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Koalas continue to occupy their previous home-ranges after selective logging in *Callitris–Eucalyptus* forest

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Abstract. The koala (*Phascolarctos cinereus*) is a charismatic, high-profile species whose conservation needs are commonly perceived to be incompatible with logging. However, koala biology and the results of chronosequence studies elsewhere suggest that this species may tolerate a degree of habitat alteration caused by logging. In this study, 30 koalas, five in each of six areas available for logging within a mixed white cypress pine (*Callitris glaucophylla*)–*Eucalyptus* forest in north-western New South Wales, were radio-tracked for one year during 1997–1998 to determine their movements, home-range sizes and tree preferences. Five months after the study began, three of these areas were logged selectively for sawlogs and thinnings of the white cypress pine, a tree that is important to koalas for daytime shelter. This removed about one-quarter of the stand basal area, but the eucalypt component was unaffected. The remaining three areas were left undisturbed as controls. Radio-tracking continued in all six areas for another seven months. Koalas continued to occupy all or part of their previous home-ranges after selective logging, and home-range sizes remained similar between logged and unlogged areas. Home-ranges for both sexes overlapped and were ~12 ha for males and 9 ha for females. Koala survival and the proportions of breeding females were similar in logged and unlogged areas. The principal food trees of the koala were red gums, mainly *Eucalyptus blakelyi* and *E. chloroclada*, and the pilliga box (*E. pilligaensis*), none of which were logged in this study. These results suggest that selective logging for white cypress pine does not appear to adversely affect koala populations and that koalas may not be as sensitive to logging as previously thought. Further work is required to determine thresholds in the level of retention of koala food trees in logging operations.

Introduction

Habitat loss is recognised as the key problem for long-term survival of the koala (*Phascolarctos cinereus*) in New South Wales (Reed and Lunney 1990; Reed *et al*. 1990; Lunney *et al*. 2000). However, logging has sometimes been grouped with forest clearing for agricultural and urban developments as processes threatening the koala. It could be argued that the koala is unlikely to display the same sensitivity to logging as most other arboreal marsupials because it does not require cavities within old trees for breeding and diurnal shelter (Martin and Handasyde 1995; Gibbons and Lindenmayer 2002). However, the issue has been difficult to resolve because there have been no experimental studies of the effects of logging on koalas.

Correlative studies have been interpreted to suggest that logging may either improve or reduce the quality of habitat for koalas, depending on the silvicultural practice and the structural characteristics of the forest after logging. For example, on the north coast of New South Wales, koalas were sparse or absent in young, single-species eucalypt plantations established after clearfelling, but were most abundant in uneven-aged forests comprising several favoured food tree species that had been subject to a long history of selective logging (Smith 2004). This pattern of logging resulted in a multi-layered forest structure with young, mature and some older-aged trees. Also in north-eastern New South Wales, koalas were recorded most frequently in forests that had been selectively logged several times previously, although not recently, and in older-aged mixed-species eucalypt plantations (Kavanagh *et al*. 1995). Elsewhere, a radio-tracking study near Eden on the south coast of New South Wales found that koalas commonly used logged areas within a mosaic of logged and unlogged forest (Jurskis *et al*. 1994; Jurskis and Potter 1997). However, all of these studies were limited by a lack of knowledge about the prelogging condition of the forest at each location and its associated fauna.

The extensive forests of the Pilliga region in north-western New South Wales contain a large and previously unstudied population of koalas, many of which live in forests long used for wood production (Rolls 1981; van Kempen 1997; Kavanagh and Barrott 2001). In this study, we posed the hypothesis that, in the short term (one year), selective logging does not adversely affect the conservation of koalas in the Pilliga forests. We examined this hypothesis in terms of koala survival and fecundity, home-range size and fidelity, movements and tree preferences in a planned logging experiment that incorporated a before-after-control-impact design, with replication.

Materials and methods

Study area

The Pilliga forests (535 000 ha) stretch across the flat, sandy plains and low hills between the Warrumbungle Mountains (near Coonabarabran) and Narrabri, representing the single largest chunk of inland plains forest in Australia (30°45′S,

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149°07′E) (Fig. 1). At the time of this study, ~390 000 ha was managed as State Forest, 75 000 ha as the Pilliga Nature Reserve, and 70 000 ha was freehold and vacant crown land (Anon. 1986). Recent changes in land tenure have greatly increased the area allocated to nature conservation (~232 000 ha) compared with that available for timber production (~233 000 ha). Baradine (~510 km north-west of Sydney), is the closest population centre to the forest. The climate is hot and dry with a mean daily maximum temperature of 33.2°C in January and mean daily minimum of 2.1°C in July (Commonwealth Bureau of Meteorology for Baradine 1944–96). On average, temperatures of 40°C or more can be expected on 1.7 days per year. Mean annual rainfall at Baradine is 633 mm (during 1944–98), with rain spread fairly evenly throughout the year and a slightly wetter summer. The study was conducted during the third wettest year on record (1998; 972 mm), and rainfall during the three previous years was above average. Nonetheless, hot dry conditions were experienced during the first half of the study, with temperatures exceeding 40°C (up to 46°C) on at least 12 days during fieldwork in the study areas. Creek lines are dry sandbeds that flow only during prolonged heavy rain, and this occurred several times during July–September 1998.

The predominant vegetation type in the study areas, and throughout most of the Pilliga, is a mixture of white cypress pine (*Callitris glaucophylla*) and several eucalypt species including, variously, red gums (mainly Blakely's red gum (*Eucalyptus blakelyi*) and dirty gum (*E. chloroclada*), but also river red gum (*E. camaldulensis*)), the endemic pilliga box (*E. pilligaensis*), narrow-leaved ironbark (*E. crebra*), poplar box (*E. populnea*) and, less commonly, western grey box (*E. microcarpa*), yellow box (*E. melliodora*), white box (*E. albens*) and silver-leaved ironbark (*E. melanophloia*). The rough-barked apple (*Angophora floribunda*) is commonly found near creek lines, and bull oak (*Allocasuarina luehmannii*) is widespread.

The Pilliga forests have had a long history of anthropogenic disturbance. Controversy exists about the nature of the pre-European vegetation of the region (Rolls 1981; Norris *et al*. 1991; Benson and Redpath 1997; Lunt *et al*. 2006), although parts of the area were certainly burnt regularly by the indigenous people creating a grassy, open forest structure. Europeans arrived in the 1830s and cleared many areas for sheep and cattle grazing, particularly in the western half of the Pilliga. The combination of low stock-carrying capacity of the pasture, the lack of reliable surface water and drought caused many farmers to abandon their properties in the late 1870s. The subsequent reduced grazing pressure, infrequent burning regime, and several wet years resulted in dense regeneration of the native white cypress pine in many areas by the early 1890s (Rolls 1981; Anon. 1986; Norris *et al*. 1991; Van Kempen 1997; Lunt *et al*. 2006). Thinning of cypress pine regeneration and associated culling of competing eucalypts began in 1930 and continued until the early 1980s. Harvesting of ironbarks for sawlogs and railway sleepers has continued for the past 100 years. The stand structure in all study areas displayed evidence of major disturbance ~50 years ago (or longer) when regenerating stands of white cypress pine were thinned and many eucalypts were ringbarked or logged.

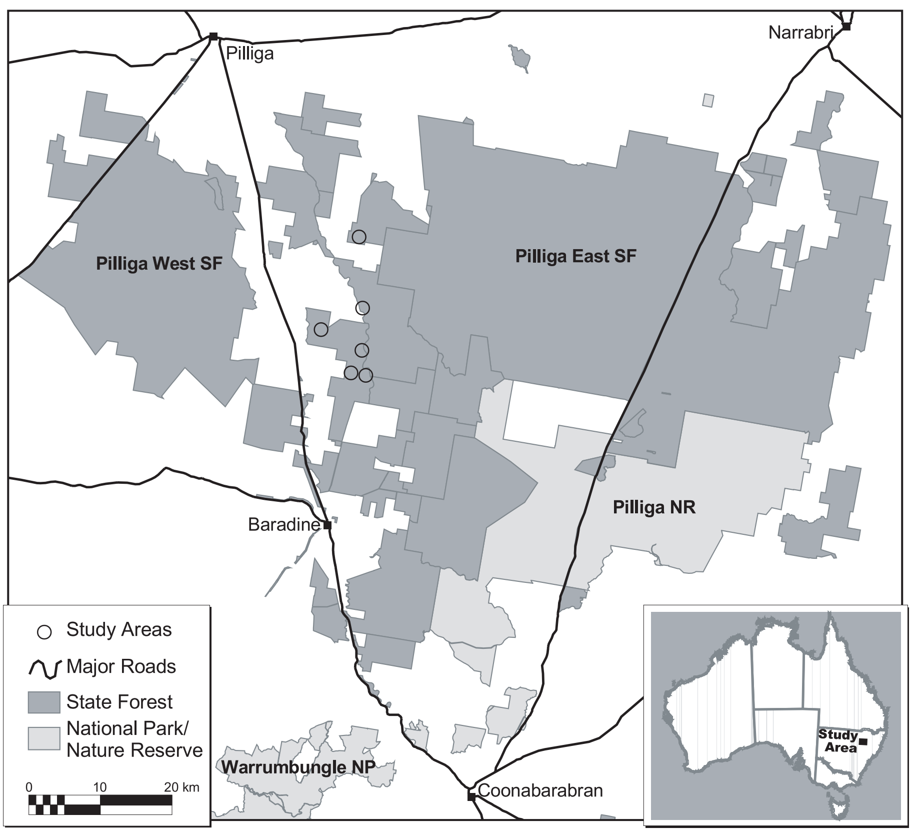

Fig. 1. Location of the six study areas in the Pilliga forests of north-western New South Wales.

Experimental design

Six study areas were identified, each of which was at least 2 km apart and scheduled for commercial thinning or final cutting of the white cypress pine component of the stand (Fig. 1). The study areas were located on the western edge of the Central Pilliga near Kenebri and Gwabegar in Cumbil State Forest (Compartments 211, 208, 206 and 201), Euligal State Forest (Compartment 196) and Cubbo State Forest (Compartment 181) within the Cumbil Forest Creek, Etoo Creek and Tinegie Creek drainage systems.

Thirty koalas, five in each of the six areas, were captured in October 1997, tagged and radio-tracked for a year to determine their movements, home-range sizes and tree preferences. Four to six months after the study began (February to April 1998), three of these areas (Compartments 208, 201 and 196) were logged selectively for white cypress pine sawlogs and thinnings, but the *Eucalyptus* component of the stands was not logged. The remaining three areas (Compartments 211, 206 and 181) were left undisturbed as controls. Animals were recaptured in October 1998 to remove the radio-collars and then released.

Logged study areas were subject to the standard harvesting (conservation) protocols as used in white cypress pine logging operations in the Pilliga. That is, 30-m-wide strips of forest either side of creeklines were excluded from logging, and small clumps of trees (including white cypress pine) centred around observed 'high-use' koala trees (>50 faecal pellets) were retained. The harvesting protocols were applied 'blind' by persons who had no knowledge of the trees used by koalas during the first half of the study.

Characteristics of the vegetation before and after logging were assessed on (usually) three (range 1–4) 0.1-ha (20×50 m) plots ($n = 80$) located randomly in each animal's home-range. This ensured that ~14 (range 11–15) vegetation plots were measured on each compartment. Counts were made of all trees and shrubs taller than 3 m and their diameters were measured. This resulted in data being collected for 9118 trees before logging and 8036 trees after logging on all vegetation plots. Also recorded were the numbers of old and new cut stumps and the numbers of stems of two species of introduced cacti, prickly pear (*Opuntia stricta*) and tiger pear (*O. aurantiaca*).

Sampling procedure

Koalas were radio-tracked daily, or at least 1–2 times per week, throughout the study. All tracking was confined to daylight hours because the (eucalypt) trees occupied by koalas during the day are known to provide a useful indicator of the trees in which koalas feed at night, either during the previous morning or the following evening (Robbins and Russell 1978; Lithgow 1980; Hindell *et al*. 1985; Melzer 1995; Pieters and Woodall 1996; Ellis *et al*. 2002). Each record consisted of tree details (location, species, diameter, height, crown width, crown condition, pellet count), site details (presence of other tree species, presence of cacti, logging treatment), koala attributes (activity, health, proximity to other individuals) and weather (wind, rain and temperature) at the time of sampling.

Exact locations of all trees used by koalas were obtained using an AUSNAV™ real-time differential Global Positioning System in conjunction with a Garmin™ 2+ unit with data averaging (reported to be accurate to within 1–5 m).

Analysis

The home-range areas of koalas were calculated using the fixed kernel (95%) and adaptive kernel (95%) methods of Worton (1989) and the minimum convex polygon (100%) method of Mohr (1947). The adaptive kernel (AK) and minimum convex polygon (MCP) methods were calculated using the CALHOME software program (Kie *et al*. 1994) and the fixed kernel (FK) method was calculated using the Animal Movement Extension available in Arcview ver. 3.2 (Hooge and Eichenlaub 1997). CALHOME has received favourable review, compared with other software programs, for its implementation of the AK and MCP methods (Larkin and Halkin 1994; Lawson and Rogers 1997). Home-range calculations using the AK method employed the 50×50 grid cell option and the default bandwidth (smoothing parameter) selected by the program. The FK method used a grid size of at least 300×300 cells and the minimum value for least-squares cross-validation as the smoothing factor. In this study, the AK method resulted in consistently larger home-range estimates for animals than the FK method, due to the inclusion of larger amounts of unused area around animal locations. In contrast, the FK method tended to give a better estimate of the size of animal activity areas but these were often unconnected. In their tests, Seaman and Powell (1996) found that the FK method was always more accurate and reliable than the AK method. The MCP method is the simplest and most frequently used home-range estimator, providing a useful comparison between studies (Harris *et al*. 1990). Accordingly, we based our analyses on the results of the FK and the MCP methods, opting to present a summary only for the AK method for comparison with other studies.

Home-range estimates tend to increase initially and then reach a plateau or decrease with increasing sample size (Harris *et al*. 1990). Asymptotes (i.e. the number of samples required to make a reliable estimate of animal home ranges) were calculated for each animal by plotting the FK95% home range as a function of increasing sample size. This was done using the bootstrap method in Arcview to randomly draw (with replacement) subsets of data in multiples of 10 samples. The process was repeated 25 times for each animal. These data showed that FK95% home-range asymptotes for nearly all animals were reached within 10–50 samples. The median sample size for all animals in this study was 88 locations, indicating the reliability of home-range estimates.

The extent to which koalas shifted their apparent home ranges as a response to logging (or season of the year) was determined for each animal by calculating the area (ha) of overlap in FK95% home ranges between the two periods October–February and March–October and expressing this as a percentage of the area used in October–February (i.e. prelogging).

Differences in sizes of koala home range between treatments, seasons and sexes were determined using the Wilcoxon (Mann–Whitney) rank sum (two-sample) test ($\alpha = 0.05$) with continuity correction of 0.5 in SAS ver. 9.1. Contingency Chi-square tests were used to assess tree species and tree size preferences of koalas in relation to tree availability, represented respectively as either tree species basal area or as basal area in different-diameter size-classes (indices of foliage biomass), within the vegetation plots located randomly in each animal's home range. Selection for, or avoidance of, particular tree species by koalas was determined by iteratively deleting species (or tree size-classes) having the greatest contribution to total Chi-square until $P > 0.1$. For compartments selectively logged during the study, tree use by koalas was analysed in relation to the mean basal area of trees before and after logging. The abundance of only one tree species, white cypress pine, was altered significantly as a result of logging.

Results

Changes in forest structure and floristics after logging

White cypress pine represented, on average, nearly half of the tree basal area of the forest in the study areas, with eucalypts comprising most of the remainder (Table 1). The dominant eucalypts in the association were, variously, the locally endemic pilliga box, the narrow-leaved ironbark, and one or more species within the red gum group. The poplar box was common in some areas. The main non-eucalypt component of these forests was the localised rough-barked apple, and the bull oak, which was widespread in all study areas.

After logging there was, on average, ~25% reduction in tree basal area on the logged plots (27.2% reduction on Compartment 208, 24.9% on Compartment 196, 21.1% on Compartment 201), nearly all of which occurred within the 20–40-cm-diameter (at breast height) size class of white cypress pine (Fig. 2). No eucalypts or other tree species were logged during the study; however, some incidental loss of smaller trees occurred during logging operations. The basal area reduction for white cypress pine was 40.5%, 36.7% and 34.0% on Compartments 208, 196 and 201, respectively.

Tree preferences

Koalas were observed on 2254 occasions during the radio-tracking study. Of these observations, 705 (31.3%) occurred in white cypress pine, 633 (28.1%) in pilliga box, 244 (10.8%) in narrow-leaved ironbark, 240 (10.7%) in two similar red gums (mainly *E. blakelyi* and *E. chloroclada*), 87 (3.9%) in a third species within the red gum group, *E. camaldulensis*, 116 (5.1%) in rough-barked apple, 87 (3.9%) in poplar box, 29 (1.3%) in bull oak, 23 (1.0%) in western grey box, 14 (0.6%) in each of yellow box and white box, 13 (0.6%) in silver-leaved ironbark, 5 (0.2%) in other eucalypts (*E. sideroxylon*, and hybrids of both *E. crebra* and *E. populnea*), 4 (0.2%) in dead trees, 11 (0.5%) in other trees and tall shrubs (including *Brachychiton populneus* and *Geijera parviflora*), and 29 (1.3%) records on the ground, either sheltering in a hollow log, stump or burrow (23), or among low and fallen vegetation (6).

Individually, most koalas displayed their strongest preferences for occupying pilliga box and the red gums (2–3 species), and one or more of these species was present in every animal's home-range (Table 2). Pilliga box was always preferred by koalas or used in proportion to its availability. Red gums were 'avoided' by only one individual, and this was due to extensive use of pilliga box within this animal's home-range (Table 2). Other boxes (i.e. poplar box, western grey box, yellow box and white box) were used in proportion to their availability by all animals. The rough-barked apple was also often preferred by koalas or used in proportion to its availability. The two ironbarks (narrow-leaved and silver-leaved), although preferred in two home-ranges, were generally used in proportion to their availability and were more likely to be avoided by koalas (in the pres-

Table 1. Tree use by koalas, and the mean basal area of each tree species in the study areas

Species	No. of koala observations	Mean tree basal area (m^2 ha^{-1}) Control blocks	Treatment blocks Before logging	Treatment blocks After logging
White cypress pine, *Callitris glaucophylla*	705	9.94	9.64	5.84
Pilliga box, *Eucalyptus pilligaensis*	633	2.27	4.07	3.91
Red gums		2.28	1.12	0.98
E. blakelyi	240			
E. chloroclada	–			
E. camaldulensis	87			
Ironbarks		2.59	2.98	2.87
E. crebra	244			
E. melanophloia	13			
Rough-barked apple, *Angophora floribunda*	116	1.16	0.28	0.28
Other boxes		0.72	0.81	0.84
E. populnea	87			
E. microcarpa	23			
E. melliodora	14			
E. albens	14			
Bull oak, *Allocasuarina luehmannii*	29	3.23	0.76	0.58
Other eucalypts	5	0.11	0.51	0.44
Tall shrubs	11			
Stumps	0	7.44	8.67	10.23
Dead trees	4			
On ground / in logs, etc	29	–	–	–
Total	2254			
Mean basal area (m^2 ha^{-1}) live trees		22.19	19.66	15.30
Total basal area (m^2 ha^{-1}) including stumps, dead trees		29.74	28.84	25.97

ence of pilliga box and/or the red gums) than preferred (Table 2). Compared with most other tree species, the white cypress pine was avoided by koalas. However, this tree species was used extensively by koalas for daytime shelter, and its lack of 'statistical preference' was influenced by its abundance in all home ranges. Koalas occasionally occupied bull oak but this tree species was usually ignored.

Across all six study areas, the frequencies of tree species or tree species groups selected by koalas was dependent on the amount of basal area (an index of foliage biomass) available for each tree species as measured on vegetation plots throughout the study area ($\chi^2 = 285.4$, d.f. = 6, $P < 0.01$). Inspection of the data suggested that koalas used several tree species differently from others. When bull oak, white cypress pine, ironbarks and the rough-barked apple were excluded and the data reanalysed, there were no differences between the relative frequencies of koala observations in the remaining three tree species groups and their relative abundance in the forest ($\chi^2 = 0.69$, d.f. = 2, n.s.). Thus, overall, koalas occupied pilliga box, other boxes and red gums in the proportions expected, but this was done at the expense of bull oak, white cypress pine, ironbarks and the rough-barked apple.

Koalas displayed a strong seasonal preference for tree species ($\chi^2 = 118.1$, d.f. = 6, $P < 0.01$). In particular, koalas utilised white cypress pine extensively (by day) during the hot

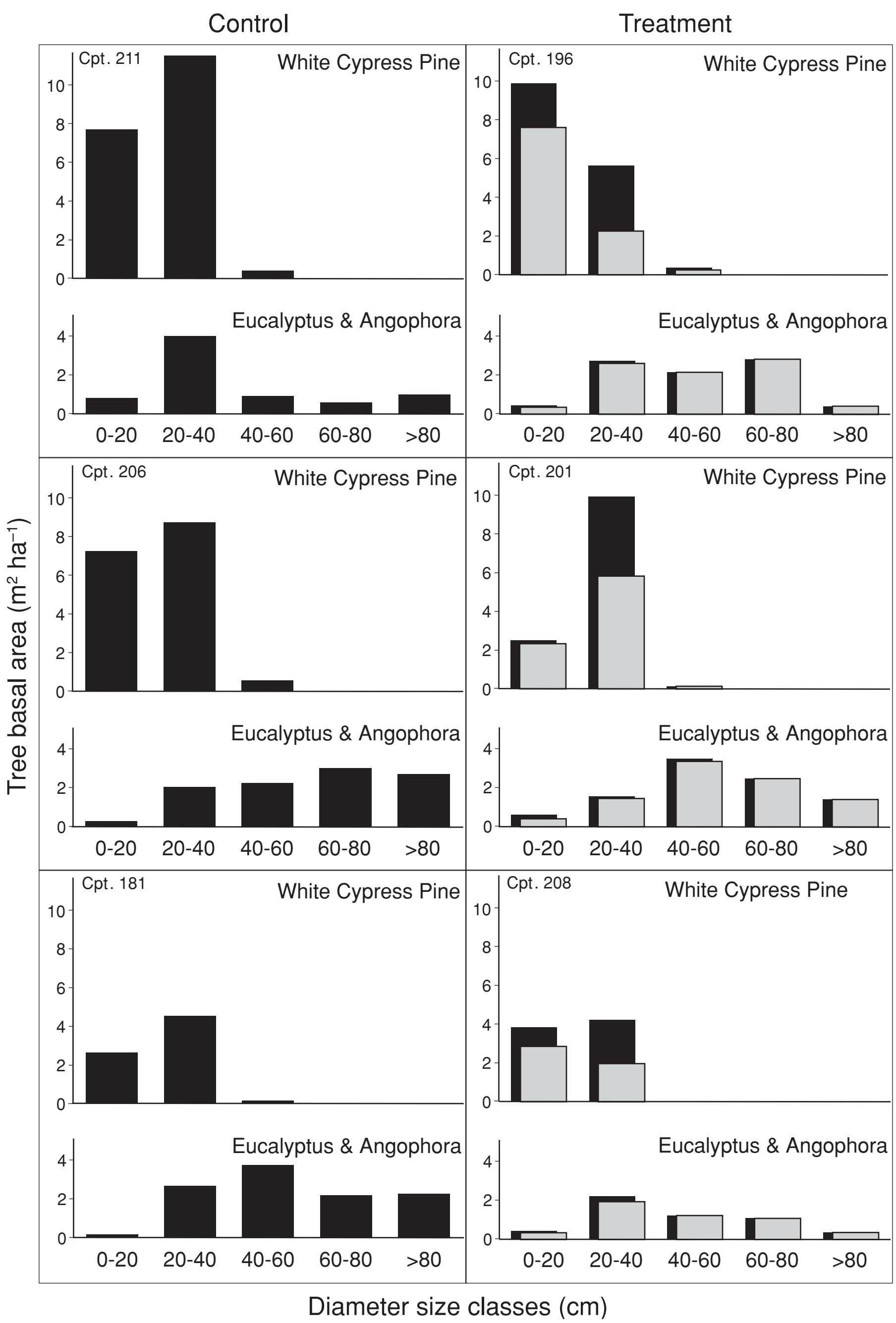

Fig. 2. Mean basal area (m^2 ha^{-1}) of trees on the three control areas (Compartments 211, 206 and 181) and before and after selective logging on the three treatment areas (Compartments 196, 201 and 208). Grey bars indicate post-logging data.

summer months, and rough-barked apple was also used more in summer than winter (Table 3). These two tree species appeared to offer the best opportunities for koalas to find shade in hot weather. Other boxes also contributed (inversely) to this observed pattern; that is, they were used less in summer than in winter. When the data for these three tree species, or tree species groups, were excluded and the data reanalysed, there were no differences between the relative frequencies of koala observations in the remaining four tree species groups in summer compared with winter (χ^2 = 5.34, d.f. = 3, n.s.). Thus, selection for shade trees in summer appears to be an important factor influencing (daytime) tree preferences of koalas in the Pilliga forests.

Koalas used the full range of available tree-diameter size-classes while resting and foraging (range 7–150 cm DBH, median = 37 cm DBH) (Table 4), but they preferred particular size-classes (χ^2 = 22.1, d.f. = 5, P < 0.01). This was due to the avoidance by koalas of trees in the smallest-diameter size-class (0–20 cm), especially those of the white cypress pine in this size category. When trees of all species within size-class 0–20 cm diameter were excluded and the data reanalysed, there was no significant dependence of the frequency of tree-diameter size-classes selected by koalas in relation to the size-classes of trees available in the forest (χ^2 = 3.37, d.f. = 4, n.s.). The same result was obtained when only white cypress pine within this smallest

Table 2. Tree preferences of individual koalas

Significance levels indicated for Chi-square tests using 3–6 degrees of freedom (***, P < 0.01; **, P < 0.05; *, P < 0.1; n.s., not significant). Selection (+) or avoidance (–) for particular tree species is indicated, as determined by iteratively deleting species having the greatest contribution to total Chi-square until P > 0.1. Blank cells indicate that tree use is proportional to the representation of that tree species within the home range. Absence of a tree species from an animal's home range is indicated by *a*

Koala ID	No. of records	Significance level	Tree species						
			Red gums	Pilliga box	Other box	Ironbarks	White cypress pine	Rough-barked apple	Bull oak
Compartment 211									
150.1	87	***	+	+				+	
150.2	36	n.s.		*a*					
150.3	93	***					–		–
150.4	19	***	+	*a*	*a*	+		+	
150.5	88	***	*a*	+				*a*	
Compartment 206									
150.18	88	**	+	*a*					
150.28	89	**				+			
150.38	23					No vegetation data collected			
150.48	67	***					–		–
150.58	65	n.s.							*a*
150.68	11	***	+	*a*	*a*	*a*			
Compartment 181									
150.6	87	***			*a*			*a*	–
150.7	86	***	*a*		*a*	–		*a*	–
150.8	38	*	+		*a*			*a*	
150.9	88	**		+					
151.6	16	***		+	*a*		+	*a*	
Compartment 208									
151.1	21					No vegetation data collected			
151.2	107	n.s.	*a*		*a*			*a*	
151.3	85	***	*a*				–	*a*	*a*
151.4	14					No vegetation data collected			
151.5	100	n.s.	*a*					*a*	
151.7	77	***	*a*	+			–	*a*	*a*
Compartment 201									
150.14	45	n.s.						*a*	
150.24	88	***	+			–		*a*	
150.34	99	n.s.						*a*	
150.44	100	***					–	*a*	*a*
150.54	95	***	+	+		–		*a*	–
Compartment 196									
151.18	92	***							–
151.28	37	***	+	+	*a*				
151.38	91	**	+	*a*					
151.48	81					No vegetation data collected			
151.58	92	***	–						
Prefer (% home-ranges)			40.9	30.4	0	7.4	3.6	14.3	0
Avoid (% home-ranges)			4.6	0	0	11.1	17.9	0	25

Table 3. Seasonal use by koalas for each of the main tree species, or tree species groups, across all study areas
Data represent the number of koala observations

Tree species	Summer October–February	Winter March–October
Red gums	148	179
Pilliga box	287	346
Other box	51	87
Ironbarks	131	126
White cypress pine	485	220
Rough-barked apple	73	43
Bull oak	9	20
Total	1184	1021

size-class 0–20 cm were removed ($\chi^2 = 3.60$, d.f. = 5, n.s.). Thus, for all other tree species, koalas occupied trees of all size-classes in the proportions expected, but avoided white cypress pine trees smaller than 20 cm diameter.

Home-range size and fidelity

The median size of a koala's annual home range in the Pilliga forests (n = 30) was 8.9 ha (range 2.6–93.6 ha) using the FK 95% method, 11.2 ha (range 1.1–107.2 ha) using the MCP 100% method, and 16.6 ha (range 2.0–77.7 ha) using the AK 95% method (Table 5). Six young animals (≤3 years), four males and two females, showed very large movements shortly after initial capture, so data for these individuals were included in the above calculations only after they had settled into a stable home range (Table 5). Estimates of the FK 95%, MCP 100% and AK 95% areas (ha) utilised or traversed by these six animals during this settling period were, respectively, 180, 363 and 544 for Koala 150.10; 570, 223 and 437 for Koala 150.28; 1914, 634 and 1108 for Koala 150.38; 255, 237 and 441 for Koala 150.70; 386, 265 and 405 for Koala 151.10; and 88, 56 and 87 for Koala 151.48.

No differences were found (Z = –0.85, P = 0.39; FK95%) between the sexes in annual home-range size. The median size of a male FK 95% home range was 12.1 ha (range 2.9–93.6 ha, n = 16) (15.5 ha, range 1.1–107.2 ha for the MCP 100% home-range, n = 16), while the median size of a female FK 95% home range was 8.9 ha (range 2.6–25.5 ha, n = 14) (10.5 ha, range 2.2–36.9 ha for the MCP 100% home range, n = 14) (Table 5).

Similarly, there were no differences (Z = 0.06, P = 0.95; FK 95%) in koala home-range size between seasons (FK 95% median 9.1 ha and MCP 100% median 7.7 ha for October–February, n = 30, and FK 95% median 6.5 ha and MCP 100% median 11.1 ha for March–October, n = 23) (Table 5).

Plots of the size and shape of FK 95% home ranges for all animals are shown in Fig. 3. The home-range sizes for koalas remained similar before and after selective logging on the three treatment areas and, following logging, the animals continued to occupy most of their previous home ranges. Home-range overlap between these two periods, as a percentage of the October–February home range, was median 55% (n = 23) for all animals. The median home-range overlap for animals in the logged areas (55%, range 14–88%, n = 13) was similar to that in the unlogged areas (55%, range 10–82%, n = 10). The plots also demonstrate that koala home-ranges overlap extensively, even (though not displayed) within the same sex. Additional untagged koalas (not shown) also occupied the same general areas as the tagged animals.

Over the whole study, there were no differences (Z = 1.12, P = 0.26 for FK 95%) in koala home-range sizes between the control (FK 95% median 13.3 ha, MCP 100% median 11.8 ha, n = 15) and treatment study areas (FK 95% median 8.8 ha, MCP 100% median 10.6 ha, n = 15) (Table 5). Also, there were no differences in koala home-range sizes between the periods 'before logging' and 'after logging' on both the control (n = 15 and n = 10) (Z = 0.14, P = 0.89 for FK 95%) and treatment (n = 15 and n = 13) (Z = 0.14, P = 0.89 for FK 95%) areas. The same result (P > 0.05) was obtained when the data were partitioned by sex.

Home-range composition

While the eucalypts in this study were not logged, they clearly are important to koalas as they represent the primary food source for these animals. An indication of the minimum number of eucalypt trees ha^{-1} required by koalas within their home ranges in this mixed-species forest is given in Fig. 4 (excludes one outlier: Koala 150.7, 123 ha and 67 stems ha^{-1}). These data suggest that a threshold in habitat quality for the koala may exist corresponding to the presence of at least 20 eucalypt trees ha^{-1} that are each larger than 20 cm in diameter (at breast height).

Table 4. Use of trees of different sizes by koalas for each of the main tree species, or tree species groups, across all study areas
Data represent the number of koala observations. The proportional representation of total basal area by diameter size class for all trees measured in the 80 vegetation plots is also provided

Tree species	Tree diameter class (cm) 0–20	20–40	40–60	60–80	80–100	100+	Total
Red gums	21	96	93	81	17	14	322
Pilliga box	33	189	193	160	38	17	630
Other box	5	42	50	28	5	7	137
Ironbarks	4	70	93	63	20	5	255
White cypress pine	129	528	43	1	–	–	701
Rough-barked apple	1	13	45	27	21	9	116
Bull oak	15	13	1	–	–	–	29
Total	208	951	518	360	101	52	2190
Tree basal area available (%)	28.5	44.8	11.5	9.2	4.3	1.6	

Table 5. Home-range sizes (ha) for koalas in the Pilliga forests

The age (estimated using Gordon 1991) and bodyweight of koalas were assessed at the time of initial capture. An asterisk indicates animals for which only data representing 'stabilised' home-ranges have been presented (see text). AK, home-range calculated using the Adaptive Kernel (95%) method; FK, home-range calculated using the Fixed Kernel (95%) method; MCP, home-range calculated using the Minimum Convex Polygon (100%) method

Koala ID	Sex	Age (years)	Weight (kg)	October–February 'before logging'				March–October 'after logging'				Full year (or whole period)			
				No. of records	AK	FK	MCP	No. of records	AK	FK	MCP	No. of records	AK	FK	MCP
Control (unlogged) blocks															
Compartment 211															
150.1*	F	2	4	27	8.67	7.42	5.4	39	17.6	14.39	13.51	66	18.95	13.28	16.33
150.2	F	9	7	37	5.24	2.49	3.36	–	–	–	–	37	5.24	2.57	3.36
150.3	M	4.5	8.4	52	27.29	26.37	23.28	45	13.98	10.28	14.17	97	36.56	23.05	30.75
150.4	M	Adult	8.6	19	17.06	18.92	11.8	–	–	–	–	19	17.06	19.52	11.8
150.5	F	7.5	7.5	44	3.27	2.41	2.53	44	11.37	5.83	8.85	88	11.06	8.12	10.41
Compartment 206															
150.18	M	3.5	7.5	45	18.7	16.64	14.68	44	64.53	41.71	39.61	89	37.35	30.86	41.89
150.28*	F	2	4.1	15	13.56	9.51	3.39	42	7.18	5.79	6.57	57	7.66	7.33	9.13
150.38*	M	2.5	5.2	–	–	–	–	–	–	–	–	–	–	–	–
150.48	M	8.5	8.7	45	34.5	33.29	25.61	24	21.03	24.33	11.57	69	35.32	33.65	27.97
150.58	F	5.5	6.6	43	34.52	25.42	35.57	26	5.02	3.99	6.43	69	32.4	12.31	36.86
150.68	M	5	7.9	11	2	2.79	1.08	–	–	–	–	11	2	2.9	1.08
Compartment 181															
150.6	F	4	6	45	8.31	6.71	5.73	42	4.02	4.9	3.46	87	7.78	6.79	6.41
150.7*	M	3	6	31	16.04	14.38	13.48	42	68.51	122.75	80.84	73	77.65	93.64	107.2
150.8	F	4	5.6	39	5.84	7.11	4.2	1	–	–	–	40	5.84	7.33	4.2
150.9	F	4	7.7	45	25.79	20.04	20.96	43	17.07	16.33	14.21	88	22.51	19.32	23.51
151.6	F	7.5	6.5	17	16.96	15.48	10.07	–	–	–	–	17	16.96	16.05	10.07
Treatment (logged) blocks															
Compartment 208															
151.1*	M	3	6.2	–	–	–	–	–	–	–	–	–	–	–	–
151.2	M	4.5	7.4	53	2.4	1.01	2.67	55	7.5	6.48	6.12	108	6.6	3.64	7.03
151.3	F	4	6.8	51	14	8.61	9.98	35	8.99	5.1	5.52	86	12.24	8.78	10.61
151.4	M	Adult	6.6	14	17.22	8.32	5.46	–	–	–	–	14	17.22	8.8	5.46
151.5	F	4	7.8	46	20.15	19.4	14.65	54	23.01	20.63	16.87	100	21.17	25.47	20.31
151.7	F	Ad.	7.5	25	2.4	1.83	1.71	54	2.96	2.29	1.83	79	2.74	2.58	2.18
Compartment 201															
150.14	M	5	6.8	51	2.76	2.93	2.01	2	–	–	–	53	2.8	3.06	2.01
150.24	M	4.5	6.6	48	4.72	4.26	4.36	44	3.44	3.19	2.53	91	6.03	4.14	5.04
150.34	F	Adult	7.3	50	12.58	9.8	9.04	50	6.53	3.03	5.28	100	15.31	9.24	12.34
150.44	M	3	6.8	50	11.1	4.42	7.72	51	4.27	2.31	2.88	101	6.93	4.41	7.72
150.54	M	5	7.5	48	7.89	3.53	7.68	51	17.22	14.25	12.81	99	23.17	7.86	29.24
Compartment 196															
151.18	M	3	7.5	32	8.39	8.2	5.43	63	20	20.16	19.87	95	16.6	18.08	20.2
151.28	M	7	8.2	33	11.77	9.91	7.68	8	3.01	4.52	1.63	41	12.06	8.66	8.06
151.38	F	5.5	6.8	32	16.51	14.31	10.68	59	15.72	6.2	11.11	91	16.6	9.08	13.6
151.48*	M	3	6.4	19	17.7	16.53	9.89	50	17.64	13.07	27.62	69	28.2	15.34	30.6
151.58	M	8	9.2	33	19.13	19.31	10.12	59	22.31	24.72	19.94	92	27.31	25.54	23.16

Movements

The median daily distance moved by koalas during radio-tracking on sequential days was 63 m (68 m for males and 59 m for females) (Table 6). The mean daily movement for all animals was 89 m. This mean value is strongly weighted by the few individuals that moved large daily distances (up to 897 m) on several occasions, particularly during October–December when young animals were dispersing (see Fig. 3). Females appeared to move less than males during winter after the main period of dispersal had ended (Table 6). No differences in koala daily movements ($Z = –1.54$, $P = 0.12$) were found between the logged (median 57 m) and unlogged (median 58 m) study areas (Table 6).

Breeding success

Reproductive assessments were made for 13 of the 14 female koalas captured in October 1997. Two animals were young (~2 years old; age estimated using Gordon 1991) and had not yet reproduced. Two others (aged ~4 and 9 years old) showed no evidence of having bred in 1997. The remaining nine animals produced young in 1997, having either a large joey in their

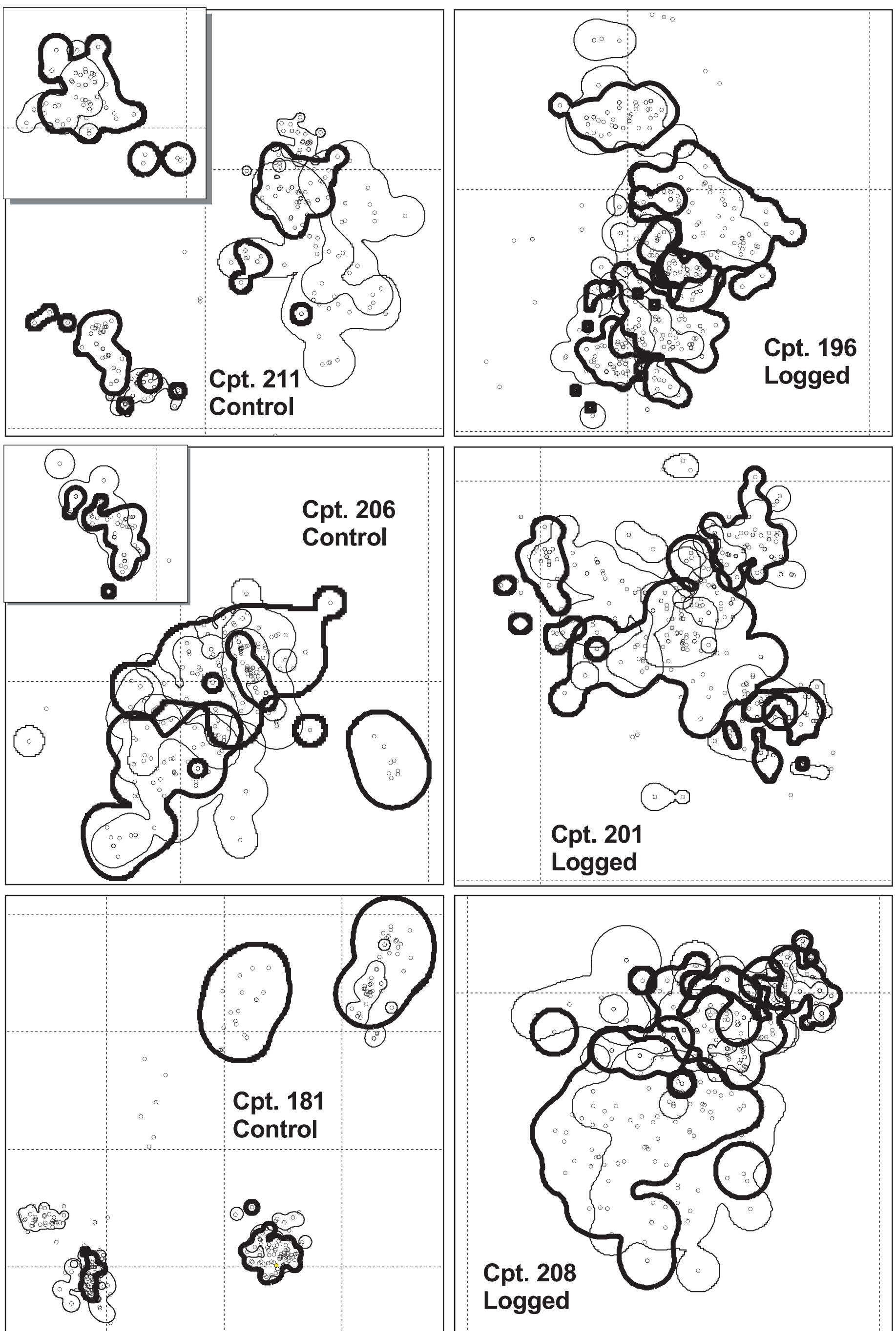

Fig. 3. Home-range overlap (FK95%) for 30 radio-tagged koalas before and after selective logging. Thin lines indicate home ranges during the pre-treatment period (October–February); thick lines indicate home-ranges during the post-treatment period (March–October). The position of each tree utilised is indicated. Scale varies between study areas, but 1-km grid squares are displayed. Inset maps (Compartments 211 and 206) show home-ranges for two animals distant from the others.

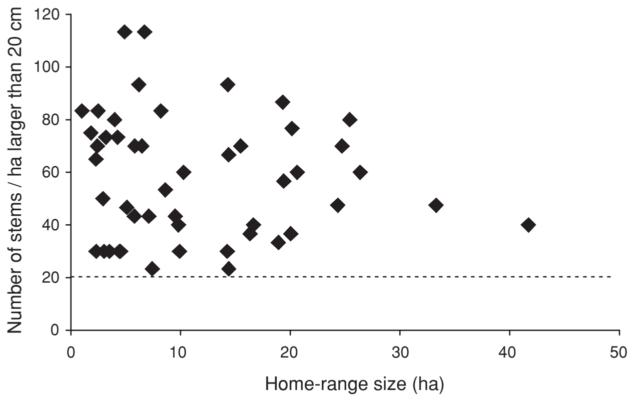

Fig. 4. Number of eucalypt stems (larger than 20 cm DBH) per hectare occurring within the home ranges of radio-tagged koalas in the Pilliga. Data include the home range and corresponding mean tree density for all animals during both the pre-treatment (n = 27) and post-treatment (n = 22) periods. Home ranges were calculated using the Fixed Kernel (95%) method.

pouch or one that had recently vacated the pouch and was clinging to the mother's back.

The following year, 7 of the 10 females still alive in October 1998 had produced young, while the other three failed to breed in that year. Four females produced young in both 1997 and 1998, and three others produced young in only one of those two years. Four of the six adult females on the unlogged study areas produced one young each in 1998 (67%) compared with 3 of 4 adult females on the logged study areas (75%).

All pouch and/or back young were estimated to be 6–12 months (mainly 8–9 months) old when their mothers were captured in October 1997 and October 1998, suggesting that koalas in the Pilliga forests normally give birth during summer.

Mortalities

Eight animals died during the study; seven of these received a post-mortem examination by an experienced veterinary officer. Septicaemia (from tiger pear thornstick injuries) was implicated in the death of two animals. Pneumonia and/or lung congestion was associated with both of the above cases and with two others, one of which also tested positive for *Chlamydia pecorum*

Table 6. Median daily distances moved by radio-tracked koalas
Data are based on 915 daily locations for 32 koalas (18 males, 14 females) when they were radio-tracked on sequential days only. Summer: October–February, pre-logging period; winter: March–October, post-logging period

Season	Sex	Median daily movements (m)		
		Control blocks	Treatment blocks	All blocks
Summer	M	93	52	73
	F	65	83	69
	Both	76	55	71
Winter	M	96	75	85
	F	42	49	46
	Both	58	57	58
Whole year	M	94	53	68
	F	57	62	59
	Both	67	57	63

(P. Timms and J. McKee, pers. comm.). Two animals died during a period of particularly hot, dry weather, one of dehydration and the other after being trapped inside a rabbit burrow to which it sought shelter from the heat and smoke generated by a nearby wildfire. Two animals were eaten by predators; one of these may have been displaced from a tree during concurrent logging operations. Three of the eight deaths occurred on the control study areas, and one of the remainder occurred several months before logging began. Two animals that died on the treatment areas did so several months after the logging operations had been completed. Thus, only two animals died on the logged areas during the period of logging, one of septicaemia and/or pneumonia and the other from predation (possibly facilitated by tree felling).

Two other animals were initially diagnosed with clinical signs of the disease chlamydia. One animal (with *C. pecorum*) disappeared from the study within the first few weeks because it wandered off and could not be relocated. The other (with *C. pneumoniae*) displayed no apparent ill-effects of the disease, producing one young in 1998.

Tiger pear

Tiger pear was abundant on five of the six study areas: Compartment 201 had significantly more than the other areas (1000 stems ha^{-1}) and, although this cactus was present in Compartment 181, only 0 stems ha^{-1} were encountered on the vegetation-measurement plots. Stem density for tiger pear on the other four compartments was 489, 391, 302 and 275 stems ha^{-1} for Compartments 196, 206, 208 and 211, respectively. On average, 41.0 stems of tiger pear were counted on each of the eighty 0.1-ha vegetation plots (mean per compartment ranged from 0 to 100 stems) and 0.4 stems of prickly pear (mean per compartment ranged from 0 to 1.5 stems). This corresponded to an average of 410 stems ha^{-1} of tiger pear within each koala home range (range 0–1227 stems ha^{-1}) and an average of 3.9 stems ha^{-1} of prickly pear (range 0–27 stems ha^{-1}).

Discussion

This was the first experimental study of the effect of a logging operation on koala populations. The principal findings were that koalas continued to occupy all or part of their previous home ranges after selective logging, and that home-range sizes remained similar between logged and unlogged areas. This result was not unexpected because, unlike most other arboreal marsupials, koalas do not require hollows in old trees for breeding or for diurnal shelter (Martin and Handasyde 1995; Gibbons and Lindenmayer 2002) and they are less demanding of foliage nutrient quality than some other arboreal folivores, in part because of their larger size (Kavanagh and Lambert 1990; Hume 1999; Moore *et al*. 2004). Also, selective logging, as applied in this study, did not remove the *Eucalyptus* food trees of the koala. Survival and fecundity in this study suggests that animals were not simply persisting in unsuitable habitat following selective logging, as has been observed for other arboreal marsupials following more extensive habitat removal (Tyndale-Biscoe and Smith 1969; Newell 1999). The observed logging intensity, which reduced tree basal area by 25% mainly from the 20–40-cm-DBH tree size-class, is typical of logging operations conducted in these forests over the past 20 years (Anon. 1986). For example, the residual basal area of white cypress pine was

13.7 m^2 ha^{-1}, 7.8 m^2 ha^{-1} and 7.7 m^2 ha^{-1} for Compartments 196, 208 and 201, respectively, and the management plan recommends the retention of 6–10 m^2 ha^{-1} of white cypress pine following commercial thinning operations (Anon. 1986).

The few retrospective studies of koala occupancy within wood-production forests also indicate that this species can tolerate a history of forest disturbance caused by logging (Kavanagh *et al*. 1995; Jurskis and Potter 1997; Smith 2004). For example, in the tall, coastal forests of north-eastern New South Wales, koalas were recorded at much greater frequency in logged than in unlogged forests, in contrast to another arboreal marsupial, the greater glider (*Petauroides volans*), which was much more likely to be encountered in unlogged forests (Kavanagh *et al*. 1995). However, that regional study was partially confounded by the greater frequency of logged forests at lower elevations where koalas are thought to be more abundant.

Koala tree preferences may also provide an indication of the sensitivity of this species to logging. Koalas are well known to forage preferentially for a limited range of tree species at any one location (Hindell *et al*. 1985; Martin 1985; Hindell and Lee 1987, 1988, 1990; Gordon *et al*. 1988; Phillips 1990; White and Kunst 1990; Melzer 1995; Phillips *et al*. 2000), a result also found in this study. The strong preferences displayed by the koala for pilliga box and for one or more of the available red gums demonstrates the need to carefully manage numbers of these tree species in future logging operations. Others have recommended that the 'primary feed tree species' of the koala be recognised and protected during logging operations or to mediate the effects of other (e.g. urban) developments (Phillips *et al*. 2000; Smith 2004).

Koalas are known to select trees for foraging within the middle range of diameter size-classes (30–90 cm DBH) (Jurskis and Potter 1997; Smith 2004). They have also been reported to prefer larger trees, but the preferences for tree species appear to be more important (Hindell and Lee 1987). In the Pilliga forests, koalas occupied eucalypts from across the range of tree size-classes available, including small trees, avoiding only white cypress pines (used mainly for diurnal shelter) within the smallest size categories (<20 cm DBH). Within these mixed-species forests, where white cypress pine forms the principal commercial species, it is important to maintain a minimum number of eucalypt trees per hectare for koala habitat. Preliminary findings from this study, in which all koala home ranges contained at least one preferred (primary food) tree species, suggest a minimum threshold of 20 eucalypt trees larger than 20 cm DBH be retained per hectare to maintain habitat quality for koalas (Fig. 4). This result needs to be treated with caution because unoccupied forest patches were not sampled.

Ultimately, the most important indicators of species sensitivity to disturbance are population survivorship and breeding success. In this study, we found that koala mortality was similar between the control and treatment (recently logged) areas, with only one death possibly attributed to logging. Likewise, a similar proportion of females was recorded with young in both the control and treatment areas following logging. No other studies have reported on koala survivorship or breeding success in relation to logging. The observed summer breeding period for koalas in the Pilliga is in accordance with other studies (Martin and Handasyde 1990).

Home ranges for koalas in semi-arid forests and woodlands are reported to be much larger (>100 ha) than in temperate forests nearer the coast (<3 ha), and there may be less overlap between individuals (Hindell and Lee 1988; Mitchell 1990; Hasegawa 1995; Melzer 1995; White 1999; Ellis *et al*. 2002). The home ranges we estimated (median 8.9 ha, mean ± se 15.1 ± 3.14 ha, FK95%) were therefore smaller than expected because the study area was nearly 400 km inland. Most previous studies have reported the home ranges of males to be larger than those of females, but we found no significant differences. We also observed shorter daily movements for the koalas than those reported by several other studies (Melzer 1995; Pieters and Woodall 1996; Jurskis and Potter 1997).

Home-range size is likely to be a function of population density and the availability of important resources, particularly high-quality food. The Pilliga forests are known to support a large population of koalas, estimated at more than 15 000 animals at the time of this study (Kavanagh and Barrott 2001), and this may explain the relatively small home ranges observed. In contrast, larger home ranges (median 194 ha, range 67–2063 ha, MCP) have been reported for coastal forests near Eden in south-eastern New South Wales, where koalas occur at very low population density (Jurskis and Potter 1997). The eucalypt component of the forest in our study comprised several tree species (red gums and narrow-leaved ironbark) that have been consistently identified as important food trees for the koala elsewhere. The preferred food tree, the pilliga box, is endemic to the Pilliga forests and nearby areas. One or more red gums and/or the pilliga box were recorded within the home ranges of every animal in this study. The nutrient composition of the foliage of eucalypts in the study area has not yet been established and this is likely to be an important factor accounting for the population density of arboreal folivorous marsupials (Kavanagh and Lambert 1990; Moore *et al*. 2004). Melzer (1995) explained the larger home ranges observed in his study in terms of the lower density of preferred food trees than at other locations.

Koala population density in semi-arid environments, such as the Pilliga, is reportedly greatest in the forests and woodlands occurring near inland rivers and intermittent watercourses (Gordon *et al*. 1988, 1990; Munks *et al*. 1996) and this has been explained by the higher moisture content of eucalypt leaves and the increased production of young nutritious foliage in these areas (Munks *et al*. 1996). We found that koalas were widely distributed throughout the Pilliga, including within many areas distant from drainage lines (Kavanagh and Barrott 2001). It is unknown whether this pattern of distribution, and other aspects of koala ecology reported here, were influenced by several years of above-average rainfall that preceded this study.

The major threats to koalas living in the Pilliga forests appear to be stress caused by high summer temperatures, infections caused by thorns from the introduced cactus *Opuntia aurantiaca*, and possibly wildfire. There are significant health and survivorship issues for koalas in some parts of the Pilliga owing to periodic infestation by tiger pear and this cactus needs to be kept under control. The immediate effects of wildfire on koala populations have not been comprehensively studied, but are thought to be catastrophic unless there are opportunities for recolonisation from unburnt areas. However, post-wildfire survival and reproduction of koalas released following treatment for burn injuries was similar to that of animals living in nearby unburnt forest (Lunney *et al*. 2004). In coastal forests, especially those near urban areas, predation by dogs and collisions with motor vehicles on roads are among the most significant causes of koala mortality (Dique *et al*. 2003; Lunney *et al*. 2004), but these threats were of lesser importance in our study.

The limitations of our study include its short duration (one year). For example, it is unknown whether there is a lag period before any adverse effects of logging become apparent, or whether logging would have had a greater impact had the study been carried out during a drought year. It is possible that survivorship or fecundity could be influenced during hot, dry summers by the reduced availability of foliage of white cypress pine, which is used extensively for diurnal shelter. Logging in this study did not alter the numbers of koala food trees and provision was made, depending on evidence (faecal pellets) of frequent use, for the retention of some large white cypress pine trees in logged areas. Another limitation includes the assessment of koala 'food' tree preferences on the basis of trees occupied during the day for diurnal shelter. However, studies by Hindell *et al*. (1985), Melzer (1995), Pieters and Woodall (1996) and Ellis *et al*. (2002) have shown that koalas typically use only 1–3 trees per day, and that koalas are highly likely to feed in the tree, if it is a eucalypt, that is occupied during the day for shelter. Finally, the home-range areas reported in this study, although based on a relatively large number of animal locations spread over one year, do not include for some young animals the periods during which they moved extensively (several kilometres) before settling into their 'stable' home ranges. Most dispersing koalas are 20–36 months of age and travel ~3.5 km from their natal to breeding home ranges (Dique *et al*. 2003).

In conclusion, our observations of koala survival and fecundity, home-range size and fidelity, movements and tree preferences failed to reject the null hypothesis that selective logging for white cypress pine does not adversely affect, in the short term, the conservation of koalas in the Pilliga forests.

Management implications

Logging intensity varies widely from one forest type and geographical location to another depending on a range of silvicultural objectives, environmental constraints, and market availability for wood products. In this study, white cypress pine only was logged, retaining the eucalypt component of the stand to redress the imbalance caused in previous years by extensive ringbarking and cull felling of eucalypts (Anon. 1986). Eucalypt foliage is clearly the principal food source for the koala, so a negative impact of logging was unlikely to have occurred in this study. Nonetheless, logging caused a significant alteration to the habitat of at least 13 koalas without apparent adverse effects, although circumstantial evidence was found for the death of one animal from logging. More work is needed in other regions to determine thresholds in the level of retention of koala food trees. Existing harvesting protocols, as applied during cypress logging operations in the Pilliga forests, do not appear to adversely affect koala populations, at least in the short term.

The Pilliga forests are now recognised for their significant contribution to koala conservation in New South Wales (Kavanagh and Barrott 2001), despite being underestimated in previous state and national assessments of koala population status (Gall and Rohan-Jones 1978; Phillips 1990; Reed *et al*. 1990; ANZECC 1998). It is important to safeguard and link the large Pilliga population with other smaller populations in north-western New South Wales by developing a cross-tenure regional conservation plan that includes revegetation along the banks of inland rivers and drainage lines in strategic areas. Koalas in this study did not require high floristic diversity among the food trees in their habitat: just two favoured tree species (pilliga box and one of the forest red gums) appeared to be adequate. In addition, white cypress pine provides useful shelter from hot summer temperatures. As a precautionary measure, logging should be excluded from buffers either side of drainage lines. These areas are likely to serve as drought refuges within this semi-arid landscape and, owing to the greater availability of moisture in the soil, are likely to contain trees with the most nutritious foliage available for koalas.

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References

Anon. (1986). Management Plan for Pilliga Management Area. Forestry Commission of New South Wales, Sydney.

ANZECC (1998). National koala conservation strategy. Australian and New Zealand Environment and Conservation Council. Environment Australia, Canberra.

Benson, J. S., and Redpath, P. A. (1997). The nature of pre-European native vegetation in south-eastern Australia: a critique of Ryan, D. G., Ryan, J. R. and Starr, B. J. (1995). The Australian landscape – observations of explorers and early settlers. *Cunninghamia* **5**, 285–328.

Dique, D. S., Thompson, J., Preece, H. J., de Villiers, D. L., and Carrick, F. N. (2003). Dispersal patterns in a regional koala population in south-east Queensland. *Wildlife Research* **30**, 281–290. doi:10.1071/WR02043

Ellis, W. A. H., Melzer, A., Carrick, F. N., and Hasegawa, M. (2002). Tree use, diet and home range of the koala (*Phascolarctos cinereus*) at Blair Athol, central Queensland. *Wildlife Research* **29**, 303–311. doi:10.1071/WR00111

Gall, B., and Rohan-Jones, W. (1978). Koala survey. *Parks and Wildlife* **2**(2), 64–67.

Gibbons, P., and Lindenmayer, D. (2002). 'Tree Hollows and Wildlife Conservation in Australia.' (CSIRO Publishing: Melbourne.)

Gordon, G. (1991). Estimation of the age of the koala, *Phascolarctos cinereus* (Marsupialia: Phascolarctidae) from tooth wear and growth. *Australian Mammalogy* **14**, 5–12.

Gordon, G., Brown, A. S., and Pulsford, T. (1988). A koala (*Phascolarctos cinereus* Goldfuss) population crash during drought and heatwave conditions in south-western Queensland. *Australian Journal of Ecology* **13**, 451–461. doi:10.1111/j.1442-9993.1988.tb00993.x

Gordon, G., McGreevy, D. G., and Laurie, B. C. (1990). Koala populations in Queensland: major limiting factors. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 85–95. (Surrey Beatty: Sydney.)

Harris, S., Cresswell, W. J., Forde, P. G., Trewhella, W. J., Woollard, T., and Wray, S. (1990). Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* **20**, 97–123.

Hasegawa, M. (1995). Habitat utilisation by koalas (*Phascolarctos cinereus*) at Point Halloran, Queensland. M.Sc. Thesis, University of Queensland, Brisbane.

Hindell, M. A., and Lee, A. K. (1987). Habitat use and tree preferences of koalas in a mixed eucalypt forest. *Australian Wildlife Research* **14**, 349–360. doi:10.1071/WR9870349

Hindell, M. A., and Lee, A. K. (1988). Tree use by individual koalas in a natural forest. *Australian Wildlife Research* **15**, 1–7. doi:10.1071/WR9880001

Hindell, M. A., and Lee, A. K. (1990). Tree preferences of the koala. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 117–121. (Surrey Beatty: Sydney.)

Hindell, M. A., Handasyde, K. A., and Lee, A. K. (1985). Tree species selection by free-ranging koala populations in Victoria. *Australian Wildlife Research* **12**, 137–144. doi:10.1071/WR9850137

Hooge, P. N., and Eichenlaub, B. (1997). Animal movement extension to Arcview version 1.1. Alaska Science Center, Biological Science Office, US Geological Survey, Anchorage, AK.

Hume, I. D. (1999). 'Marsupial Nutrition.' (Cambridge University Press: Cambridge.)

Jurskis, V., and Potter, M. (1997). Koala surveys, ecology and conservation at Eden. State Forests of New South Wales Research Paper No. 34. State Forests of New South Wales, Sydney.

Jurskis, V., Rowell, D., and Ridley, D. (1994). Survey techniques and aspects of the ecology of the koala near Eden. State Forests of New South Wales Research Paper No. 22. State Forests of New South Wales, Sydney.

Kavanagh, R., and Barrott, E. (2001). Koala populations in the Pilliga forests. In 'Perfumed Pineries: Environmental History of Australia's *Callitris* Forests'. (Eds J. Dargavel, D. Hart and B. Libbis.) pp. 93–103. (CRES, Australian National University: Canberra.)

Kavanagh, R. P., and Lambert, M. J. (1990). Food selection by the greater glider *Petauroides volans*: is foliar nitrogen a determinant of habitat quality? *Australian Wildlife Research* **17**, 285–299. doi:10.1071/WR9900285

Kavanagh, R. P., Debus, S., Tweedie, T., and Webster, R. (1995). Distribution of nocturnal forest birds and mammals in north-eastern New South Wales: relationships with environmental variables and management history. *Wildlife Research* **22**, 359–377. doi:10.1071/WR9950359

Kie, J. G., Baldwin, J. A., and Evans, C. J. (1994). 'CALHOME: Home Range Analysis Program.' (USDA Forest Service, PSW Research Station: Fresno, CA.)

Larkin, R. P., and Halkin, D. (1994). A review of software packages for estimating animal home ranges. *Wildlife Society Bulletin* **22**, 274–287.

Lawson, E. J. G., and Rogers, A. R. (1997). Differences in home-range size computed in commonly used software programs. *Wildlife Society Bulletin* **25**, 721–729.

Lithgow, K. (1980). Aspects of the feeding ecology of the koala *Phascolarctos cinereus* in Victoria. B.Sc.(Honours) Thesis, Monash University, Melbourne.

Lunney, D., Curtin, A. L., Ayers, D., Cogger, H. G., Dickman, C. R., Maitz, W., Law, B., and Fisher, D. (2000). The threatened and non-threatened vertebrate fauna of New South Wales: status and ecological attributes. NSW National Parks and Wildlife Service Environmental and Heritage Monograph Series No. 4. NSW National Parks and Wildlife Service, Sydney.

Lunney, D., Gresser, S. M., Mahon, P. S., and Matthews, A. (2004). Post-fire survival and reproduction of rehabilitated and unburnt koalas. *Biological Conservation* **120**, 567–575. doi:10.1016/j.biocon.2004.03.029

Lunt, I. D., Jones, N., Spooner, P. G., and Petrow, M. (2006). Effects of European colonisation on indigenous ecosystems: post-settlement changes in tree stand structures in *Eucalyptus–Callitris* woodlands in central New South Wales, Australia. *Journal of Biogeography* **33**, 1102–1115. doi:10.1111/j.1365-2699.2006.01484.x

Martin, R. W. (1985). Overbrowsing and decline of a population of the koala, *Phascolarctos cinereus*, in Victoria. I. Food preference and food tree defoliation. *Australian Wildlife Research* **12**, 355–365. doi:10.1071/WR9850355

Martin, R., and Handasyde, K. (1990). Population dynamics of the koala (*Phascolarctos cinereus*) in southeastern Australia. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 75–84. (Surrey Beatty: Sydney.)

Martin, R. W., and Handasyde, K. A. (1995). Koala. In 'The Mammals of Australia'. (Ed. R. Strahan.) pp. 196–198. (Reed Books: Sydney.)

Melzer, A. (1995). Aspects of the ecology of the koala, *Phascolarctos cinereus* (Goldfuss, 1817), in the sub-humid woodlands of central Queensland. Ph.D. Thesis, University of Queensland, Brisbane.

Mitchell, P. (1990). The home ranges and social activity of koalas – a quantitative analysis. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson) pp. 171–187. (Surrey Beatty: Sydney.)

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *American Midland Naturalist* **37**, 223–249. doi:10.2307/2421652

Moore, B. D., Wallis, I. R., Marsh, K. J., and Foley, W. J. (2004). The role of nutrition in the conservation of the marsupial folivores of eucalypt forests. In 'Conservation of Australia's Forest Fauna'. 2nd edn. (Ed. D. Lunney.) pp. 549–575. (Royal Zoological Society of New South Wales: Sydney.)

Munks, S. A., Corkrey, R., and Foley, W. J. (1996). Characteristics of arboreal marsupial habitat in the semi-arid woodlands of northern Queensland. *Wildlife Research* **23**, 185–195. doi:10.1071/WR9960185

Newell, G. R. (1999). Responses of Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*) to loss of habitat within a tropical rainforest fragment. *Biological Conservation* **91**, 181–189. doi:10.1016/S0006-3207(99)00083-X

Norris, E. H., Mitchell, P. B., and Hart, D. M. (1991). Vegetation changes in the Pilliga forests: a preliminary evaluation of the evidence. *Vegetatio* **91**, 209–218. doi:10.1007/BF00036058

Phillips, S., Callaghan, J., and Thompson, V. (2000). The tree species preferences of koalas (*Phascolarctos cinereus*) inhabiting forest and woodland communities on Quaternary deposits in the Port Stephens area, New South Wales. *Wildlife Research* **27**, 1–10. doi:10.1071/WR98054

Phillips, W. (1990). 'Koalas. The Little Australians We'd All Hate To Lose.' (Australian National Parks and Wildlife Service: Canberra.)

Pieters, C. W., and Woodall, P. F. (1996). Daily movement patterns and habitat utilisation of koalas (*Phascolarctos cinereus*) exposed to different levels of habitat modification. In 'Koalas – Research for Management'. (Ed. G. Gordon.) pp. 23–28. (World Koala Research Incorporated: Brisbane.)

Reed, P. C., and Lunney, D. (1990). Habitat loss: the key problem for the long-term survival of koalas in New South Wales. In 'Koala Summit: Managing the Koala in NSW'. (Eds D. Lunney, C. A. P. Urquhart and P. C. Reed.) pp. 9–31. (NSW National Parks and Wildlife Service: Sydney.)

Reed, P. C., Lunney, D., and Walker, P. (1990). 1986–1987 survey of the koala *Phascolarctos cinereus* (Goldfuss) in New South Wales and an ecological interpretation of its distribution. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 55–74. (Surrey Beatty: Sydney.)

Robbins, M., and Russell, E. (1978). Observations on movements and feeding activity of the koala in a semi-natural situation. In 'The Koala: Proceedings of the Taronga Symposium on Koala Biology, Management and Medicine'. (Ed. T. J. Bergin) pp. 29–44. (Zoological Parks Board of New South Wales: Sydney.)

Rolls, E. (1981). 'A Million Wild Acres: 200 Years of Man and an Australian Forest.' (Nelson: Melbourne.)

Seaman, D. E., and Powell, R. A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* **77**, 2075–2085. doi:10.2307/2265701

Smith, A. P. (2004). Koala conservation and habitat requirements in a timber production forest in north-east New South Wales. In 'Conservation of Australia's Forest Fauna'. 2nd edn. (Ed. D. Lunney.) pp. 591–611. (Royal Zoological Society of New South Wales: Sydney.)

Tyndale-Biscoe, C. H., and Smith, R. F. C. (1969). Studies on the marsupial glider, *Schoinobates volans* (Kerr). III. Response to habitat destruction. *Journal of Animal Ecology* **38**, 651–659. doi:10.2307/3041

van Kempen, E. (1997). 'A History of the Pilliga Cypress Pine Forests.' (State Forests of New South Wales: Sydney).

White, N. A. (1999). Ecology of the koala (*Phascolarctos cinereus*) in rural south-east Queensland *Wildlife Research* **26**, 731–744. doi:10.1071/WR98002

White, N. A., and Kunst, N. D. (1990). Aspects of the ecology of the koala in south-eastern Queensland. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 109–116. (Surrey Beatty: Sydney.)

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–168. doi:10.2307/1938423

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