptions

The results clearly showed that different harvest systems have the potential to impact differently on Superb Parrot nest trees (Table 2). A 20-metre exclusion zone adjacent to watercourses and water bodies was the single-most effective prescription to ensure the retention of a large proportion (60%) of Superb Parrot nest trees in Cuba State Forest. Retaining all unmerchantable trees protected a further 19 per cent, living trees (dbhob >150 cm) 16 per cent, and dead trees 2.5 per cent.

Only three per cent of all known nest trees in Cuba State Forest were considered to be at risk using Harvest System #1, which was based solely on STS silviculture, because only two nest trees contained sawlog-quality timber that were not protected by other prescriptions. Harvest systems involving both STS and AGS posed a greater threat to nest

TABLE 2

Number of Superb Parrot nest trees (n = 81) afforded protection and at risk under different harvest systems. NB. While some trees qualified for protection under more than one prescription, the results are non-additive.

Prescription	Harvest system #1	Harvest system #2	Harvest system #3
1. Habitat corridor (0–20 m zone only)	49	49	49
2. Upper diameter felling limit	13	–[1]	13
3. Stag retention	2	2	2
4. Merchantability	15	–[1]	10
Number of nest trees at risk[2]	2	30	7

[1]The risk to known nest trees could not be assessed as AGS openings were not able to be marked in the field.
[2]The risk calculation does not take into account the contribution of habitat trees.

trees. In particular, 30 nest trees (37%) were at risk of being felled using Harvest System #2. However, Harvest System #3, which removed uncertainty in the 20–50 metre zone of habitat corridors and retained all trees greater than 150 centimetres dbhob, brought about a fourfold reduction to the risk calculation, to only seven nest trees (9%).

Synthesis of spatial information

THE HOLLOW RESOURCE

A total of 318 hollow-bearing trees were recorded within the three segments, containing 778 visible hollows (Table 3). The abundance of hollow-bearing trees in each segment was within the range expected in undisturbed temperate woodlands (7–17 hollow-bearing trees/ha; Gibbons and Lindenmayer 2002) despite Cuba State Forest having a long management history. Around 12 per cent of hollow-bearing trees and 6 per cent of visible hollows contained Superb Parrot nests. Living hollow-bearing trees provided the bulk of the hollow resource (>90%), and all data were subsequently pooled to contain both living and dead trees.

Measures of Superb Parrot occupation differed greatly between segments. Importantly, all occupation measures in segment 1 (4.5 nests/ha; 19.5% of hollow-bearing trees contained nests; 10.4% of visible hollows contained nests) were much higher than in segment 3 (1.8; 7.9; 3.4), despite segment 3 containing around 25 per cent more hollow-bearing trees and visible hollows than segment 1. Notwithstanding the comparatively low abundance of hollow-bearing trees and hollows in segment 2, occupation measures within this segment were also disproportionately smaller.

Such a disparity in the level of hollow occupation suggests that, at the very least, hollow availability is not limiting the number of Superb Parrot nesting within colonies 2 and 3. To illustrate this assertion, on a proportional basis and all other things being equal, the number of nests in segment 3 could increase threefold (i.e. 24 additional breeding pairs) before the hollow occupancy rate equals that evident in segment 1. The hypothesis that the size of the breeding population of Superb Parrots in Cuba State Forest is limited by hollow availability is therefore not supported by the available information.

With the exception of the 0–20 metre zone in segment 3, the distribution of hollow-bearing trees and hollows within each of the segments was relatively uniform with respect to distance from the river (Figs 4a and 4b respectively). However, the density of Superb Parrot nests in segments 1 and 3 was highly skewed, with the average density of nests in the 0–30 metre zone of these segments being three times greater than in the 30–80 metre zone (Fig. 4c). Despite this observation, the proportion of hollows occupied by Superb Parrots showed no consistent trend within any of the segments (Fig. 4d). The fact that nest placement was skewed towards the edge of the river independently of hollow abundance indicated that Superb Parrots did not occupy hollows at random within colonies.

FORAGING PATCH SIZE

All measures of Superb Parrot occupation were positively correlated with the area of extant woodland vegetation within five kilometres of colonies (Fig. 5). This trend also existed for all measures of occupation up to a foraging range of nine kilometres. The available information therefore supports the hypothesis that food availability is a factor regulating the population size of Superb Parrots in Cuba State Forest.

The original and extant woodland area increased more-or-less linearly with increasing distance from each colony (Fig. 6). Some overlap existed in the area of woodland vegetation before and after clearing up to a distance of five kilometres from each colony. However, at distances greater than five kilometres, the area of original woodland vegetation exceeded that currently available to any of the colonies. Mainly as a result of disproportionately higher levels of clearing within five kilometres of colonies 2 (71% of the original cover cleared) and 3 (75%) than colony 1 (37%), more than 2 000 hectares of woodland vegetation has been retained within five kilometres of colony 1 only.

A conclusion from these data could be that prior to clearing, colonies were centrally located around foraging patches of about 2 000 hectares. The hypothesis that Superb Parrot colonies are spaced to partition resources between different breeding groups may, therefore, have some foundation.

TABLE 3

Raw data and measures of Superb Parrot occupation within 6.5 hectare segments of colonies 1–3.

	(Row)	Colony 1	Colony 2	Colony 3
Raw data				
Segment area (ha)	...(1)	6.5	6.5	6.5
Number of Superb Parrot nest trees	...(2)	22	2	11
Number of Superb Parrot nests	...(3)	29	3	12
Number of hollow-bearing trees	...(4)	113	65	140
Number of hollows	...(5)	279	141	358
Measures of occupation				
Number of Superb Parrot nests per ha[1]		4.5	0.5	1.8
Proportion of hollow-bearing trees containing nests (%)[2]		19.5	3.1	7.9
Proportion of hollows containing Superb Parrot nests (%)[3]		10.4	2.1	3.4

[1]Row 3 divided by row 1
[2]Row 2 divided by row 4 × 100
[3]Row 3 divided by row 5 × 100

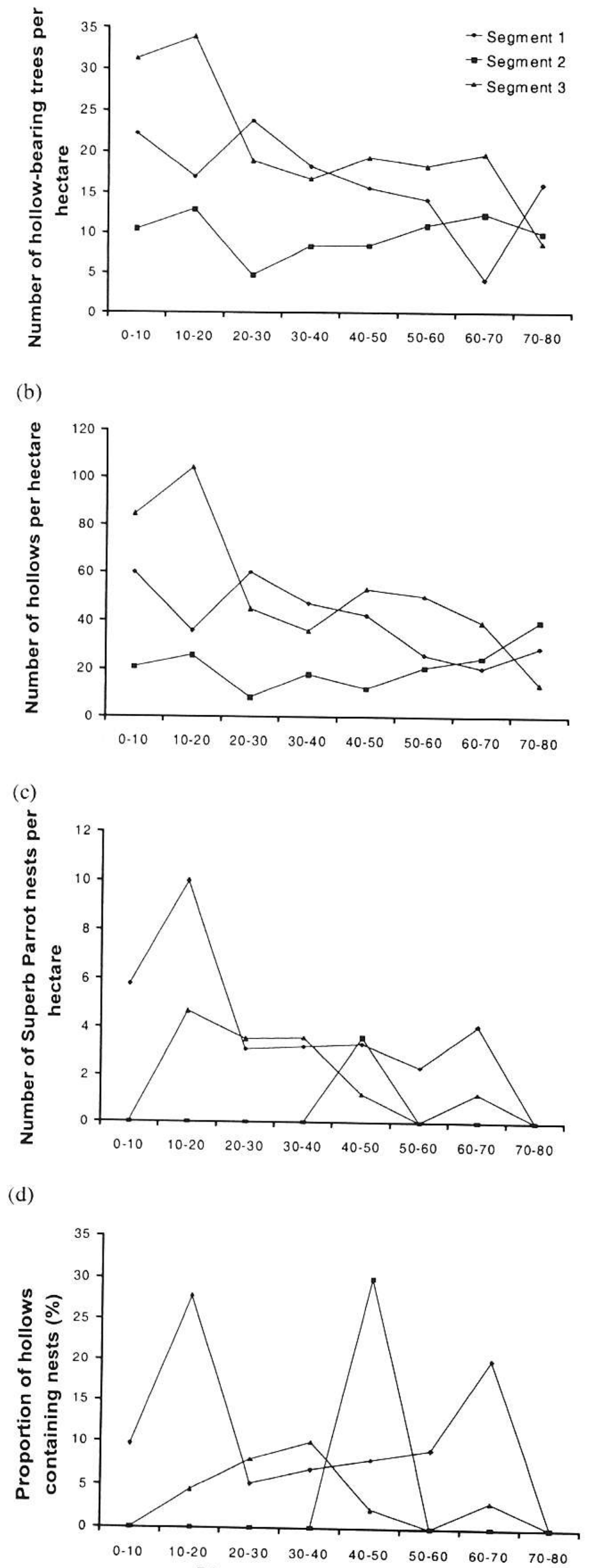

Figure 4. Distribution of hollow-bearing trees within each segment from the Murrumbidgee River.

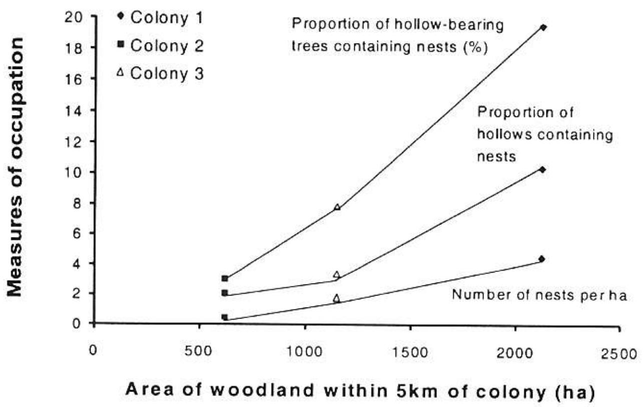

Figure 5. Relationship between area of woodland within five kilometres of colonies and measures of Superb Parrot occupation (refer to Table 3 for calculation method).

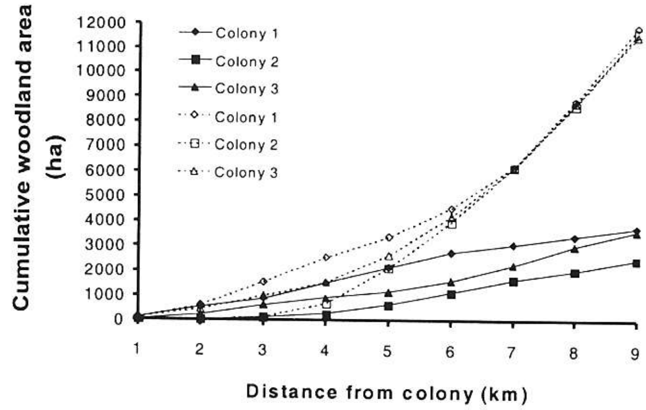

Figure 6. *Cumulative woodland area adjacent to colonies 1–3. Dashed lines show pre-clearing vegetation; solid lines show current vegetation.*

DISCUSSION

River Red Gum harvest practices

In this study, physical and spatial characteristics of Superb Parrot nest trees were used to assess the efficacy of different timber harvest systems in conserving the hollow resource upon which this species depends. The harvest prescriptions were repeatable and therefore quantitative. Such an approach to hollow assessment is unusual in Australia, as methods typically employed by researchers estimate the demand placed on the hollow resource by all species in order to establish habitat tree retention rates (e.g. Smith 1994; Lamb *et al.* 1998). In other words, the approach used in this study provides a measure of the condition of the hollow resource, rather than a resource condition target.

Timber harvesting was shown to be capable of removing a variable proportion of Superb Parrot nest trees in Cuba State Forest. Nevertheless, the current breeding population does not appear to be constrained by harvest practices spanning greater than a 100 years, as the existing hollow resource could potentially support a much larger number of breeding pairs. This augers well for the sustainability of the River Red Gum timber industry.

However, future harvest practices must continue to include prescriptions to perpetuate the hollow resource. Excluding harvesting in a 20 metre riparian zone was shown to be the single-most effective prescription to ensure the retention of a large proportion Superb Parrot nest trees, as most nest trees (60%) are located within 20 metres of watercourses and water bodies. Retaining large trees, as well as trees with no sawlog value, within areas available for harvesting also made sizeable contributions.

The presence of large hollows in the main stem or branches of a River Red Gum reliably indicates the existence of internal timber defects, which usually renders the tree of relatively little or no value for sawlog production. Not surprisingly, the results show there is minimal risk to Superb Parrot nest trees using STS silviculture as the characteristics of a good timber tree are generally opposite to those of a good habitat tree. Such an outcome highlights that prescriptions designed to retain hollow-bearing trees are not an essential facet of STS silviculture. Conversely, as most trees desirable for harvesting in River Red Gum forests will eventually contain hollows suitable for occupancy by Superb Parrots, the stability or persistence of breeding populations could be compromised if formal provisions did not exist to recruit hollow-bearing trees through time and space. Accordingly, careful attention must be given in STS silviculture to retain trees that are best able to develop hollows during the next 1–2 cutting cycles (one cutting cycle is nominally 20–25 years).

Australian Group Selection silviculture has the potential to significantly deplete the hollow resource because all trees within an AGS opening are felled. However, by restricting the location of AGS openings to areas where only a small proportion of Superb Parrot nests occur (i.e. stands located more than 50 m from the first tree line adjacent to watercourses and water bodies), the risk imposed by AGS silviculture on Superb Parrot nest trees is likely to approach that of STS.

In order to achieve the habitat and recruit tree retention targets in stands subject to AGS silviculture, 10–20 per cent of the harvestable area needs to be excluded from AGS silviculture over the length of at least two rotations (one rotation is nominally 100 years). This measure not only provides sufficient growing space for retained habitat and recruit trees, but also sufficient time for recruit trees to develop hollows. Prescriptions that retain hollow-bearing trees *and* provide for their recruitment are therefore essential facets of AGS silviculture.

It is important to understand that this study calculated the risk to Superb Parrot nest trees imposed by harvest systems at a temporal scale of a cutting cycle and a spatial scale of a timber catchment. That is, the risk cannot be viewed as an annual impact within individual harvesting areas. For example, under Harvest System #3, and not taking into account the standard habitat tree retention requirements, seven Superb Parrot nest trees within Cuba State Forest would potentially be placed at risk by timber harvesting over a period of 20–25 years, or approximately one nest tree on average every three years. The presence of hollows in excess of current demand, as well as the development of hollows suitable for occupancy through the same period of time, offset such a loss to the nest tree resource. While it was outside the scope of this paper to quantify the rate of development and loss of hollows through natural processes, recruitment of suitable nest hollows for Superb Parrots could exceed losses from harvesting at a rate of 2.1×10^{-4} per hectare per year (i.e. seven nests at risk in a period of 20 years, over an area of 1 660 hectares).

Spatial organization of Superb Parrot nest trees

This study found evidence of intra-population variation in the level of hollow occupation by Superb Parrots at colony and landscape scales. Importantly, no measure of occupation was obviously related to the abundance of hollow-bearing trees or hollows. Rather, the distribution of colonies and the density of nests within colonies appeared to be associated with the area of woodland within the foraging range of parents. Food availability is therefore likely to be a factor regulating the population size of Superb Parrots in Cuba State Forest.

INTRA-COLONY VARIATION

The distribution of nest trees within high-use colonies was skewed towards the edge of the Murrumbidgee River. This observation may possibly be explained by habitat and/ or social considerations.

Soil water availability has a pronounced affect on the growth of River Red Gum (Bacon *et al.* 1993). It is plausible that the larger trunk and crown dimensions attained by trees growing close to watercourses produce internal hollow characteristics that best match the occupancy requirements of Superb Parrots. Such affects on tree (and thus hollow) development could be expected to decrease with increasing distance from a permanent water source (Bacon *et al.* 1993).

Superb Parrots do not defend large territories around their nest (pers. obs.), possibly because their nesting and foraging habitats do not coincide (see von Haartman 1957). Instead, only their nest hollow and its immediate vicinity are defended against competitors (pers. obs.). As a consequence, trees with large crowns and numerous hollows are able to support more than one Superb Parrot nest, and nests of other hollow-dependent avifauna including Yellow Rosella *Platycercus elegans flaveolus*, Sulphur-crested Cockatoo *Cacatua galerita*, Long-billed Corella *C. tenuirostris* (pers. obs.), and Sacred Kingfisher *Todiramphus sancta* (D. Parker, pers. comm.).

However, there is likely to be a level of hollow occupancy above which intra- and inter-specific competition for hollows results in less preferred habitat being utilized. Agonistic interactions between male conspecifics (and between Superb Parrots and Yellow Rosellas) are commonly observed when female Superb Parrots are selecting a hollow (pers. obs.). In this way, superior competitors could be expected to occupy high quality nesting habitat and displace late or inexperienced breeders to inferior habitat located on the edges of the colony, or to a different colony altogether. For example, Moller (1995) showed that despotic territorial behaviour in blackbirds maintained a population distribution in which superior competitors excluded conspecifics from preferred habitat, and thereby achieved higher reproductive success.

Inter-colony variation

As imposition on the energy budget of breeding birds can have a major bearing on the number and quality of offspring, variation in intra-population reproductive success is commonly the result of adults matching their clutch or brood size to their individual foraging efficiency (e.g. Masman *et al.* 1989; Moreno *et al.* 1997; Tinbergen and Verhulst 2000; Burness *et al.* 2001; Przybylo *et al.* 2001; Takagi 2002; Stauss *et al.* 2005).

Regular flight has been estimated to elevate avian energy expenditure by at least ten times basal metabolic rate (e.g. Nudds and Bryant 2000). Considerable potential therefore exists to achieve energy efficiencies and reproductive advantages by commuting short distances to feed in areas where gross foraging efficiency is high. Parents travelling large distances to obtain food, or having greater search or foraging times to gather the same net energy, not only require higher inputs to meet their own energy demand, but they may also expose their chicks to a restriction in energy content and/or nutritional quality of their food. Brood size consequently diminishes if underfed chicks die from passive starvation or siblicide: malnourished fledglings are also less likely to recruit into the breeding population (e.g. Tinbergen and Boerlijst 1990).

As birds are expected to distribute themselves in heterogeneous landscapes in relation to resource availability (Bernstein *et al.* 1991), the number of breeding pairs in a colony can be a reliable indicator of habitat quality and hence reproductive success. For example, Smith and Bruun (2002) showed that colony size and nestling survival of European Starlings *Sturnus vulgaris* was positively related to the area of pasture close to breeding colonies. Furthermore, after considering the parental foraging effort (costs) of Blue Tits and the quality and number their offspring (benefits), Stauss *et al.* (2005) calculated the benefit-cost-ratio was two to three times higher in the high quality than in the low quality foraging habitat.

It is therefore reasonable to speculate that the level of hollow occupation evident in colony 1 is not only associated with the area of adjacent woodland but also with high reproductive success. As a consequence, intra-specific competition for nest hollows is likely to take place within (and adjacent to) that colony, yet its spatial coverage was limited to a single bend in the river.

A simple interpretation of the colonial nest dispersion of Superb Parrots is that nest sites are clustered because tree hollows also have a clustered distribution. However, hollow-bearing trees are more-or-less continuously distributed along the banks of the Murrumbidgee River as well as interior portions of Cuba State Forest (pers. obs.), and yet Superb Parrot nests are not equally dispersed throughout the hollow resource. Nest-site limitation alone is therefore unlikely to induce coloniality in Superb Parrots.

The results indicate that the distribution of colonies may be an artefact of the pre-clearing woodland assemblage, whereby colonies were spaced to minimize inter-group competition for food. As Superb Parrots are not territorial on their foraging ground (pers. obs.), the foraging range of different breeding groups may overlap, but birds within nearby nest sites could be expected to exploit adjacent food resources more efficiently. At a colony scale, the density of nests may be a reflection of competition factors driven, in the first instance, by the area of nearby foraging patches, then subsequently by the availability of nest hollows that become less suitable for occupation by Superb Parrots with increasing distance from a permanent water source.

Paradoxically, in the absence of competition for hollows, nest site fidelity may mean that Superb Parrots continue to utilize traditional breeding sites where their reproductive performance may no longer be optimal due to habitat loss or degradation. The present day distribution of nests may therefore not accurately reflect optimum habitat requirements, but be more about historical landscape factors that no longer exist. Population density, as an indicator of habitat quality, should therefore be accompanied by information on reproductive success (Godfrey 2003).

A CONCEPTUAL MODEL

Beyond a certain density level, the benefits to individuals of co-operative nesting and foraging increase at a diminishing rate compared to the cost of intra-group competition (Zemel and Lubin 1995). Furthermore, to maintain a stable group size where fecundity regularly exceeds mortality, excess individuals must leave the group, and consequently they may disperse to lower quality habitats where their reproductive success is diminished (Martin 1995).

I postulate that the number of breeding pairs in a Superb Parrot colony is a manifestation of the delicate balance between the benefits of co-operation, such as predator avoidance and information sharing, and intra-group competition for nest hollows and food. Metapopulation stability may occur through differential reproductive success and dispersal between colonies. I also predict that flight energetic costs have major implications for the foraging behaviour and reproductive success of Superb Parrots. Understanding this complex picture requires further reasoning supported by ecological research and physiological evidence.

Recovery planning

A universal recovery objective for threatened species is to increase the abundance and distribution of wild populations across their natural range (e.g. NPWS 2002, 2003). Recovery actions require knowledge of species ecology, threats, effectiveness of abatement measures and recovery timeframes. Given that the basic population demography of Superb Parrots is poorly known, including age-sex structure, mortality, fecundity and dispersal, there is an obvious need to improve the knowledge base before threats and recovery actions can be confidently identified. Little information also exists in the literature regarding benefits of the communal foraging and nesting strategies employed by Superb Parrots.

As the greatest proportional mortality in many birds occurs in their first year of life (Lack 1954), addressing pre-recruit mortality is an obvious recovery priority for Superb Parrots. But should recovery actions aim to improve the survival of nestlings or older young?

Immediately after fledging, young birds and their attendant parents commonly form large cohesive flocks (or crèches) in woodlands located beyond the foraging range of parents during the breeding season. Soon after young reach independence, smaller groups disperse over a wide geographic area (R. Webster, pers. comm.; pers. obs.). Consequently, mortality among juveniles arising from a lack of proficiency in behavioural skills, such as foraging, avoiding predators and interacting with competitors, is independent of the location of their natal area. The strength of the next generation could, therefore, be most sensitive to mortality during the early stages of life.

Consequently, a research priority should be to more fully investigate the strength of the relationship between Superb Parrot reproductive success and the area, condition and connectivity of adjacent woodland. Should a causative relationship be confidently established, recovery actions clearly need to focus on managing woodland vegetation adjacent to *existing colonies with low occupation levels*. This assertion is based on the premises that: (i) Superb Parrots have limited capacity, compared to other Psittaciformes, to extend their distribution into new nesting habitat (possibly because Superb Parrots faithfully return to their natal area to breed, and may have difficulty perceiving habitat quality); (ii) that hollows are unlikely to be limiting where occupation levels are low (because population density may be related to food resource availability where hollows are not limiting), and; (iii) new plantings would become functional for commuting and foraging well before the generation time of new tree hollows (e.g. three year-old *Acacia* spp. produce seeds that are consumed by Superb Parrots).

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