Koala density, habitat, conservation, and response to logging in eucalyptus forest, a review and critical evaluation of call monitoring.

by

Andrew P. Smith and John Pile

November 2023

Setscan Pty Ltd. Currumbin Qld. 4223 setscan@gmail.com

DOI:10.13140/RG.2.2.23675.28968

Koala density, habitat, conservation, and response to logging in eucalyptus forest, a review and critical evaluation of call monitoring.

Andrew P. Smith[1] and John Pile[2]

[1]Setscan Pty Ltd. PO Box 4130 Elanora Qld 4221. Email setscan@gmail.com

[2]647 Valery Road, Valery NSW 2454

Key words: koala, habitat, density, folivore, logging, GIS models, song meters, predation.

Abstract

This study is the second in a series that examines the habitat requirements and response to logging of koalas inhabiting tall eucalypt forests of north-east NSW. It compares and reviews the effectiveness of call counting, direct observation (spotlighting) and koala scat surveys for defining, modelling and mapping koala habitat for the purpose of koala conservation and management in timber production forests. It shows that koala habitat is more complex than previously considered and cannot be adequately described by the abundance of primary and secondary koala food trees or by models that rely on mapped GIS layers, especially those based on acoustic monitoring of male koala calls. It validates the findings of earlier studies that high quality core (breeding female) koala habitat is characterized by complex forest structure and a high diversity of local food tree species and is eliminated by intensive clear-fell harvesting. The study area was classified and mapped by grid-based ground survey into 5 zones of decreasing logging intensity and increasing koala habitat quality, and the accuracy of this mapping was tested by simultaneous koala call counts and spotlight surveys over two consecutive years. Average koala density increased steeply from 0.02 – 0.20/hectare with increasing mapped habitat quality, forest age, forest structural complexity and tree species diversity, and this relationship was driven primarily by breeding females. The number of calling male koalas did not correlate with habitat quality or with koala density determined by spotlighting. Male koalas were widely distributed across the landscape and more prevalent than females in low quality, non-breeding, sink habitats. These findings show that previous koala habitat modeling and logging impact studies that relied on remotely deployed acoustic monitors (song meters) to measure male koala abundance, and assumed that male calling is indicative of female breeding success, should be disregarded as incorrect and unsuitable for koala conservation and management. Koalas maintained a stable density of 0.29/ha. (3 hectares/ koala) in highest quality (least disturbed) habitat over a period of 15-25 years where they consumed about 1-2 % of annual leaf production. It is hypothesized that koala density is regulated at low or benign levels by feedback from host trees that increases toxicity of new and old

leaf growth in response to excess folivore browsing. Koalas changed food trees frequently and fed on almost all available tree species (16+) within their home ranges. Large home ranges, complex mature forest structure, a high diversity of food tree species and a diverse gut microbiome should allow females to rotate food trees, minimize induced toxicity, and select individual leaves with a dry matter and nitrogen digestibility and water content sufficient to satisfy the requirements of breeding and lactation, with minimal risk of predation. Abnormally high koala population densities in woodlands and open forests (> 0.6/ha) are largely limited to areas where koalas have been introduced or re-introduced to plantations or natural areas where aboriginal hunters and dingos were historically present but are now absent and where food trees have not been selected for resistance to koala browsing pressure. Remnant mid to low elevation tall wet forests in northeast NSW where the climate is mild and extensive wildfire is rare, can be considered core areas for koala conservation where cessation of timber harvesting and increased reservation is a priority.

INTRODUCTION

The koala (*Phascolarctos cinereus*) was recently (DAWE 2022) classified as endangered and is one of more than 100 mammal species classified as vulnerable, endangered, critically endangered, or extinct in mainland Australia under the Environment Protection and Biodiversity Conservation Act 1999. Australian native mammals have undergone a greater level of extinction and decline than those on any other continent (Short and Smith 1994, Woinarski *et al.* 2015) and the most affected species have been ground dwelling mammals susceptible to hyper-predation by dogs (*Canis familiaris)* introduced Red Foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) in regions where predator abundance has been greatly elevated by fast breeding introduced rabbits (*Oryctolagus cuniculus*), mice (*Mus musculus*) or native rodents in the genus *Rattus* (Smith and Quin 1996, Smith unpublished). Only six arboreal mammal species are listed as threatened, and the most common cause of decline in this group is loss of tree hollows (used for shelter and reproduction) in timber production forests where intensive logging or clear-fell harvesting has replaced structurally complex old growth forests with young, uniform aged, regrowth harvested on rotations too short for replacement hollows to develop (Smith 1982, 2010, 2019, Smith and Lindemayer1988, Eyre and Smith 1997). The koala does not depend on tree hollows but sleeps in the open which reduces its susceptibility to old growth logging but increases its exposure and vulnerability to hunting (Warnecke 1978), drought (Gordon *et al.* 1988), wildfire (Lunney and Leary 1988, Lunney et a 2004) and predation by dogs (Smith 2004, Allen *et al.* 2016), especially in the more open forests and woodlands where koalas must come to the ground more often to move between trees.

Prior to European settlement the koala was an easy target for Aboriginal hunters and dingoes in frequently burnt grassy open forests and woodlands and is likely to have been eliminated or reduced to rarity in habitats in well populated coastal inland and riverine areas. Domestic dogs can locate koalas in trees by smell and trained sniffer dogs are sometimes used to locate koalas in surveys (Cristescu *et al.* 2015). Koalas were not recorded by early explorers (Oxley and Mitchell) in open forest and woodlands on the northern inland slopes of the Great Dividing Range in NSW and sightings were few until the population expanded rapidly in the vicinity of Gunnedah after about 1970 (Smith 1992, Ellis *et al*. 2016)). Similarly, in Victoria koalas were scarce or absent from inland low elevation forests and woodlands prior to European settlement and largely confined to tall open forests of the Eastern Highlands (Warneke 1978). There are no records of koalas from 1850's mammal surveys carried out in riverine and open forests in western Victoria and the Murray River system prior to the spread of pastoralism and the introduction of rabbits and foxes (Menkhorst 2009). However, koalas were reported by pioneer settlers (Committee of the South Gippsland Pioneers Association 1920) to be abundant in tall, dense, wet forests in the ranges and foothills to the east of Melbourne where aboriginal tribes were sparse or absent. Firsthand accounts of the "big timber" and "scrub" clearing in South Gippsland at the time of settlement in the 1870's describe native bears as being numerous with up to 6 individuals to be seen at one time in tall, giant gum trees (*E. globulus and E. rubida*), "*more than 100 foot up without a branch to rest on*" (Elms 1920). Today this pattern is reversed, koalas are scarce or absent from tall wet forests of the Victorian Highlands and only locally abundant in dispersed low elevation woodlands and low open forests where they have been mostly introduced or re-introduced (Menkhorst 1995, Whisson *et al.* 2016). It is now commonly assumed that koalas prefer woodland and low open forest habitat (Lee and Carrick 1989) where they attain high densities and are easily studied, but this preference may be an artifact of post European expansion following the exclusion of dingoes or wild dogs from much of the koala's geographic range by fencing, baiting and bounty hunting. The anatomy of the koala has been described as suited to movement by leaping from tree to tree (Strahan 1978) rather than coming to the ground, suggesting that the ancestral habitat of the koala may have been taller forests with more closely spaced trees rather than dry open forests and woodlands where predation risk was high. Remnant tall forests are widespread along the Great Dividing Range of Eastern Australia from Victoria to Southern Queensland in a network of scattered National Parks embedded within a matrix of State Forests managed for wood production. Today, koalas are sparse or absent from large tracts of these forests and continue to decline across most of their geographic range, especially in areas that have been extensively fragmented, frequently burnt, or intensively logged (McAlpine *et al.* 2015). Extensive surveys of tall open forests conducted for logging impact studies in northern NSW during the 1990's found koalas to occur at less than 2% of survey sites in the Glen Innes, Tenterfield and Walcha-Nundle-Styx River Forest Management Areas on the Northern Tablelands and less than 9% of sites in the Grafton, Casino, Coffs Harbour and Urunga Forest Management Areas on the mid north coast (Smith *et al.* 1992,1994, 1995). Koalas were only abundant (40% of sites) in lower elevation parts of the Urbenville and Murwillumbah Forest Management Areas, close to the Queensland border, in areas with a history of a low intensity logging that retained mature and structurally complex multi-aged forest (Andrews *et al.* 1995). In south-east NSW forests koala populations declined after European hunting for hides, burning and clearing for agriculture early last century (Lunney and Moon 2012) and more recently after clear-fell harvesting for woodchip (compounded by the effects of drought and warming) and have since remained scarce (Lunney and Leary 1988, Lunney *et al.* 2014).

Detailed ecological studies of koalas in tall wet forests are few and largely limited to radiotracking and scat surveys in the Pine Creek State Forest and Bongil Bongil National Park region of northern NSW (Smith and Andrews 1997, Smith 2004, AMBS 2011, Radford Miller 2012), and modelled associations between koala survey records and environmental variables across a broad range of forested regions (Lunney 1987, Smith *et al.* 1992,1994, 1995, Kavanagh *et al.* 1995, Andrews *et al.* 1995, Law *et al.* 2017, 2022a, Goldingay *et al.* 2022). Scat surveys in the Pine Creek State Forest found koalas to prefer floristically diverse and structurally complex multi-aged forests in areas of high site quality with a high stocking of larger trees, an abundance of preferred koala food trees (KFT), and no recent intensive logging (Smith and Andrews 1997, Smith 2004, Radford Miller 2012). Despite these findings and the well-known preference of koalas for larger trees (Hindell and Lee 1987, Lunney *et al.* 2000, Phillips and Callaghan 2000, Moore and Foley 2005, Matthews *et al.* 2007, Ellis *et al.* 2009), the threat to koalas from intensive timber harvesting in tall productive forests appears to have been largely overlooked in conservation planning and management. The National Recovery Plan for the koala (DAWE 2022) does not recognize timber harvesting as a significant threat. The NSW Government Koala Strategy (Department of Planning and Environment 2022) called for "*research into koala response to intensive harvesting of native forests*" by the NSW Natural Resources Commission (NRC) to "*deliver an independent research project to better understand how koalas are responding to intensive harvesting on the NSW North Coast*". Following delivery of research projects undertaken by the Department of Primary Industries Forest Science Unit (not an independent institution) and others, the NSW National Resources Commission (NRC 2021,22) claimed that "*intensive harvesting occurring in the past five to 10 years is unlikely to have impacted koala density*". This conclusion is based primarily on the results of studies by Law *et al.* (2018, 2022a, b) reported in NRC (2021,22) which used remote call monitors or autonomous recording units (ARUs) to record and identify male koala calls and model male calling frequency as a function of mapped environmental variables and logging history in NSW timber production forests. These studies relied on an untested assumption that male and female koalas have similar habitat requirements and a similar response to logging. The acoustic monitoring studies of Law *et al.* (2018, 2022b) failed to detect any adverse impacts of timber harvesting on (male) koala populations leading the authors to claim that "*native forestry regulations provided sufficient habitat for koalas to maintain their density, both immediately after selective harvesting and 5–10 years after heavy harvesting*". This conclusion is now being cited as justification for expansion of timber harvesting in northern NSW State Forests (NRC 2022) using intensive clear-fell practices comparable with those in early woodchip operations in southern NSW and Victoria associated with significant arboreal mammal declines (Recher *et al.* 1980, Lunney 1987, Lunney *et al.* 2014, Smith *et al.* 1985, Smith 2004, 2019, 2020, 2021).

The results of acoustic modelling surveys are inconsistent with the findings of earlier studies that relied on koala scat counts, radio-tracking and spotlighting surveys of both male and female koalas (Smith and Andrews 1997, Smith 1997, Smith 2004, Radford Miller 2012). This discrepancy can be explained by limitations of acoustic monitoring and in particular its failure to measure female koala distribution and abundance. This study tests and rejects the assumption of Law *et al.* (2018, 2020, 2022ab) and the NRC (2021,22) that the habitat requirements and response to logging of male and female koalas are the same, and validates the earlier findings of Smith and Andrews (1997) and Radford Miller (2012), by undertaking simultaneous counts of male and female koalas and male call counts along a gradient of increasing koala habitat quality and decreasing logging intensity. Male koala calling was found to be widespread, frequent (too frequent for rigorous frequency of occurrence habitat modelling), and uncorrelated with female breeding habitat, making call monitoring unsuitable for identifying core koala habitat and for koala conservation planning and management in general. This study also reviews the density, stability and habitat requirements of natural koala populations and provides an alternative paradigm for koala habitat definition, modelling, mapping and conservation that takes into account: actual breeding female koala distribution and abundance; forest productivity; forest structure; the diversity and abundance of locally important food trees; long term local koala population stability (determined by wildfire, drought, logging, predation and hunting disturbance history) and its effects on heritable and induced toxicity of local tree species; the effects of site variation (provenance) on toxicity of local tree species; and the effect of local specialization in koala gut microbiomes in reducing leaf toxicity and determining local food tree preferences.

METHODS

Study Area

The 6400-hectare Pine Creek State Forest study area includes portions of both Pine Creek State Forest and the adjacent Bongil Bongil National Park (BBNP) gazetted in 2003 and is located in coastal northern New South Wales (NSW) approximately 18 km south of Coffs Harbour, on undulating to hilly topography up to 160 m elevation (Figure 1). The study area is divided into two portions dissected by the Pacific Highway and collision with motor vehicles has been identified as a significant threat to koalas in the immediate vicinity of the highway but is not considered a threat elsewhere in the study area (Smith 1997, Lunney *et al.* 2022). Annual rainfall is high (about 1600 mm/annum) and falls year-round but is heavier in summer and lower in winter and early spring. Maximum temperatures are moderate ranging from mean monthly values of 19 C in winter to 27 C in summer (Bureau of Meteorology 2022). Drought and water shortage is not likely to represent the level of threat to koala density reported on the drier margins of its range (Ellis *et al.* 1995). Soils are typically of low to moderate fertility (Milford 1999) but productivity is high with forests attaining heights of 40-60m in gullies and on protected aspects. The Pine Creek State Forest has been extensively logged at low to moderate intensity since the later 1800's and comprises a mosaic of floristic types and structures which do not necessarily reflect the original forest distribution (SFNSW 2000). The area supports four major floristic communities: 1) native plantation forest in areas clear-felled and replanted with Flooded Gum (*Eucalyptus grandis*), Blackbutt (*Eucalyptus pilularis*) or Blue Gum (*Eucalyptus saligna*) and undergoing varying degrees of naturalization by seeding from surrounding forest; 2) Dry Blackbutt (E. *pilularis*) dominated forest on the ridges and more exposed aspects; 3) Tallowwood (*Eucalyptus microcorys*) and Moist Blackbutt (*E.pilularis*) dominated forest on sheltered aspects and lower slopes; and 4) Moist Hardwood forest dominated by natural Flooded Gum, Tallowwood, Blue Gum, Brush Box (*Lophostemon confertus*) and palms in the moist gullies (Smith and Andrews 1997). Forest Oak (*Allocasuarina torulosa*) and a range of other species including Turpentine (*Syncarpia glomulifera*), Grey Gum (*Eucalyptus propinqua*), White Mahogany (*Eucalyptus acmenoides*), Bloodwood (*Corymbia intermedia*), Red Mahogany (*Eucalyptus resinifera*) and Ironbark (*Eucalyptus sideraphloia*) are also widespread, especially in non-plantation forest types. Understorey vegetation is predominantly moist, and a network of rainforest and gully wet sclerophyll forest provides koalas with good shelter from heat and drought and refuge from wildfire.

The study area is largely isolated from other areas of koala habitat by the Bellinger River to the south, the Pacific Highway and coast to the east, and cleared land to the north and west except for two narrow forest corridors about 400-700 m wide that link with more extensive forests along the Great Dividing Range to the northwest across Tuckers Knob State Forest and private land (Figure 1). The study area supports one of the largest known regional koala populations in NSW comprising about 400 individuals (Smith 1997) and has a higher density of koalas than any other arboreal marsupials. It is centrally located within the proposed Great Koala National Park, a plan by the National Parks Association of NSW and affiliated organizations to protect 315,000 hectares of high-density koala habitat in northern NSW by linking 140,000 hectares of existing National Parks with 175,000 hectares of surrounding State Forest. The NSW government (Department of Planning and Environment) has recently announced a process to establish the Great Koala National Park and to halt timber harvesting operations in 106 koala hubs within the area being assessed for the park (www.environment.nsw.gov.au).

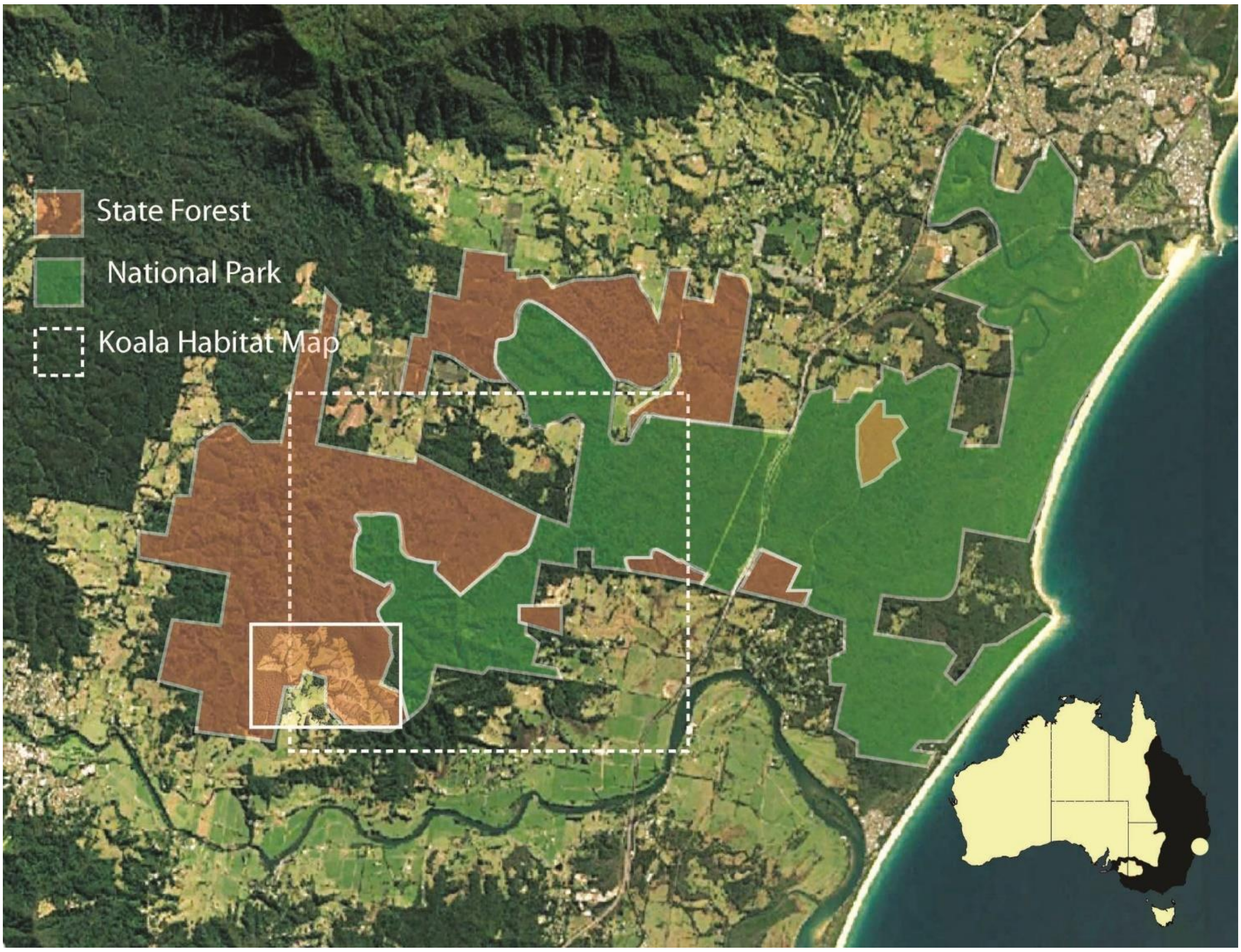

Figure 1. Pine Creek and Bongil Bongil National Park study area (adapted from Google Earth 2023) showing the occurrence of State Forest, National Park, private forest, and forest cover links to the north-west. The large dashed white square identifies a subset of the study area in which koala habitat mapping and the location of transect survey sites are illustrated in Figure 2. The small white square identifies the location of clear-fell timber harvesting undertaken in 2010 shown in more detail in Figure 3. Inset shows koala distribution (black) in Australia and location of the study area near Coffs Harbour NSW (yellow spot).

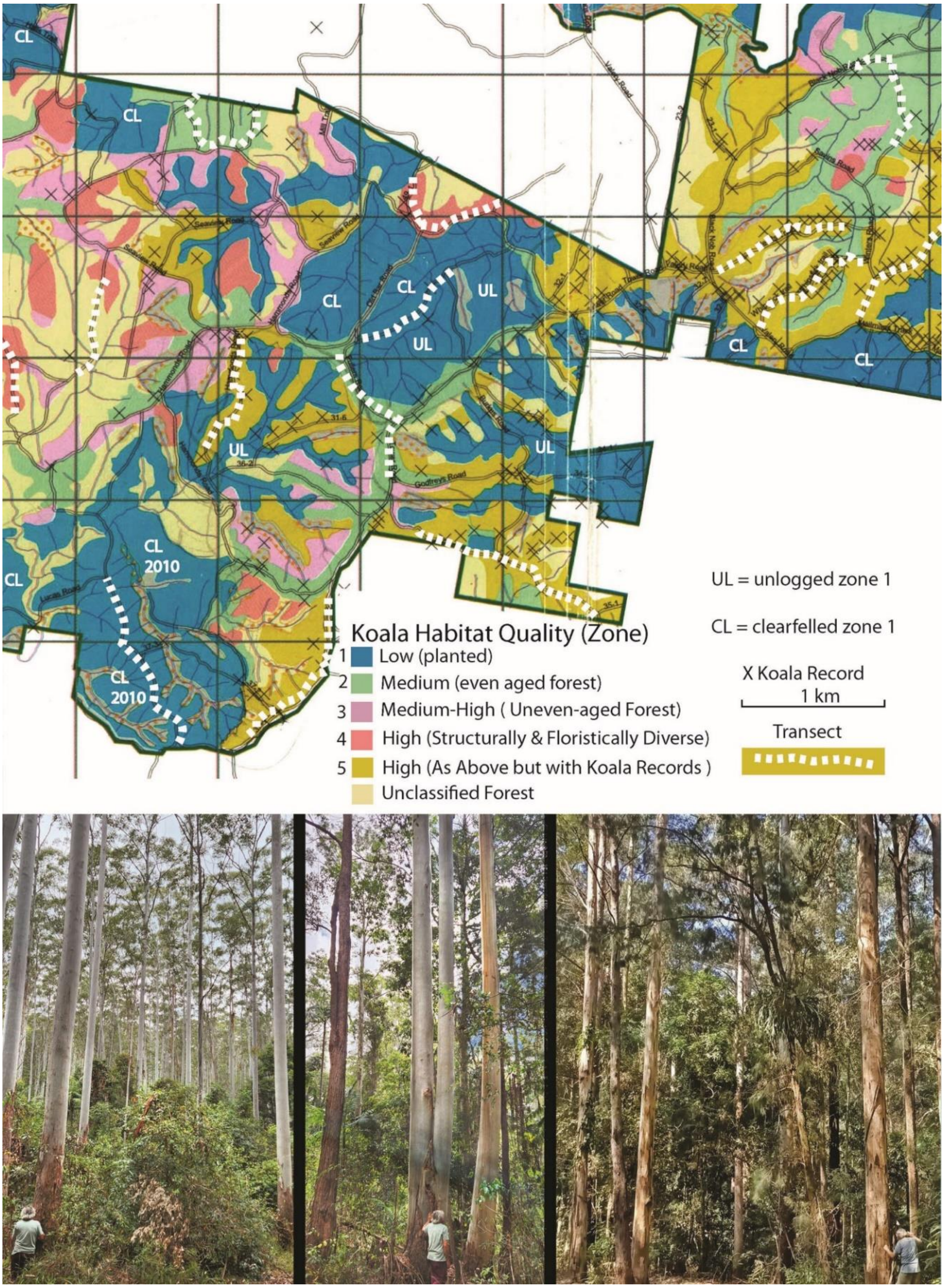

Figure 2. Top. A sample region from the study area showing koala habitat quality mapping (after SFNSW 2000) ranked on a scale of 1-5, the location of transects surveyed in 1998 and 1999, and the location of recent (post 2005) clear-fell timber harvesting operations (CL). Bottom. Examples of forest in zone 1 low quality habitat (left), zone 3 medium quality habitat (centre) and zone 5 high quality habitat (right) photographed (J. Pile) in 2023 to show increasing structural complexity along the gradient.

Logging History

The Pine Creek State Forest has a long history of timber harvesting since the late 1800s (Newman and Partners 1997). Early harvesting concentrated on selective removal of large, good quality stems from a small number of merchantable species within rainforests along gullies which were soon exhausted. By 1969 many of the previously cleared and logged rainforest gullies had been regenerated by sowing or planting with Flooded Gum giving rise to "plantation like" young regrowth forests with a relatively uniform structure and a predominance of stems under 40 cm diameter. In recent years these forests have undergone naturalization to varying degrees following seedling establishment from surrounding native forest, especially by shade tolerant Tallowwoods and Grey Gums preferred by koalas. The surrounding natural forest and intervening areas were subject to small patch harvesting and Timber Stand Improvement (TSI) to remove large old and senescent trees (typically with many large hollows) and reduce competition from logging regrowth. During the 1970's and 1980's harvesting was more selective and large mature trees deemed capable of further growth were retained to provide sawlogs in subsequent cutting cycles (SFNSW 2000). In 1994 intensive large gap clear-felling that removed all standing trees irrespective of size and economic value, re-commenced in the Pine Creek State Forest, and in 1995 the National Parks and Wildlife Service (NPWS) withdrew logging consent after the local community voiced concerns about the impact of clear-fell harvesting on the local koala population (Smith 2004). A committee including representatives of the community, State Forests or NSW (SFNSW), NPWS, timber industry, and conservation groups was formed to oversee preparation of a koala plan of management for Pine Creek State Forest. A scientific study of koala habitat requirements and response to timber harvesting was undertaken in 1996-97 (Smith and Andrews 1997, Smith 1997, Smith 2004) and the resulting findings and recommendations (Florence *et al.* 1997) were considered in preparation of a koala plan of management for the region by SFNSW (2000). Koala habitat was classified into 6 management zones with increasing ratios of conservation to wood production emphasis. The lowest quality, predominantly plantation, habitat in Pine Creek State Forest was zoned for "*wood production emphasis*" but with an overall objective to "*maintain the distribution and abundance of koalas*". The highest quality habitat was zoned for "*koala emphasis*" with an objective to "*enhance the distribution and abundance of koalas as a potential source population for surrounding areas and addition to the interim reserve*." Intensive logging in Pine Creek State Forest recommenced in 2001 with little consideration to these management plan objectives and in response to subsequent community concerns just under half of Pine Creek State Forest was added to Bongil Bongil National Park in 2003 (Smith 2004). In about 2006 clear-felling of the lowest quality forests commenced in the remaining Pine Creek State Forest and by 2011 about 1500 hectares had been cleared and replanted with high wood value species including Blackbutt (Figure 3a).

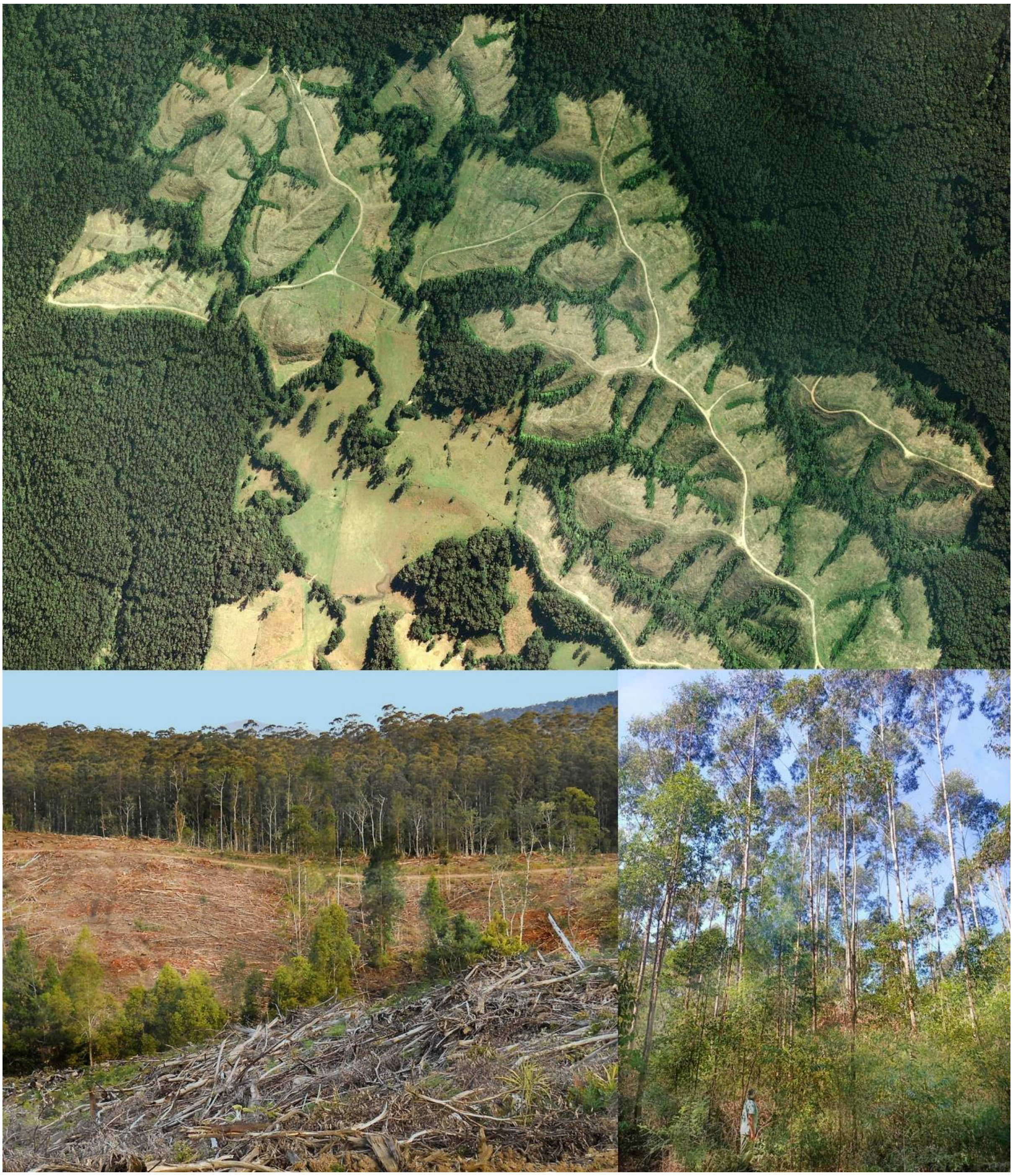

Figure 3 Top, aerial view of a portion of southwest Pine Creek State Forest in 2010 (modified from Google Earth) showing approximately 200 ha of clear-felled forest logged at high intensity on either side of survey transects TB 6 where one koala was seen and five koalas were heard in 1998, representing an estimated density of 0.08 koalas/hectare or a population of about 15 koalas in the cleared area. Lower left, ground view of clear-felling in 2011 and (lower right) ground view of clear-felling regrowth in 2023, 12 years later (J. Pile) showing crowded small diameter stems.

An aerial photograph of the southwest portion of Pine Creek State Forest in 2010 (Figure 3b) shows approximately 200 ha of clear-felled forest on either side of a 1333 m survey transect (TB 6) where one koala was seen and five koalas were heard in 1998, and an estimated population of about 15 koalas was present. In 2012 the Pine Creek State Forest Koala Plan of Management was suspended, and clear felling continued. In 2022 the NSW NRC endorsed an expansion of the large gap clear-felling of the type shown in Figure 3 and carried out in former plantation forest within Pine Creek State Forest to more extensive regions of native forest in northern NSW.

Previous Koala Research in the Pine Creek State Forest

In 1996 NSW State Government funds were provided for an ecological study of koala distribution, abundance, diet, habitat requirements and response to logging with a view to devising ecologically sustainable harvesting strategies consistent with koala conservation. A scientific study conducted in 1996-7 modelled associations between koala scat density and measured environmental variables at 116 stratified sites (Smith and Andrews 1997, Smith 2004). Significant positive correlations were found between koala density and a range of environmental variables including the abundance of locally preferred koala food tree species (Tallowwood, Grey Gum, Flooded Gum, Blue Gum, White Mahogany, Blackbutt, Swamp Mahogany (*Eucalyptus robusta*), Forest Red Gum (*Eucalyptus tereticornis*) and Forest Oak) koala food tree species richness, the abundance and basal area of mature trees (50-80 cm diameter), forest structural complexity, soil type and fertility, and distance away from "plantation" forest. The study concluded that koala conservation in Pine Creek State Forest was inconsistent with clear-felling and high intensity logging that produced low diversity forests with uniform regrowth structure. The study recommended that koala habitat in Pine Creek State Forest be mapped and zoned into areas of increasing koala habitat quality and decreasing harvesting intensity for koala conservation and management (Smith 1997, Florence *et al.* 1997). Following this study and recommendation, koala habitat across Pine Creek State Forest was mapped by the Coffs Harbour Pine Creek koala Support Group under contract to the NSW Government, and the resulting map (Figure 2) provided the foundation for preparation of a koala management plan prepared by SFNSW (2000). The findings and hypotheses of the 1997 study (Smith and Andrews 1997) were tested and validated in part by a postgraduate study of koalas by radio-tracking, spotlighting and diet analysis throughout Pine Creek State Forest between 1999 and 2002 by Radford Miller (2012) who concluded that "*the uneven-aged, species-rich, koala feed tree-rich zones, including the zone based largely on the presence of prior koala records, did indeed have the highest estimated koala densities*". Mapped preferred koala habitat was found to include a higher basal area and species richness of known koala food tree species, and trees > 20 cm diameter. The median asymptotic home range of 7 radio collared female koalas in the Pine Creek State Forest was 6 ha and median male home range of 8 koalas was 6 times higher at 37 hectares, and on average 40% of the home range of both sexes overlapped with other koalas (Radford Miller 2012).

Koala Habitat Mapping

In 1997 koala habitat in Pine Creek State Forest was mapped using Geographic Information Systems (GIS), after the methods of Ferrier and Smith (1992), Smith *et al.* (1997) and Smith *et al.* (2002) to interpolate and extrapolate the predictions of modelled statistical associations between koala records and mapped environmental variables. Only a limited number of indirect mapped environmental variables (topography, geology, forest type, soil type and compartment logging history) could be used in this process because no maps were available for the most important predictor variables (abundance of locally preferred koala food trees (KFTS), koala food tree species richness, and forest structural complexity). Consequently, the resultant maps although significant, when tested against actual koala distribution determined by spotlighting surveys, only explained a small portion of the total variability in koala distribution and abundance. These initial GIS generated habitat maps were only considered suitable for predicting extreme differences between plantation and non-plantation forest and lacked the accuracy necessary to predict and map variations in koala distribution and density within areas of more natural, non-plantation forest. SFNSW forest type maps, based on aerial photograph interpretation (API) of Baur (1965) forest types, were not found to be useful for koala habitat mapping because no significant correlation was found between koala distribution or KFTS abundance and mapped forest type (Smith and Andrews 1997, Smith 2004).

Limitations of koala habitat modelling and mapping using GIS and mapped attributes in Pine Creek State Forest were subsequently addressed by carrying out ground surveys of preferred koala floristic and structural attributes (identified by Smith and Andrews 1997) throughout most of the forest on a 200 m grid. Each grid square was classified into one of 5 habitat suitability classes by engineering surveyors, John Pile and John Murray on behalf of the Coffs Harbour Pine Creek koala Support Group in 1997. This mapping was endorsed by the Scientific Working Group (Florence *et al.* 1997) responsible for advising on koala management and was subsequently incorporated, with some amalgamations and boundary adjustments, into 6 management zones that provided a foundation for the SFNSW (2000) Pine Creek State Forest koala Plan of Management. Zones 1- 5 reflected a gradient of increasing habitat suitability based on forest structure, floristics and site quality (Table 1). Zone 6 included unclassified, degraded and partially cleared areas of variable habitat quality, including high quality areas of some rare communities such as Swamp Mahogany. A sample of this mapping is reproduced in Figure 2 along with photographs of sample habitats from zones 1,3 and 5 photographed in 2023. The accuracy of koala habitat mapping for classifying forest structure and floristics in Pine Creek State Forest was independently validated between 1999 and 2002 by Radford Miller (2012) who measured forest floristics and structure in sample plots across the region and found that KFTS species richness varied strongly across the mapped zone gradient (from less than 1 KFTS in zone 1 to 3.5 species in zone 5) and that the basal area of all KFTS increased strongly (more than 10-fold) across zones 1-4. The mean number of tree stems per hectare also increased from zone 1 to zone 5 and stand basal area was lower in zone 1 but relatively constant across zones 2-5. Forest structure in Pine Creek State Forest has changed in the 23 years since this survey was undertaken, exhibiting a general increase in tree diameter in all unlogged areas and an increase in structural complexity and floristic diversity in unclassified areas and zones 1-2 as these areas have been gradually invaded by non-plantation species.

Zone	Forest Structure	Baur 1965 Forest Type in order of predominance	Site Quality	KFTS Species Richness & Stocking #	Koala Records	Area (ha.)	Koala Habitat Quality Class^
1	Even-aged Plantation	18 (Plantation)	variable	0-1		1972	1
2	Even-aged Native Forest	37 (Dry Blackbutt) 60 (Mahogany, Ironbark Grey Gum)	Low-medium	0-1		844	2&3
3	Uneven-aged regrowth	37, 36 (Moist Blackbutt) 60	medium	1		706	3A-4
4	Uneven-aged mature & occasional senescent	47 (Tallowwood Blue Gum) 48 (Flooded Gum) 60	high	High (2 or more KFTS)		261	4
5	Uneven-aged mature & occasional senescent	47, 48 , 60	high	High (2 or more KFTS)	Known Hot Spot*	950	5
6/0	Variable, uneven-aged to tree-less	Unclassified,	variable	variable		868	0-4

* area with a known high density (> 3 per 400 m) of community koala records
# koala food tree species (KFTS): tallowwood, grey gum, blue gum, forest oak.
^ after (SFNSW 2002 Appendix 2)

Table 1 Criteria used for classification and mapping of koala habitat into management zones (adapted from SFNSW 2000).

Koala Survey Methods

Koala surveys were carried out in 1996, 1998 and 1999 during favourable weather conditions (no strong winds or rain) in the months of October to December by two observers using a walk, listen, spotlight count method. One observer stopped for a 10-minute call listening period every 200m while the other observer continued walking, slowly spotlighting and recording calls between listening stops. In 1996 observers recorded the estimated distance and angle to animals heard and marked call locations on a map where possible to prevent double counting. Calls recorded by both observers from the same koala were identified by triangulation which acted as a check on distance estimation. Faint, distant and poorly discernible calls considered to be more than 200-250+ m away were recorded but not mapped. In 1998/99 surveys calls were allocated to 50 m distance classes from the transect. The sex, age (juvenile or adult), tree selection, tree size and behaviour of all animals was noted where possible. Sex determinations were mostly limited to adult females accompanied by dependent young. Surveys commenced between 1930 and 2030 hours and finished before midnight. In 1996 surveys were conducted on 20 transects with an average length of 2.23 km at road/track locations randomly distributed across Pine Creek State Forest. In 1998 35 survey transects were relocated to fit within mapped habitat zones, with 4-10 replicates in zones 1-5 and 2 replicates in zone 6. Transects in zone 6 were located in relatively tree-less or degraded (failed plantation) habitat and were consequently ranked as class 0 habitat suitability in some statistical gradient analyses. Transects were slightly variable in length depending on the size of mapped habitat zones and averaged 1.04 km in length and about 75 minutes in survey duration. In 1999 surveys were repeated at the same locations as 1998 under similar conditions using the same methods. Sighting data for 1998 and 1999 on the same transect were summed and converted to counts/km to increase the range of values and normalize data distribution for quantitative statistical analyses or were converted to frequency data (presence-absence/transect) for logistic regression analysis using Statistica.

Koala Long Term Monitoring in the Pine Creek State Forest

Koala abundance on five 1.5km long transects located within high quality (zone 5) koala habitat in the Bongil Bongil National Park has been monitored annually by the NSW National Parks and Wildlife Service Coffs Coast Area Staff since 2013 using a consistent method. Transects are surveyed during the mating season (September -October) using a call playback-listen-walk spotlight technique undertaken by supervised volunteer observers. Koala calls are broadcast at four sites spaced at 500 m intervals along each transect. Health, sex and reproductive status (presence of females with young) are recorded where possible. All koalas seen and heard are recorded. Four of the five monitoring transects used by NPWS are located on transects surveyed for this study in 1998/99 and a fifth is close to a transect surveyed in 1998/99 in similar habitat. Koala monitoring data were made available to the authors for the purpose of this study.

RESULTS

Koala Spotlight Counts

Survey effort and the number of koalas observed on walk-listen-spotlight transects during the mating season in 1996, 1998 and 1999 are summarized in Table 2. The number of koalas sighted in 1996 declined rapidly with distance from the transect line and was effectively zero beyond 50 m due to increasing obstruction of koalas from view by tall dense forest vegetation (Figure 4). A polynomial decline function fitted to koala sightings in 10 m distance classes away from the observer found that on average 63% of koalas were concealed from view out to a distance of 50 m. This decline function was used to estimate average koala density across all transects from the density of animals in the first distance interval category (10 m), or by applying a correction factor (2.6) for multiplying with total koala counts out to 50m either side of the transect line to allow for animals not seen. This decline function and correction factor was almost identical to that previously reported (Smith & Andrews 1997) for 161 km of vehicle spotlighting undertaken in an independent survey on all roads in the Pine Creek State Forest in 1996-97. Average koala density on all transects was 0.12 animals/hectare (8.3 hectares per koala) in 1996 and 0.10 animals/hectare (9.9 hectares per koala) in 1998 and 1999 (Table 2).

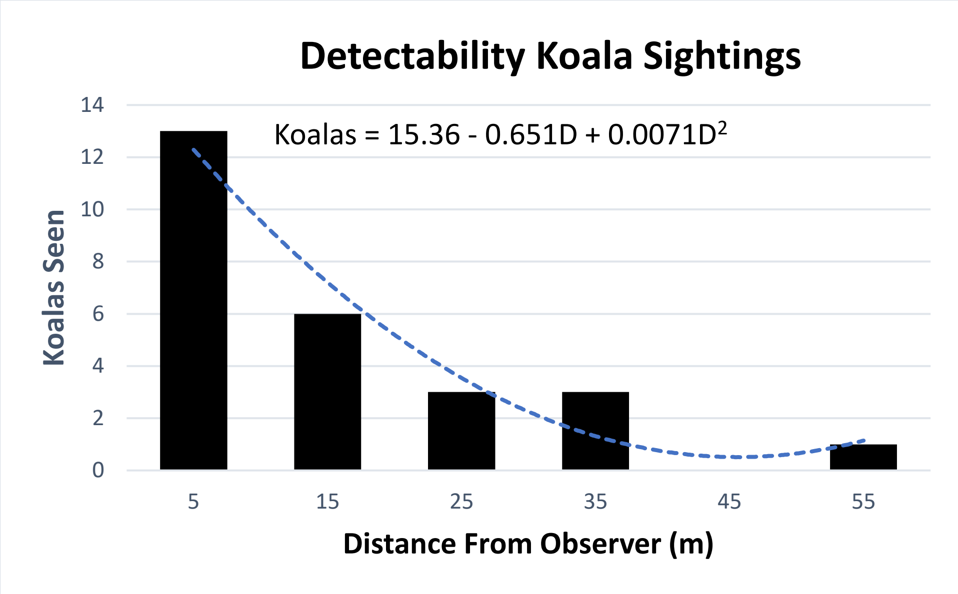

Figure 4 Showing the decline in number of koalas sighted at increasing 10 m distance intervals from the observer.

Survey Year	**1996**	**1998**	**1999**
Sightings			
Total Transect Length (km)	44.500	35.71	35.71
Area surveyed Sightings 100 m strip (ha.)	445	357	357
Area Surveyed Calls 600 m strip (ha.)	890	714	714
Av. Transect Length (m)	2225	1056	1056
Number of Transects	20	34	34
Survey Date	15 Oct-30 Dec	22 Oct-27 Nov	25 Oct-15 Dec
Av. Survey Duration (min)	144	60	-
Koalas Seen to 50m	25	14	14
Koalas Seen/km.	0.56	0.39	0.39
Koalas seen corrected for detectability (x 2.6)	65	36	36
Density Koalas Seen (koalas/ha.)	0.146	0.10	0.10
Calls			
Koalas Heard (inc. faint)	95	84	81
Koalas Heard/km. (Inc faint)	2.13	2.35	2.27
Male Koalas Calling within 150 m	74	63	67
Area Surveyed Calls 300 m strip (ha.)	1335	1071	1071
Males Calling /ha	0.055	0.058	0.062
Ratio of Calls to All Sightings	3.8	6.0	5.8

Table2. Results of koala call counts and koala sightings 1996-1999.

Koala Call Counts

The results of koala call counts are summarized in Table 1. On average koalas were heard 6.3 times more often than they were seen and one koala was heard for every half kilometre walked or every half hour of survey. The number of calls varied with distance from observer but not as steeply, or in the same manner, as the decline in koala observations with distance. The number of calls recorded within 50 m distance classes from the observer (Figure 5) shows that koalas were reluctant to call when observers were nearby (within 50 m). However, the number of calls recorded within the first 50 m right angle distance classes from the transect line (Figure 6) shows that many koalas close to the transect line called before or after observers had passed rather than when they were nearby. This response contributed noise to an overall trend of declining koala calls with distance from the observer. The general pattern of call decline suggests that all or most calls were heard out to distances of about 150 m after which call detectability fell, reaching low levels at distances over 250 m. Twelve percent of all calls in 1996 and 14% in 1998/99 were classified as “faint”, or so far away that their distance could not be estimated reliably, and their location could not be triangulated or mapped. Faint calls are included in the largest (275 m) distance class for the purpose of decline analysis (Figures 5,6) but are likely to have included a spread of distances less and greater than 275 m., rather than a cluster as shown. The largest triangulated distance to a call was 249m.

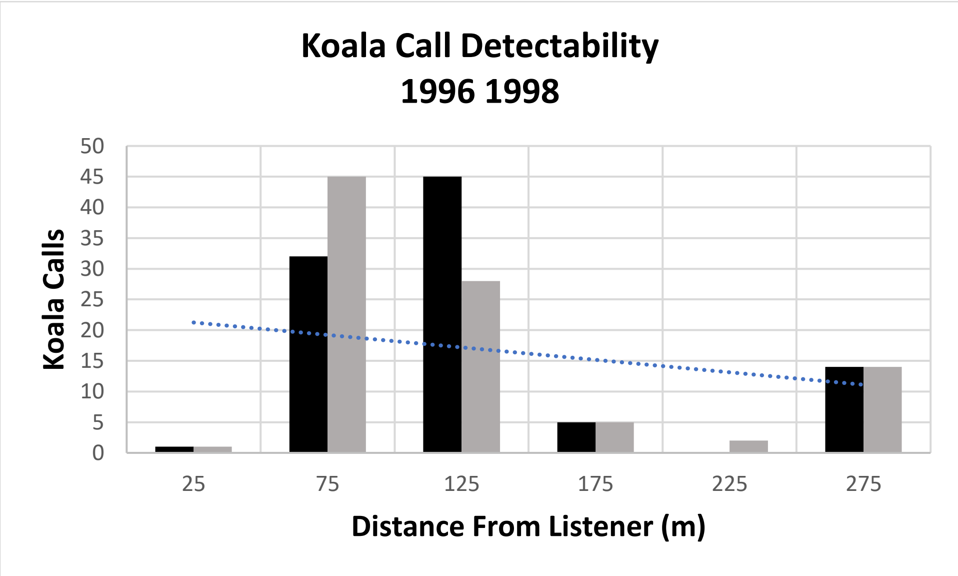

Figure 5 Showing the number of koalas calling in estimated 50 distance intervals from the listener.

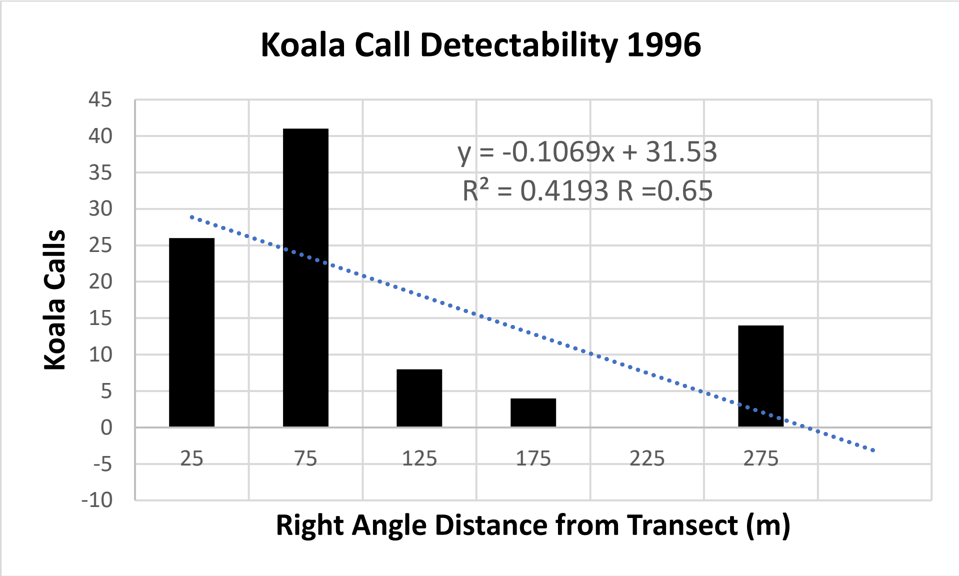

Figure 6 Showing the number of koalas calling in estimated 50 distance intervals from the transect line.

Koala calls can theoretically be used to estimate male koala density if several key variables are known. Firstly, observers must move forward continuously and triangulate calling animals to ensure that none are double counted. Secondly, the rate of decline (detectability decline) of calls with distance from the transect line must be known and used to limit or correct the number of calls counted to estimate density. Thirdly, the proportion of koalas within the sample population that call while observers are passing must be determined. The rate at which koala calls decline with distance suggests that all or most calls are detectible within 150 m, so counts to this distance can potentially be used for density estimation when faint or distant calls and those more than 150 m from the observer are excluded. In 1996, 1998 and 1999 a small percentage (average 4%) of all calls were attributed to females because they were quieter, or involved screaming rather than bellowing, and were sometimes made in response to male bellowing. Our data provide no direct information on the proportion of male koalas in the sample population that called during the period of about 10-20 minutes while observers were passing. However, it is possible to get a rough estimate of this portion by comparing the density of calling koalas with the expected density (calculated as half the density of koalas seen by spotlighting) assuming an even sex ratio across the sample population. This comparison revealed that the density of calling koalas was about two thirds of the level expected from direct sightings in 1996 if all males called and sex ratio was parity, and equal to or slightly higher than expected in 1998 and 1999. Koala populations typically include a higher proportion of resident females (Martin and Handasyde 1990, Gordon *et al.* 1990, Thompson 2006, Ellis *et al.* 2002a) and sex ratios may be male biased in dispersing (transient), non-breeding or sink habitats (see subsequent sections). The ratio of koalas heard to koalas seen per kilometre of transect was lower (3.8) in 1996 than in 1998/99 (5.8 to 6.0), but these values are not directly comparable because transects in 1996 surveyed different habitats which may have had a higher proportion of females (see next section). Koala calling has been reported to decline when it is warm, raining, or windy (Ellis *et al.* 2011; Hagens *et al.* 2018; Law *et al.* 2018; Law *et al.* 2020). Annual rainfall in the nearest meteorological station to Pine Creek State Forest with continuous data (Lower Bucca) was much higher in 1996 than 1998/99 but monthly rainfall in the survey months of September and October was similar (Bureau of Meteorology 2023).

Relationship Between Koalas Seen and Koalas Heard

We initially expected male koala call rates to be a constant multiple of koala sightings, and to test this hypothesis, we correlated calls with sightings after standardizing all calls and sightings to rates per kilometre for each transect to account for variations in transect length. In 1996 there were no apparent trends or significant correlations ($r^2 = 0.02 - 0.04$) between call rates and koala sightings/km (Figure 7). When data were analysed separately for 1998 and 1999 there was a low ($r^2 = 0.19$) but significant ($P< 0.025$) positive correlation between calls and sightings in 1999, and a low ($r^2 = 0.11$) but significant ($P=0.05$ 1 tailed) negative association between calls and sightings in 1998. When call data were combined for the 1998/99 data these trends cancelled each other out and there was no significant correlation between calls and counts (Figure 8). The lack of correlation between calls and counts, and especially the large number of calls on transects in low quality habitats, indicates that male and female koalas are distributed differently across the Pine Creek State Forest with calling males more abundant in low quality habitat and females more abundant in high quality habitat. This hypothesis was tested by correlating the difference between numbers heard and numbers seen in 1998/99 against mapped koala habitat quality (zones 0-5) after dividing the numbers heard by 6.3 to correct them to the same mean detection rate as sightings (an average of 0.8 koalas/km). A significant ($P <0.01$) negative correlation was found between the difference between calls and sightings and habitat quality (Figure 9). Koala calls were about 90% higher than average in low quality habitat and 70% lower than average in high quality habitat. In all three survey years moderate to high numbers of koalas were heard calling on transects where no female koalas were sighted indicating that males are more widely distributed across low quality habitat that appears to be unsuitable for breeding females.

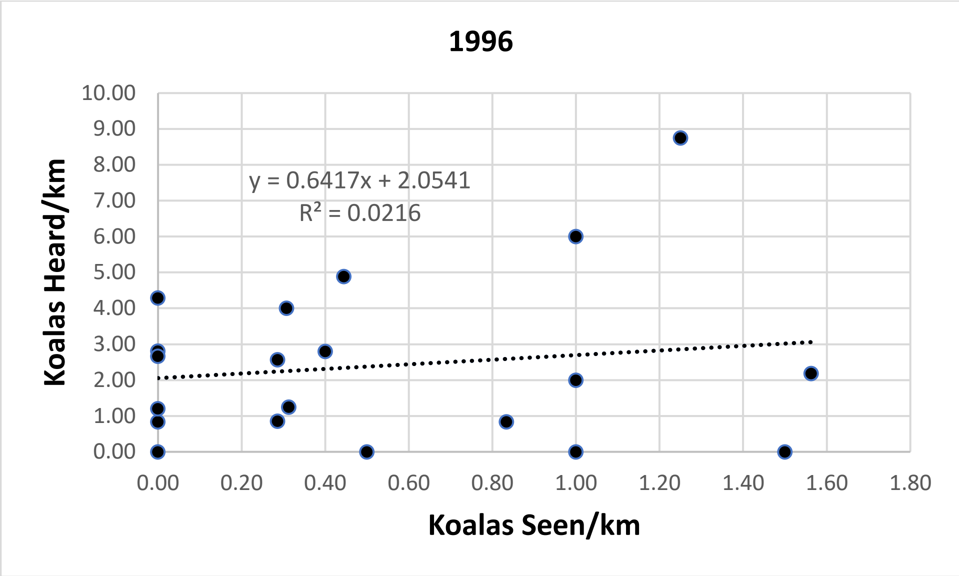

Figure 7 Relationships between number of koalas seen and heard on survey transects in 1996 showing the absence of a significant correlation or trend.

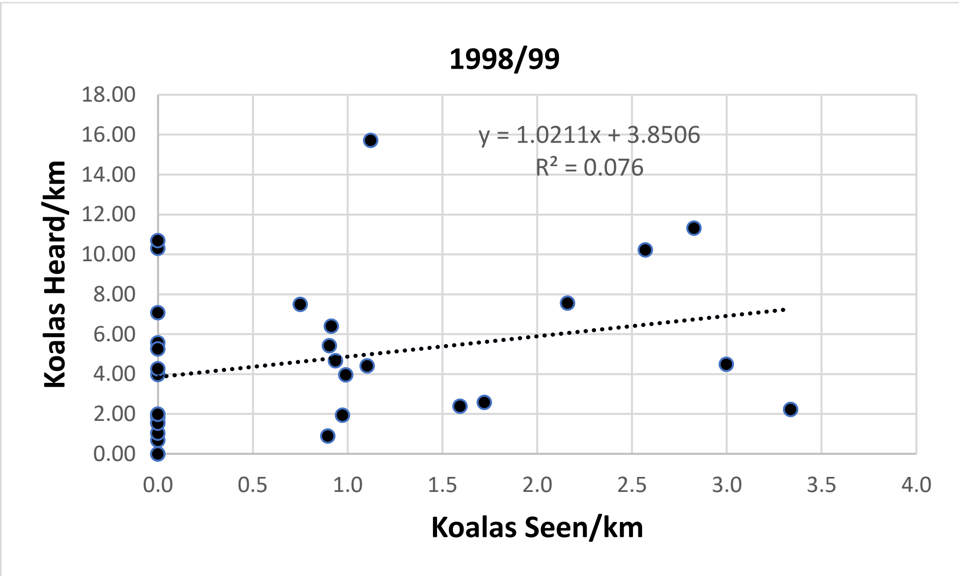

Figure 8 Relationships between number of koalas seen and heard on survey transects in 1998/99 showing the absence of a significant correlation or trend.

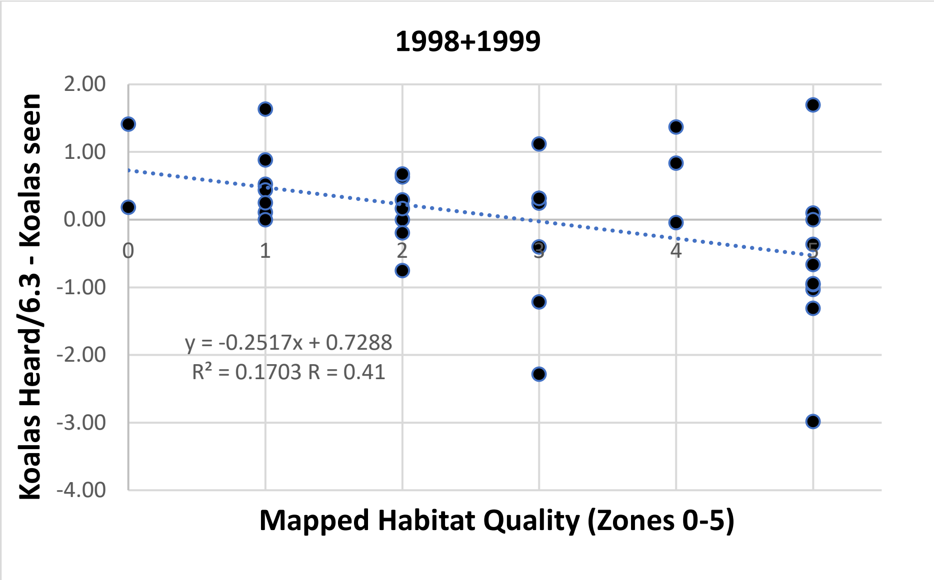

Figure 9 Difference between koala calls/km and koala sightings/km (after standardization to similar means) correlated with mapped koala habitat quality, showing an overall decline in call rate relative to sightings with increasing habitat quality.

Koala Habitat Preferences

Surveys in 1996 were randomly distributed across Pine Creek State Forest, while those in 1998 and 1999 were specifically stratified to fall within one of six mapped habitat quality classes in the Pine Creek State Forest koala Plan of Management (SFNSW 2002, Figure 2). The validity of this mapping was evaluated by correlating the frequency and number of koalas heard and seen/km on survey transects within each habitat zone against habitat quality on a scale of 0-5 and 1-5. Survey transects in 1998/99 were by necessity relatively short (mean 1.04 km) because they were located to fit within patches of the same habitat zone and quality which rarely exceeded 2 km in length. This meant that the effective area surveyed by spotlight on each transect was only about 3.8 hectares which is smaller than average koala home range (about 6 ha. female, 25-37 ha. male) in Pine Creek State Forest (AMBS 2011, Radford Miller 2012). Consequently, some koalas are likely to have been missed by chance on some transects where suitable habitat was present, resulting in some false absences and a low spread of abundance values for quantitative analysis. To reduce noise caused by this sampling problem we pooled counts for 1998/99 to give an effective spotlight search area of 7.6 hectares/transect. We also overcame the problem of small sampling area by examining relationships between habitat quality and the frequency of occurrence (presence-absence) of koalas on transects in different habitat zones using logistic regression. The effective survey area per transect for calls was much higher, about 30 hectares.

This reduced the risk of recording false absences but increased the risk of recording false positives where koala calls originated from nearby patches of a different quality to that found along the transect or from roaming males passing through unsuitable (non-resident) habitat. Many of the mapped koala habitat zones in Pine Creek State Forest are small and narrow (200-500 m wide) so that some koala calls are likely to have emanated from adjacent habitats not representative of that along the transect.

A significant ($r^2 = 0.30$ $P< 0.001$) linear correlation was found between mapped koala habitat zone and koala sightings /km (Figure 10). Koalas were scarce to absent on transects in low quality habitat (zones 1-2) and moderate to abundant on transects in high quality habitat. Logistic regression also yielded a highly significant ($P= 0.002$) relationship between frequency of koala sightings on transects and habitat quality (Figure 11). A logistic regression for sightings of healthy adult females only (predominantly females with dependent offspring) was found to be much steeper than the relationship for all koalas, indicating that reproducing females were largely confined to the highest habitat quality classes (3-5) and scarce in moderate to low quality habitat. This result is consistent with radiotracking studies of Radford Miller (2012) who found tracked female koalas to be primarily distributed in the higher quality habitat in zones 4 and 5. A linear correlation between frequency of occurrence of koalas sighted on transects in 1998/99 (combined) and habitat quality (where degraded habitat in zone 6 is ranked as zero) provided the least noisy and most statistically significant relationship with habitat quality, explaining 94% of the variation in koala frequency of occurrence (Figure 12). No significant correlation was found between the frequency of occurrence of male koala calls and habitat quality (Figures 11, 12) and no significant correlation was found between the number of calling koalas/km and habitat quality (Figure 13) indicating that male koalas were widely distributed across the landscape including areas unoccupied by breeding females.

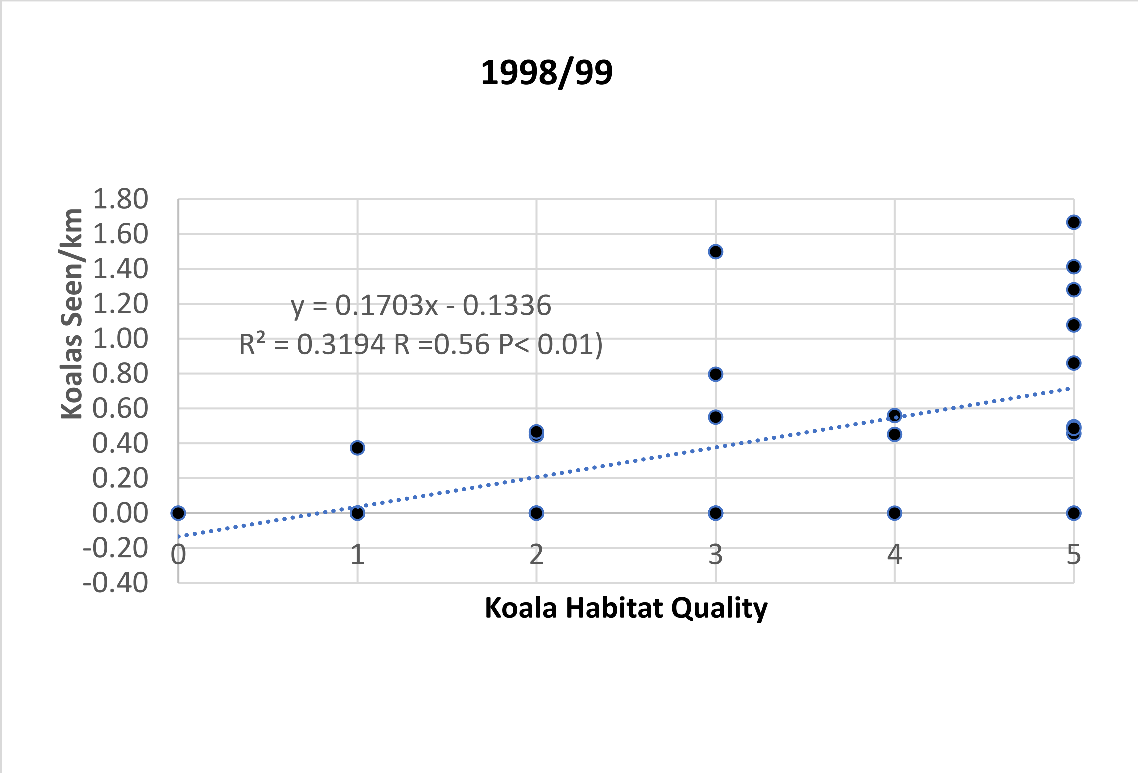

Figure 10 Correlation between koalas seen/km and mapped koala habitat quality (1-5) for combined 1998/99 surveys.

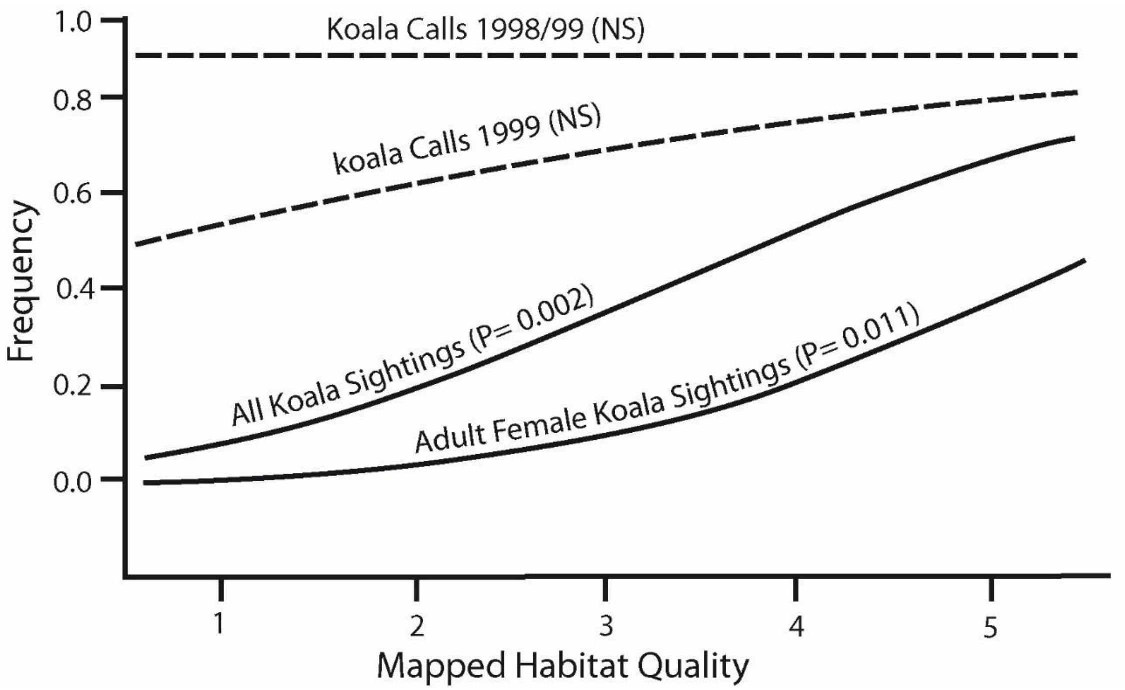

Figure 11 Results of logistic regression analysis of koala frequency of occurrence (0 - 1.0) on transects using calls 1999, calls 1998/99 combined, sightings of all koalas (1998/99 combined) and sightings of

healthy adult females only (1998/99 combined). Broken lines indicate statistically non-significant relationships.

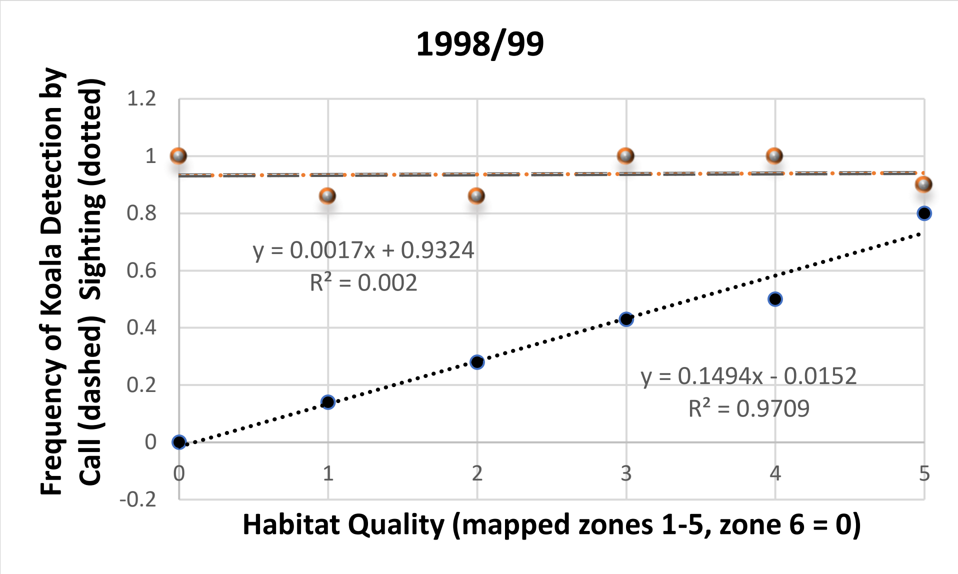

Figure 12 Best model of habitat quality showing the correlation between koala frequency of occurrence on transects and mapped habitat quality (0-5) for calls (dashed line) and sightings (dotted line) using combined data for 1998/99.

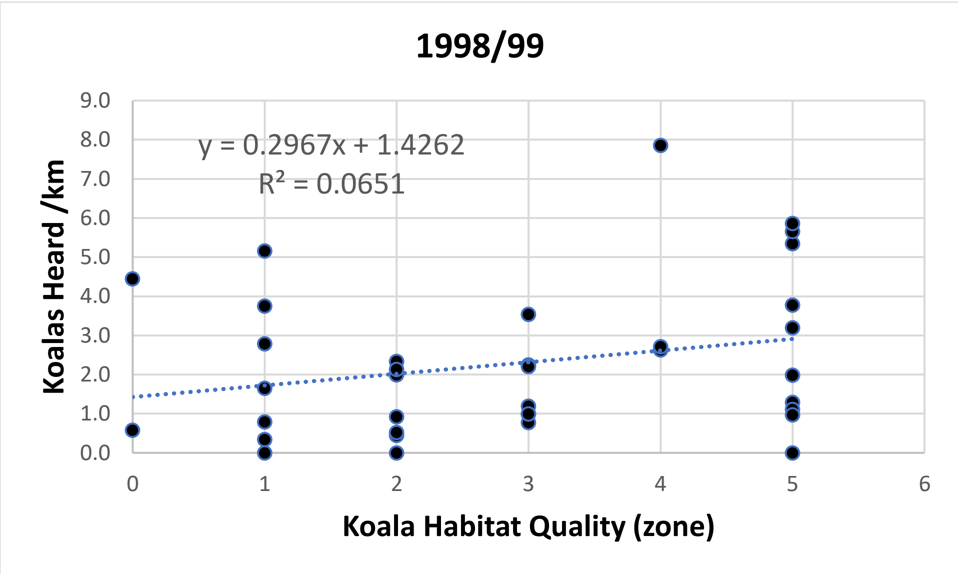

Figure 13 Showing the absence of significant correlation between koalas heard/km and mapped koala habitat quality (1-5) for combined 1998/99 surveys.

Koala Density and Population Size

Koala counts/km were converted to a measure of koala density (counts /ha) by multiplying all animals seen out to 50m either side of each transect by 2.6 (to account for animals present but not seen) and dividing by 10 (surveyed area=10 hectares). Densities were averaged for each habitat zone and multiplied by the area of each zone in the Pine Creek State Forest in 1999 based on SFNSW (2000) mapping to obtain an estimate of population size. Results are presented in Table 3. Zone 6 was not included as this area was unmapped and included low as well as some medium and high-quality habitat. Mean koala density was 0.018 koalas/ha or 56 hectares per koala in the lowest quality (Zone 1) planted native forest, about 2.5 times higher in even aged Flooded Gum with some KFTS regrowth (zone 2) at 0.053 koalas/ha or 19 hectares per koala, about 5 times higher in medium to high habitat quality forest (zones 3 and 4) and 11 times higher in zone 5 at 0.2 koalas/ha., or 5 hectares per koala. Zone 5 forest was floristically and structurally similar to zone 4 but included areas with an abundance of previously reported koala records or sightings known locally as koala “hotspots”. Overall density in selectively logged, non-plantation forest (habitats 2-5) averaged 0.13 koalas/ha. or 7.7 hectares per koala and overall density in zone 1-5 forests was 0.096/ha or 10.4 hectares per koala. These densities are broadly consistent with expected densities based on the known home ranges sizes of koalas in the Pine Creek State Forest. Radiotracking studies in 120 ha. of forest adjacent to the Pacific Highway in the Pine Creek State Forest recorded 13 koalas in 120 ha forest or O.11 koalas/ha) in an area of mixed habitat quality including significant areas of zones 4 and 5 (AMBS 2011). Radford Miller (2012) captured and radio tracked 27 koalas to more than 10 fixes in the Pine Creek State Forest and reported mean female home range of 6.4 hectares and males home ranges of 37 hectares. Female home ranges were mostly exclusive and rarely overlapped with other females while male home ranges frequently overlapped other males and females. Females shared 53% of their (95% Kernel) home ranges and males shared 34% giving unique home range areas of about 4.8 hectares for females and 31 hectares for males or 13 hectares for both males and females if each koala uses half of each overlap zone and sex ratio is parity. Koala population size is likely to have changed since surveys were undertaken in 1999, increasing in unlogged habitats due to increases in tree size in zones 3-5, and recruitment of additional food tree species such as Tallowwood in zones 1 and 2, and decreasing in areas where subsequent clear-fell logging has been undertaken.

Habitat Zone	Number of Transects	Koalas/ha.	Mapped Area*	Population
1	7	0.018	1972	35
2	7	0.053	844	45
3	7	0.098	706	69
4	3	0.083	261	22
5	10	0.203	950	193
Total	36	0.076	3783	364

Table 3 Koala densities in habitat zones 1-5 showing mean values for 1998/99 combined. Data for zone 6 (degraded or unclassified habitat) not calculated due to lack of adequate sampling. *Areas from SFNSW 2000.

Koala Long Term Monitoring and Population Trends

Long term annual monitoring of koala calls and sightings has been carried out since 2013 on or close to five of the transects surveyed in 1998/99 located in high quality koala habitat (mapped zone 5). State Forest at these locations in Pine Creek State Forest was transferred to Bongil Bongil National Park in 2003. Average koala sightings and call counts/km on these transects in 1998/99 are consistent with averages recorded at the same or nearby locations over the period 2013-2022 (Figures14, 15). No statistically significant change in koala density is apparent in high quality koala habitat (zone 5) over this time. There is a trend of declining koala sightings within high quality habitat in the National Park from 2013 to 2022 but this is not statistically significant and could be an artefact of tree growth or increased rainfall over the same period increasing foliage cover and reducing koala detectability. The ratio of calls to sightings varied considerably between 2013 and 2022 and was lower on average (2.9) than in 1998/99 (4.4). No significant correlation was found between the number of koalas seen and the number of koalas heard on monitoring transects, consistent with a similar lack of correlation across the wider Pine Creek State Forest study area found in 1998/99, providing further evidence that koala calls cannot be relied on as a measure of koala density for measuring habitat quality at local scales.

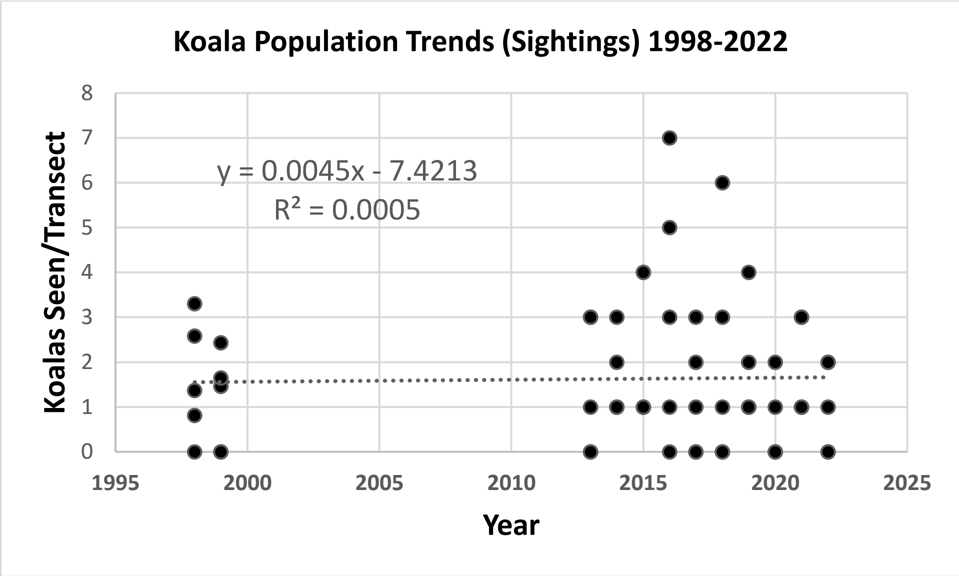

Figure 14 Koalas seen/1.5 km transect in 1998 and 1999 and 2012-2022 for five transects in high quality koala habitat.

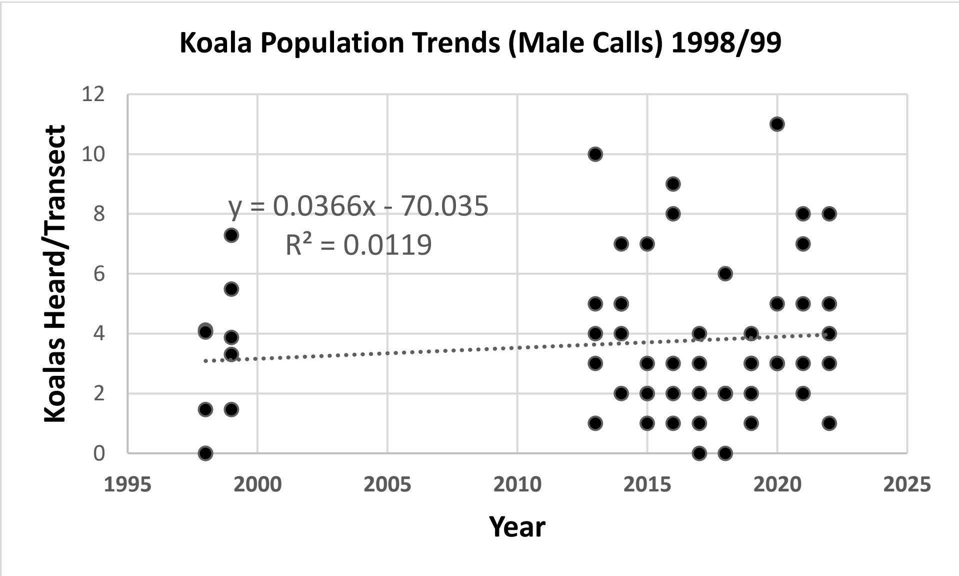

Figure 15. Koalas calls per transect in 1998 and 1999 and 2012-2022 for five transects in high quality koala habitat.

DISCUSSION

This study compared the effectiveness of call counting, direct observation (by spotlighting) and koala scat surveys for modelling and mapping koala distribution, habitat and response to logging within a 6400-hectare study area in Pine Creek State Forest and Bongil Bongil National Park in northeast New South Wales (NSW). The study area was classified and mapped (by ground survey) on a 200m grid into 5 zones of increasing koala habitat quality based on the occurrence of key, ground measured environmental site attributes previously found to be significantly correlated with koala scat abundance. These included the species richness and abundance of locally preferred koala food tree species (KFTS), forest age, forest structural complexity and the type and intensity of past logging. Habitat quality zoning is effectively a gradient of increasing time since logging, decreasing logging intensity and increasing tree species diversity or naturalness. The highest quality habitat has only been lightly selectively logged to remove large and old senescent trees and is characterized by a high diversity of tree species and a high density of trees across all size classes, while the lowest quality habitat is characterized by young (20-35 year) structurally uniform trees often of a single species regenerating after clear-fell harvesting and replanting (Figure 3). The reliability of habitat quality mapping for predicting core koala habitat was tested by undertaking simultaneous koala call counts and spotlight surveys over two consecutive years. The density and frequency of sighted koalas, especially adult breeding age females, increased with increasing koala habitat quality. Sighted koalas, especially breeding females, were scarce or absent (0.018/ha) from low quality forests (predominantly 20–35 year old Flooded Gum plantings) and moderately abundant (0.2/ha.) in structurally complex, dense, more natural forest in areas subject to historically low intensity harvesting that removed large older living and senescent trees. Male koalas were more widespread in all habitats including low quality habitat. This indicates that the male koala population is likely to comprise two parts, a resident breeding part that occupies higher quality habitat with breeding females and a second non-breeding or transient part that occupies low quality or unsuitable (sink) habitat with few or no breeding females. This pattern is consistent with the known social behaviour of male koalas including their occupation of much larger home ranges than females, aggressive territorial exclusion of smaller or unsuccessful males, and female biased sex ratios in breeding areas (Eberhard 1978, Mitchell 1989, Thompson 2006, Ellis *et al.* 2001).

Long term monitoring of koala density in a subset of mapped high-quality habitat in Bongil Bongil National Park shows that average koala density in this habitat has been relatively stable (has not significantly increased or decreased) over the past 25-year period and has fluctuated around a mean of 0.29 koalas per hectare over the past decade despite the occurrence of droughts. This comparative stability over such a long time is an indication that koala population density in Bongil Bongil National Park is likely to be at carrying capacity set by the foliage biomass and toxicity (or palatability) of local food tree species and individuals. Stable populations are those in which either reproductive rates are reduced to balance mortality, or in which those individuals surplus to population capacity are forced to disperse into surrounding unoccupied forests including sink habitats where they die prematurely and mortality exceeds reproduction. Both strategies are known to occur in koala populations. Martin (1985) reported a decline in koala fertility following defoliation of preferred food trees in Victoria, and Eberhard (1978) found that a koala population on Kangaroo Island was regulated by increased mortality amongst dispersing sub-adult koalas. The results of our surveys, in conjunction with radio-tracking studies in the same area (AMBS 2011, Radford Miller 2012), are consistent with a population regulation strategy in which surplus male koalas are forced to disperse throughout low quality habitat, (unsuitable for female reproduction) in search of vacant territories, while female koalas primarily remain within areas of high quality habitat and reproduce only in years when sufficient food of suitable quality is available to provide them with the additional nutritional and energy requirements for lactation. Lactating female koalas require up to 20% more food intake than non-lactating females (Krokenberger 1993). Vegetation in the study area is a mosaic of forest patches of different habitat quality (Figure 2) including some patches that are smaller than average koala home range. Radio-tracking studies of koalas throughout Pine Creek State Forest between 1999 and 2002 (Radford Miller 2012) have shown how koalas utilize this mosaic. Forty percent of female home ranges and 73% of male home ranges included multiple mapped habitat quality zones. Koalas were selective in their location of home ranges but once located koalas used all Eucalyptus tree species within their home range in approximate proportion to availability, except for patches containing Grey Gum that were occupied more than expected. Koala home ranges were located non-randomly with respect to forest type, with habitat zones 3-5 preferred followed by zone 2, then zone 1 and last zone 6. Vegetation within koala home ranges contained a higher density of *Eucalyptus*, and higher richness of KFTS, more KFTS, and almost twice as many Tallowwoods and three times as many Grey Gums and Iron Barks as random vegetation samples. Koala habitat was sexually segregated with males favouring areas with higher stem densities, smaller trees, and lower basal areas than females. Female home ranges also contained much greater proportions of preferred food trees Tallowwood and Grey Gum and lower proportions of Blackbutt and Flooded Gum than the male home ranges (Radford Miller 2012).

The findings of this study validate ground-based koala habitat mapping in Pine Creek State Forest (SFNSW 2000) and by inference the key underlying environmental variables used to classify and map forests into zones of increasing koala habitat quality. The absence, or low density, of breeding female koalas in young (20-30 year old) uniform aged forest dominated by a low diversity of tree species reported by Smith and Andrews (1997), and confirmed in this study, is evidence that breeding female koalas in Pine Creek State Forest are likely to be eliminated by high intensity, clear-fell logging of the type carried out in Pine Creek State Forest since 2005 (Figure 3) and currently underway in nearby forests (J. Pile, A. Smith unpublished observations). The conclusion that female koala populations in Pine Creek State Forest will be eliminated by clear fell harvesting contradicts and is irreconcilable with recent claims by the NSW National Resources Commission (NRC 2021, 22) that "*intensive harvesting occurring in the past five to 10 years is unlikely to have impacted koala density*" and findings of Law *et al.* 2022b) that "*native forestry regulations provided sufficient habitat for koalas to maintain their density, both immediately after selective harvesting and 5–10 years after heavy harvesting***".** The latter claims are based on findings and conclusions of recent surveys (Law *et al.* 2017, 2018, 2022, NRC 2021,22) that used remote call recorders to model male koala distribution and response to harvesting in NSW timber production forests. These same surveys are also currently being used to justify expansion of clear-fell harvesting in northern NSW State Forests (NRC 2022) using practices comparable with those in 1960's and 1970's woodchip production areas of southern NSW and Victoria. The conclusions of NRC (2022) and Law *et al.* (2017,2018, 2022ab) rely on an unproven assumption that male and female koala distribution and habitat preferences are identical, and that the frequency of male koala calls in intensively logged forest is a reliable and accurate indicator of core female koala habitat, or female koala abundance and long-term reproductive success, in logged forest. The findings of the current study demonstrate that this assumption is invalid. Core koala habitat has previously been defined as "*an area of land with a resident population of koalas, evidenced by attributes such as breeding females (that is, females with young) and recent sightings of and historical records of a population*" (NSW Government State Environmental Planning Policy No 44 (SEPP 44). This is an important functional definition of koala habitat because it explicitly excludes areas of forest that are occupied temporarily by transient koalas, especially males, dispersing or moving around in search of mates, and excludes low quality sink habitats occupied by surplus koalas without resident territories and where population density is unstable and mortality exceeds reproduction. The frequency of koala calls in Pine Creek State Forest did not correlate with the number of male and female koalas sighted and the distribution of male koala calls differed from that of female koala sightings. These findings show that male and female koalas are distributed differently across the landscape, with calling males widespread in both low and high quality habitat while adult breeding females are largely confined to high quality habitat. This result is consistent with the findings of independent radio tracking studies by Radford Miller (2012) who found that sexual segregation of habitat and available forage occurred within Pine Creek State Forest with female koalas monopolising habitat containing more Tallowwood and Grey Gum and larger trees, leaving males in habitats with more Sydney Blue Gum, Forest Oak, Blackbutt, Flooded Gum and smaller trees. It is also consistent with evidence from dietary studies on St Bees Island in North Queensland (Tucker *et al.* 2007) that dispersing koalas are excluded from preferred tree species and habitats by resident adults, and the reported social behaviour of koalas generally, in which population regulation is achieved by territorial exclusion and dispersal of surplus young, especially males (Eberhard 1978, Gordon *et al.* 1990). Our findings lead us to conclude that the failure of Law *et al.* 2022b to find an impact of intensive logging on koalas is an example of a type 2 statistical error (acceptance of a null hypothesis that there is no effect of timber harvesting when in fact there is) caused by widespread distribution of transient male koalas in suboptimal or sink habitat, and deficiencies in habitat modelling that rely on limited available mapped GIS layers (Smith *et al.* 2002, Law *et al.* 2017, NRC 2020, 2022, Goldingay 2022) rather than ground surveys of unmapped variables for prediction. We conclude from these findings that koala habitat models, especially those based on acoustic monitoring and large-scale GIS layers, are not reliable replacements for actual ground survey of female koalas for the purposes of koala conservation and management.

Limitations of Song meters and Call Counts

Law *et al.* (2018) proposed that acoustic surveys of male calls can account for imperfect detection of koala presence by other methods (scat surveys, spotlighting) for the purpose of koala conservation and management because large numbers of recorders can be deployed at low cost and detection frequency per site is higher than for other survey methods. We find no support for this claim, and conclude from the results of our study, and our review of other studies that have used acoustic counting methods (Law *et al.* 2017, 2018, 2021, 2022ab, NRC 2022, Goldingay 2022) that acoustic call recording is unsuitable for koala habitat modelling, mapping and impact assessment and that the findings of studies using this method should be disregarded as unreliable, for the reasons listed and discussed below.

1. Koala calls are made primarily by males (97%, this study) which have higher levels of mobility, larger home ranges and different habitat preferences and distribution patterns to females, making them unsuitable for modelling and mapping core female breeding habitat.
2. Call rates vary with season, weather, time of day (Ellis *et al.* 2011; Hagens *et al.* 2018) making them unreliable for modelling across wide regions sampled at different times of year or under different conditions.
3. Koala calls may be difficult to identify with certainty on recorders when scanned with acoustic software without time consuming manual checking for false positives and negatives (Law *et al.* (2017).
4. Not all male koalas call. Male response to other male calls may vary with the social status of the caller and listener. In Southeast Queensland adult males typically approach the calls of other males, especially small ones, while juvenile males ignore or move away from calls and females show no response (Jiang *et al.* 2022).

5. Koala calls are recorded over such large areas (up to 38 hectares) that there is a real chance of recording false presences because koalas are calling from a patch of different habitat type from that surrounding the recording locality. This is a particular problem for the logging impact studies of Law *et al.* (2022) where calling koalas may reside in small patches of retained filter strip or corridor.
6. Male koalas have much larger home ranges than females (6 x in Bongil Bongil National Park) which means that males occupy extensive areas of forest that they do not require for foraging, and which may be unsuitable for sustaining reproducing female koalas or male koalas over the long term. It also means that males must be much more mobile than females and consequently may traverse large areas of unsuitable habitat, or sink habitat, in search of mates or new territories. Results of our study show that males are widely distributed and abundant in areas of low quality habitat not occupied by breeding females.
7. The number of koala calls per site made by remote recorders cannot be used as a quantitative measure of koala abundance because it is not possible to distinguish between multiple calls made by one individual and single calls made by multiple individuals. This problem is usually overcome by measuring the frequency of sites where koalas are present as a measure of koala abundance. However, the relationship between animal frequency of occurrence and animal density is non-linear (Caughley 1997) except at low frequencies (<20%). At high frequencies (>60%,) density may increase 5 fold with only small changes in frequency (within bounds of chance or normal random variation) which means that the chance of making a type 2 error greatly increases, and significant associations with environmental variables may be missed or disguised by normal background noise when frequency of detection rates are higher than about 60%, which is often the case with acoustic monitoring because of the large area surveyed (38 hectares) and the long time period that recorders are left out (7 days or more). It has been shown (Hagens *et al.* 2018) that the probability of recording koala presence using acoustic recorders increases with the number of survey nights in low quality habitats from near zero after one night to 100% after ten nights, which indicates that male koala abundance measures determined using this method open to manipulation and effectively meaningless without standardization of survey duration. In this study we found male call frequencies to exceed 80% in combined 1998/99 survey data after just 20-40 minutes of listening which proved too high for reliable analysis of frequency associations with mapped habitat quality (Figure 11).
8. Reliance on remote recorders (song meters), or unsighted calling koalas, to record koala abundance precludes any opportunity to gather additional important information about koala

health, sex, age, and reproductive status and consequently fails to distinguish between core breeding habitat (where the population is stable or expanding) and sink habitat where the population is constantly renewed by immigration of a dispersing surplus from elsewhere.

The only merit that we perceive in acoustic monitoring is for mapping very broad koala distribution (presence/absence) at state and national scales, or for searching for new koala populations in large areas of currently, unsurveyed habitat, but even then there is no way of determining whether these records are from resident breeding individuals or transient, dispersing males in unsuitable habitat, such as those reported by Close *et al.* (2017) in the Sydney region which dispersed 45 km in nine months. One study (Hagens *et al.* 2018) has reported a significant correlation between male koala calls/hr. on acoustic recorders and koala density at 10 survey sites across the state of Victoria, which is inconsistent with our findings. We consider this correlation to be an artefact of an abnormal sampling distribution (akin to fitting a linear regression between two points or two clusters) driven by an overly steep koala density gradient arising from inclusion of unnaturally high-density koala populations (3-8 animals/ha) in a plantation at Bessiebelle (southwest Victoria) and introduced populations at Cape Otway and Phillip Island (Southern Victoria) in their database. When this correlation is re-run with just the 7 more normal density populations (<2/ha) there is no correlation between koala density and male koala calls/hour consistent with findings in this study.

Limitations of GIS layers koala Habitat Modelling and Mapping

A key aim of koala habitat models is to generate accurate maps of predicted koala distribution for conservation planning and management at local and regional scales. Habitat maps can only be generated from models that predict koala abundance as a function of a limited number of “mapped” environmental variables stored in Geographic Information Systems (GIS) layers. They cannot be generated using “unmapped” variables measured on the ground at survey sites such as forest age, forest structure, food tree diversity, the abundance of locally preferred food trees, or the occurrence of logged stumps and fire scars. This presents a significant limitation for accurate and reliable koala habitat mapping at local scales in areas such as Pine Creek state Forest and Bongil Bongil National Park where koala density may vary more than 10-fold over short distances (200 m) in complex mozaics. Smith and Andrews (1997) generated a statistically significant GIS model of koala habitat and distribution in Pine Creek State Forest using available mapped variables (elevation, topography, geology, soils, forest type and compartment logging history), but when tested by spotlight survey against actual koala distribution the model was only found to be suitable for predicting gross differences between plantation and non-plantation forest. To overcome this problem and develop a map that could more accurately predict koala density in non-plantation habitat every 200 m grid square in Pine Creek State Forest was surveyed, classified, and ranked on a scale of 1-5 (SFNSW 2000) to reflect increasing forest age, structural complexity, diversity of preferred koala food trees and koala food tree abundance. The reliability of this mapping was independently verified by Radford Miller (2012) and found to accurately reflect a gradient of increasing koala habitat suitability (as described by Smith and Andrews 1997). To the best of the author's knowledge this is the only region in Australia where the problem of unmapped environmental attributes has been overcome by undertaking complete ground surveys to map the occurrence of locally important environmental variables as a foundation for koala habitat management.

The most common approach to dealing with the limitation of unmapped variables in other studies has been to overlook the problem and develop less accurate and rigorous models using only large scale existing mapped variables, such as topography, vegetation type, geology, soil type, modelled climate, and limited (recorded) disturbance history (Smith *et al.* 2002, Law *et al.* 2015, 2017). While many of these models may be statistically significant, they seldom explain more than a small amount of the true variation in koala abundance and consequently have little or no predictive accuracy or reliability at local management scales. The inappropriate application of large-scale models to local scale management has been found to have serious adverse consequences for arboreal mammal conservation in Victorian timber production forests. Statewide models of Greater Glider distribution (Lumsden *et al.* 2013, VicForests 2019, DELWP 2020) used by VicForests as a planning and management tool to predict Greater Glider probability of occurrence in logging coupes as a substitute for undertaking local ground surveys, failed to correctly predict Greater Glider occurrence at 46 out of 58 logging coupes leading to inadequate protection on 78% of logging coupes (Smith 2021). Failure to accurately predict as little as 20% of threatened species occurrences can be considered a high conservation risk (20% population loss each logging cycle), a risk that can be avoided simply by undertaking pre-logging spotlight surveys. Even the best GIS models are unlikely to accurately predict threatened species occurrence more than 50% of the time. A common cause of this inaccuracy, in addition to lack of suitable GIS layers, is that the scale of predictions cannot, by definition, be any more spatially accurate than the scale of variation in the underlying mapped data used to make the prediction, and these data are often very coarse (kilometres to tens of kilometres), especially in the case of climate data which are extrapolated from a small number of climate stations. Law *et al.* (2017) claim to have generated a koala habitat model at a scale of 250 m resolution that could be used to guide management, but simply dividing a coarsely mapped environmental variable into small squares does not improve their predictive accuracy or reliability to the scale of division.

In 2015 the NSW Environment Protection Authority tested the predictions of five different koala habitat models generated using mapped environmental variables against actual koala scat occurrence at a range of test sites in northern NSW (Smith 2015, EPA 2016). These models included: 1) a PCT (plant community type) model based on the likely occurrence of koala food trees in different mapped vegetation communities; 2) a RN17 forest type model that equated mapped forest types of Baur (1965) with primary, secondary or non-habitat; 3) an Office of Environment and Heritage (KHM) Boosted Regression Tree model that correlated over 10,000 known koala presence and absence sites with over 140 mapped or remotely sensed environmental variables; 4) a DPI Department of Primary Industries (Law *et al.* 2015) internally validated koala habitat model that predicts koala probability of occurrence in 250 m grid squares based on algorithms that compare koala Atlas records with a range of mapped environmental and landscape variables, and 5) an Office of Environment and Heritage baseline koala map (Predavec *et al.* 2015) which predicted the likelihood of koala occurrence based on the proportion of koala records from within a suite of mammal records in 10 km × 10 km cells. No significant correlation was found between the PCT, RN17, KHM models and koala scat abundance, and a significant negative correlation was found between scat abundance and the DPI (Law 2015) model (Smith 2015). A significant, but poor, correlation (r=0.210) was found with the baseline koala map (Predavec 2015) which simply demonstrates that koalas are more likely to be found in regions where they have previously been reported. The best model (a combination of the KHM and RN17 models) was statistically significant ($r=0.21$, $p< 0.04$, $r^2 = 0.04$) but explained only 4% of the variation in koala scat abundance which is too low for koala management. Law *et al.* (2017) subsequently generated a 250 m resolution MaxEnt koala habitat model for northern NSW and south-east Queensland which the authors claim to have validated using independent acoustic surveys and a food tree model at 63 sample sites spread over geographic distance of around 500 km with a bias toward upper (28 sites) and lower slopes (32 sites) and state forests subject to timber harvesting. Findings of this study show that acoustic surveys cannot be used to validate female koala habitat because they do not measure the density of breeding females at sample sites. A significant correlation was found by Law et al. (2017) between predicted and actual male koala occurrence across the broad survey region, but much of this habitat could be unsuitable to females and simply represent sink habitat occupied by transient, roaming male koalas such as those described by Close *et al.* (2017) which moved over 45 km across the landscape in 9 months. Also, because the model of Law *et al.* (2017) was generated over a large geographical distance, the resulting statistical associations with male koala abundance are likely to have been driven largely by broad (regional scale) differences in primary productivity (eucalyptus leaf biomass) that change predictably with elevation and climate. The map of koala habitat generated by Law *et al.* (2017)

for northern NSW shows a range of 9 different habitat suitability classes that generally increase across a gradient of increasing rainfall and site productivity (foliage biomass) from west to east, and decrease with increasing elevation as productivity declines with cooling temperatures. This model predicts little variability in koala density within local regions such as the Pine Creek State Forest study area. It is also inappropriate to validate acoustic models using food tree models, because, as discussed in more detail in the next section, food tree preferences of koalas are highly variable and inconsistent from region to region.

Limitations of Primary and Secondary Koala Food Trees for Predicting koala Habitat

Koala density is broadly determined by a combination of primary productivity (the amount of leaf produced per hectare of forest) and the proportion of leaf that is palatable to koalas. Koalas are well known to be fussy eaters and to prefer a limited number of *Eucalyptus* trees commonly referred to as ‘Primary’ or ‘Secondary’ koala food trees (DECC 2008). Classification and mapping of vegetation communities according to their proportion of primary and secondary koala food trees based on listings such as those in the NSW Government Recovery Plan for the koala 2008 (now superseded) is a common approach to modelling koala habitat for conservation and management purposes (Mitchell *et al.* 2021), and has been used to ‘pseudo-validate’ koala habitat models (Law *et al.* 2017), even though there is no proven correlation between koala density and mapped forest type at local scales (Smith 2004, 2015). Smith and Andrews (1997) found no correlation between mapped forest type and koala scat density in Pine Creek State Forest. This lack of correlation is unsurprising and can be attributed to regional and local variations in primary productivity, the occurrence of locally unique food tree preferences and inaccuracies in vegetation mapping. Vegetation community mapping is generally interpolated from a small sample of survey sites classified by aerial photo interpretation (API) and validated by limited ground truthing (e.g. Watson, Elks, and Smith 1999). In the senior author’s experience API classifications are rarely more than 50% accurate at local scales. Smith and Andrews (1997) tested the accuracy of SFNSW forest type mapping in Pine Creek State Forest by ground survey at 119 sites and found that only 35% (range 0- 70%) of sites were correctly mapped.

Koala dietary preferences vary considerably between localities and regions (OEH 2018), and frequently include tree species not listed as primary or secondary koala food trees in policy and planning documents (Ellis *et al.* 2002b, Sullivan *et al.* 2003, Smith 2004, Woodward *et al.* 2008, Cristescu *et al.* 2011). The second most frequently consumed koala food tree species in Pine Creek

State Forest (*A. torulosa*) is not included on the DEC (2008) koala recovery plan list of koala food trees for the NSW north coast. An analysis of koala scats from Pine Creek State Forest (Smith 2004, MacGregor unpublished) found Koalas to feed on almost all the available *Eucalyptus* and many non-eucalypt tree species (16+ species) in the study area, but to prefer some tree species more than expected and others less than expected based on their natural occurrence. The most abundant remains in scats were from Tallowwood (39%), Forest Oak (11%) Sydney Blue Gum (9%), Grey Gum (7%) and Turpentine (6%). Sydney Blue Gum was consumed about four times more than expected, Tallowwood 2.6 times more than expected, Grey Gum 2 times more than expected, Turpentine 2.5 times less than expected and Forest Oak 1.5 times less than expected on the basis of tree occurrence in survey plots where scats were collected (Figure 16). Blackbutt, which is a common dominant tree in Pine Creek State Forest, was consumed 4 times less than expected, but is a favoured food tree on Stradbroke Island, while Brush Box (a non-eucalypt) contributed only 1% of the diet in Pine Creek State Forest but was the equal most frequent species in koala scats on Stradbroke Island (Cristescu *et al.* 2011). Eucalypts in the genus *Corymbia* were largely avoided in Pine Creek State Forest but have been reported in moderate abundance in the diet of koalas in the Sydney region (Sluiter *et al.* 2001). Red Gum, which is a well-known primary koala food tree, was eaten less than Blackbutt on North Stradbroke Island and little more than Brush Box (Woodward *et al.* 2008). Exploitation of *Syncarpia* and *Allocasuarina* appears to be locally unique in Pine Creek State Forest and Bongil Bongil National Park, and the importance of these tree species as koala food trees has been overlooked by the NSW Natural Resources Commission (NRC 2022). Feeding on Forest Oak may be important to koalas at this locality because of its nitrogen fixing capability and likely high foliage nitrogen content. Radford Miller (2012) found that female koalas increase their intake of *Allocasuarina* and Monocalyptus (Blackbutt and White Mahogany) during the breeding season and decrease their intake of Grey Gum and Blue Gum. Supplementing the diet with Forest Oak should enable koalas to increase their protein intake for reproduction and exploit more eucalypt foliage with low available nitrogen levels, including older mature leaves and the foliage of eucalypt species in the subgroup Monocalyptus (now *Eucalyptus*) which typically have high nitrogen binding tannin levels that can reduce protein intake below levels required for maintenance. Smith and Andrews (1997) found that *Allocasuarina* was scarce (10% of levels in all other forest types) in previously clear felled and re-planted forests indicating that this species is likely to be particularly sensitive to elimination or reduction under current intensive logging practices.

Local and regional variation in koala food tree preferences can be attributed to four main known causes; a) inherent (genetic) variations in palatability and toxicity between tree species and individuals,

b) environmental site variations in toxicity between individuals within the same tree species inhabiting different regions (Moore *et al.* 2004), c) induced changes in levels of leaf toxicity and palatability in response to folivore browsing pressure (Borzak *et al.* 2016), and d) differences in individual koala gut microbiomes which affect their ability to detoxify or overcome the chemical defenses of different tree species (Marsh *et al.* 2021). *Eucalyptus* trees have at their disposal a wide range of chemical defenses for reducing herbivore browsing including water content, fibre and lignin content, protein content, protein binding tannin content, toxins (particularly oils), and antifeedants that suppress intake including formylated phloroglucinol compounds (FPCs) and unsubstituted B-ring flavanones (UBFs) (Ellis *et al.* 1995, Moore and Foley 2000, 2005, DeGabriel *et al.* 2009, Marsh *et al.* 2019). Considerable variation has been reported in the levels of these chemicals between tree species, between individuals within species and between leaves within trees (especially between young and old leaves and leaves in the upper v lower crown). Habitat models for eucalyptus folivores that rely on forest type or community type, or rely on lists of so-called primary koala food trees, for mapping and impact assessment (eg Law *et al.* 2017, NRC 2022) ignore this considerable intraspecific variation in foliage quality. Moore *et al.* (2004) found that levels of phenols, FPCs and oils in Tallowwood, the most preferred koala food tree in Pine Creek State Forest, varied more than 4-fold between individual trees, increasing linearly with site quality, elevation and decreasing with mean minimum atmospheric temperature. High levels of variation between individual trees in different regions provides an environment for selective elimination of less well defended trees in habitats with high levels of folivore browsing pressure. Moore *et al.* (2004) found that koala scats were more common under larger, less chemically defended individual trees with lower levels of cineole and the koala antifeedant FPC sideroxylonol. Excessive targeting of such individual trees by koalas over time can be expected to lead to a reduction in their growth and competitiveness and their eventual displacement by more heavily defended individuals, except where these trees are able to induce higher levels of defense in response to folivory. *Eucalyptus* trees shed their leaves every 2-4 years and generally reduce the levels of nutrients in leaves as they age re-directing them to new growing foliage before they are shed (Fife *et al.* 2008). This indicates that eucalypts have the capacity to move chemicals around the canopy and potentially to increase the level of toxins and antifeedants in direct response to herbivore browsing. Plants are known to increase airborne volatile signals to neighbouring branches and to send down stem signals via the plant vascular system in response to leaf wounding (Heil and Ton 2008). When koalas chew on *Eucalyptus* leaves they release volatile compounds that are likely to alert neighbouring branches and trees of the attack, allowing the tree to mount an induced defense by raising levels of toxic chemicals and antifeedants in new or existing leaf growth. Studies of toxins in *E. globulus* trees

(Borzak *et al.* 2016) have shown that levels of sideroxylonal and cineole are 30-50% higher in new than old leaves, and that levels in new leaves are further elevated by 24-37% in trees that were partially defoliated relative to control trees that were not defoliated. The increase in toxin levels in new leaves regenerating after defoliation was accompanied by a comparable decrease in toxin levels in older retained leaves lower in the canopy indicating that this change is an induced response by the tree to increase protection of new leaves which are those most frequently targeted by insects and mammalian herbivores, particularly the smaller folivores such as greater gliders (*Petauroides volans*) (Henry 1985, Kavanagh and Lambert 1990). Condensed tannins, which are thought to inhibit browsing by mature leaf eating mammalian folivores like koalas by binding with proteins and reducing digestible nitrogen intake below maintenance levels (DeGabriel *et al.* 2008), also varied with leaf age and defoliation history but in a reverse direction. Condensed tannins were 50% more abundant in older leaves in the lower crown and increased by a further 30% in older, lower leaves of trees that were partially defoliated. These findings show that individual *E. globulus* trees can respond to defoliation by increasing the cineole and sideroxylonal content of new young leaves (by transfer from older leaves) and by increasing the condensed tannin content of old or mature leaves. The magnitude of these induced changes equalled or exceeded natural underlying genetic differences in toxin levels between individual trees sampled from different geographic regions. Inherent (genetically determined) toxicity levels were lower in *E. globulus* from Tasmania (where koalas and greater gliders are absent) than mainland Australia. These studies, which show that koala food trees are not passive participants in forest ecosystems but actively elevate their chemical defenses in response to browsing, have profound implications for koala conservation and management. They show that arboreal folivores should limit browsing of individual trees to low levels that do not trigger an induced increase in toxicity by changing food trees frequently and by not returning to a browsed tree for long periods or until after induced increases in toxicity have returned to background levels. Observations of feeding by eucalyptus folivores show that this is precisely how they behave. Greater gliders typically change individual food trees frequently, harvest only a small portion of foliage on each tree during each feeding bout and move daily despite the increased exposure to predators (Henry 1985). Koalas similarly change food trees frequently, move about 180 m daily despite the increased risk of predation when coming to the ground to move between trees, seldom feed on the same tree twice within long observation periods and progressively feed on almost all the available *Eucalyptus* tree species and individuals and many non-eucalypt trees within their home ranges (Krockenberger 1993, Matthews *et al.* 2007, Matthews et al 2016, Ellis *et al.* 2009, Radford Miller 2012). In Pine Creek State Forest Radford Miller (2012) observed koalas in trees where a koala had previously been sighted on only 78 out 711 occasions (11%)

during radiotracking surveys of up to 6 months duration. Scat analysis of koala diet in Pine Creek State Forest (Smith (2004, MacGregor K., unpublished) found an average of 10 different tree species per scat and remains of almost all the available *Eucalyptus* and many non-eucalypt tree species (16+ species) across the study area. The need to minimize induced toxicity in host foliage could also explain the findings of Smith and Andrews (1997) that koala density is strongly correlated with tree species richness or variety of food trees and not just their abundance, as different tree species are likely to have different levels and types of induced response and to require different types of gut microbiomes for digestion. Different tree species may also be required to sustain koalas in different seasons and under different weather conditions including dry periods and droughts (Ellis et al 1995). Radford Miller (2012) found that female koalas change their diets seasonally increasing intake of high nitrogen *Allocasuarina* and eucalypts in the subgroup Monocalyptus (*E. acmenoides* , *E. pilularis*) and decreasing their intake of eucalypts in the subgroup Syphyomyrtus (*E. propinqua, E. grandis, and E. saligna*) during the spring breeding season. The need to minimize induced toxicity in host trees by changing food trees after feeding and not returning for long periods explains why koalas require such large home ranges and have relatively low densities in natural forests with a long history of browsing pressure, such as those in the study area. Induced toxicity provides a simple, plausible feedback mechanism for host trees to regulate koala population density and browsing pressure in forests to levels that do not adversely affect tree growth and survival. Under this mechanism high browsing pressure increases foliage toxicity to a level that reduces dry matter (energy) and nutrient (nitrogen) intake below minimum requirements for breeding in female koalas, leading to slowed or suspended reproduction until the koala population stabilizes or declines and browsing pressure decreases.

Recent evidence indicates that the ability of koalas to exploit different tree species in different regions and seasons is related to localized variations in the occurrence of specialized microorganisms in their gut microbiomes (Marsh *et al.* 2021). Individual koalas have site specific gut microbiomes which they inherit from their mothers or other females by ingestion of special maternal faeces or ‘pap’ excreted directly from the caecum. Pap inoculates young with microflora enabling them to digest *Eucalyptus* and other leaves after weaning. Pap has a high water content (82%) and 23-41 times higher count of tannin-protein-complex degrading enterobacteria than normal faeces (Osawa *et al.* 1993). Gut microbiomes differ between individual koalas and these differences limit the tree species that individual koalas ingest. Certain streptococci and enterobacteria found in koalas that feed on Eucalypts in the subgroup Monocalyptus (characterized by high levels of tannins and low levels of available nitrogen) may be essential for releasing tannin bound proteins and making this tree group more palatable (Osawa 1992, Osawa *et al.* 1993). Similarly, Ruminococcaceae found in koalas feeding on

Messmate (*Eucalyptus obliqua*) are thought to assist koalas in the digestion of recalcitrant celluloses enabling them to maintain energy balance on the tough, highly fibrous foliage characteristic of this species (Brice *et al.* 2019, Marsh *et al.* 2021). Once these essential taxa have been lost from koala microbiomes, which is likely to occur in individuals that feed on a few easily digestible species, or single tree species, in captivity, plantations or logging regrowth, there is no evidence that they can be regained in the short term. Koalas brought into captivity and fed different tree species are unable to change their microbiome unless they are inoculated with gut microbes from other individuals adapted to different diets (Blyton *et al.* 2019). This suggests that koalas can only eat leaves from some trees species if they have an appropriate microbiota, and that composition of the gut microbiome is likely to influence and limit koala food choice. The microbiome of translocated koalas has been found to influence the species of *Eucalyptus* they ate in their new habitats (Blyton *et al.* 2023) suggesting that koalas must select tree species compatible with their gut microbiomes. A low diversity or absence of suitable gut microbiomes could explain why some dispersing and translocated koalas have been reported to move large distances (Close *et al.* 2017) and why koalas are frequently absent from large areas of apparently suitable habitat. It may also explain the existence of koala “hotspots”, and why one of the best predictors of koala occurrence is “where koalas have been recorded before” (Predavec *et al.* 2015). Together, available studies of koala diet, foraging behaviour, induced toxicity and gut microbiomes, indicate that koalas can adapt to feed on almost any available local Eucalyptus species over time, that food preferences are locally or regionally unique, and that elimination of koala populations from large areas after intensive/extensive disturbances such as wildfire, intensive logging and drought may disrupt the continuous transfer of locally adapted gut microbiomes from mothers to daughters within a population presenting a significant threat to their ongoing survival that may take many hundreds or even thousands of years to overcome.

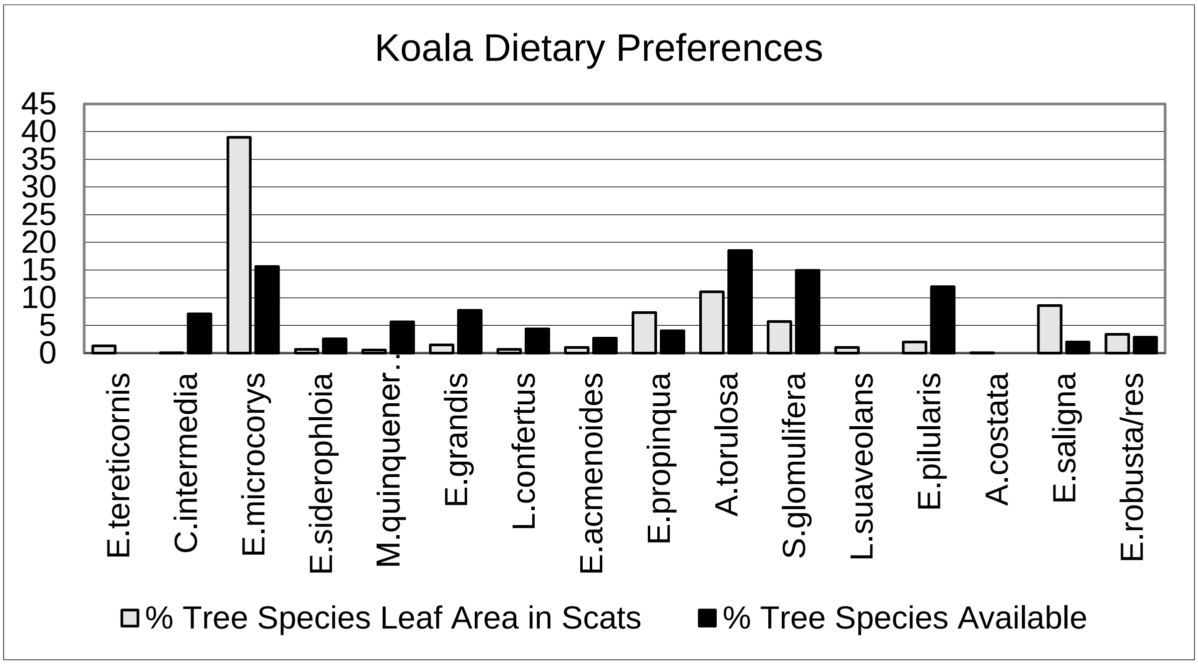

Figure 16 Percentage area of remains from different tree species in koala scats in the study area relative to tree species abundance in scat survey plots. (After Smith 2004 and MacGregor unpublished).

Koala Population Density and Long-Term Stability

Koala populations have the capacity to expand rapidly and attain abnormally high densities (1-18/ha) in some offshore islands, mainland remnants, peri-urban habitats and plantations where they have been introduced or re-introduced after long periods of prior absence. These unnaturally high densities commonly lead to dieback and death of preferred food trees and subsequent koala population declines (Masters *et al.* 2002, Menkhorst *et al.* 2019, Wallis 2013, Whisson and Shimmin 2006, Whisson *et al.* 2016, Whisson and Ashman 2020). Koala population irruptions in areas where they have been introduced after a long period (thousands of years) of scarcity or absence provides strong evidence that selective browsing pressure by koalas regulates the tree species composition of natural forests by selectively eliminating less well defended tree species and individuals over time. It follows from these observations that koala density in natural forests will be lower in forests with long term stable koala populations and a long stable history of browsing pressure. The Pine Creek State Forest and Bongil Bongil National Park study area supports a mosaic of tall wet and dry sclerophyll forest and rainforest on undulating topography across a network of moist drainage lines which provides a high level of protection against intense fire and drought enabling this region to support one of the largest and most stable koala populations in NSW (Smith 1997). Koala population density (0.29 animals/hectare) in high quality habitat (zone 5) in Bongil Bongil National Park within the study area has been relatively stable for the past 25 years despite significant climate fluctuation and drought during this period (Figure 15). Stable koala densities have also been reported in similar forest habitat in the Richmond Range region of the NSW north coast (Goldingay *et al.* 2022) and within the broader Coffs Harbour region, despite the occurrence of drought (Lunney *et al.* 2015). This relative stability of koala density in mid-low elevation north coast forests is strong evidence that koala populations in these forests are at carrying capacity or 'in balance' with their host trees. Female koalas are unlikely to occupy home ranges larger than necessary to satisfy their energy and nutritional requirements for growth and reproduction because this will increase predation risk and increase unnecessary energy expenditure. Carrying capacity in high quality habitat in the study area appears to be 0.29 koalas per hectare or a minimum 3.5 hectares of forest per female koala. Free living koalas consume about 70kg (males) to 85 kg (lactating females) of dry leaf per year (Nagy and Martin 1985, Krockenberger 1993) or up to 25 kg/hectare per year at densities of 0.29 koalas/hectare. This is around 1% of expected annual leaf production in a high rainfall forest with an annual litter fall of 5000 kg/hectare/year (of which about half is assumed to be edible leaf and the balance bud, stem and bark material, Grig and Mulligan 1999). Greater Gliders, which also feed almost exclusively on *Eucalyptus* foliage, have a similar impact on *Eucalyptus* foliage, consuming about 18 kg leaf per year (Foley *et al.*.1990) or 18 kg dry leaf per hectare per year at densities of 1/hectare. Greater Gliders are 5-6 times smaller than koalas but occur at higher densities (0.5-2.0/ha) and feed more selectively on young growing tips of larger trees rather than mature adult leaves (Henry 1985). Relatively low levels of leaf consumption by these arboreal folivores indicate that *Eucalyptus* trees in natural forests have evolved successful defensive mechanisms for limiting mammalian herbivore browsing rates to around 1-2% of total annual leaf production on average, or up to 5% of leaf production in some preferred tree species. Levels of 1-2% loss are small, relative to average annual leaf area loss in *Eucalyptus* forests of 5-15% (Gherlenda *et al.* 2016) from all sources including insects, and unlikely to adversely impact the growth and survival of host trees. However, higher levels of folivore browsing (> 2-5%) are likely to reduce tree growth rates resulting in the long-term selective elimination of susceptible individuals and increased survival of those with a greater capacity for induced or inherent defense against folivores including koalas. This implies that forest koala populations with average densities more than about 0.3 - 0.6 koalas/hectare, such as those occurring in some plantations and many introduction areas, are likely to be unstable and will trend to lower densities and possible local extinction over the long term.

On the Importance of Structure and the Effects of Timber Harvesting in koala Habitat

Numerous studies have found that koalas have a preference for larger trees for both sleeping and feeding (e.g. Lunney *et al.* 2000; Phillips and Callaghan 2000; Moore and Foley 2000; Matthews *et al.*.. 2007; Ellis *et al.* 2009). Hindell and Lee (1987) found koalas in the Brisbane Ranges of Victoria to prefer larger trees and forests with a higher density of medium to large trees. Marsh *et al.* (2013) found that Koalas spend more time resting in larger trees because they provide suitable forks for sleeping but spend time in smaller trees at night. In drier parts of their range at Gunnedah on the northwestern slopes of NSW koalas have been found to select larger and taller trees during the day to provide shelter from heat in summer (Crowther *et al.* 2014). A 10-year study of tree selection by koalas on Phillip Island found them to prefer trees of larger size but to select individual large trees with lower levels of FPCs and higher levels of nitrogen (Moore and Foley 2005). In Pine Creek State Forest Smith and Andrews 1997 found that koala scats were more abundant than expected at the base of larger trees and there was a general increase in scat abundance with increasing forest age, structural complexity, and predominance of larger stems. Scats occurred more frequently than expected in trees of 30-120 cm dbh and less than expected in trees under 20 cm dbh. Koala scats were found under 10-20 cm diameter trees but only in stands with a mixture of larger trees including some > 50 cm dbh. Koala scats were absent from uniform aged regrowth (plantation) stands less than about 35 years of age and with no stems > 50 cm dbh. Scats were most abundant in mixed age forests with a high overall tree stocking (tree density) in all size classes including young regrowth (10-40 cm dbh), advanced regrowth (41-60 cm dbh) and mature (60-80 cm dbh). There was a general linear increase in scat density with the number of tree stems > 50cm dbh per hectare. Radio tracking studies in Pine Creek State Forest have shown that these structural preferences differ between the sexes with males more prevalent in uniform young stands and females in structurally complex older stands (Radford Miller 2012). These earlier findings are corroborated by the present study which found male koalas to be widely distributed and moderately abundant in uniform aged young (20-35 yr) plantation forests in management zones 1 and 2 while breeding female koalas were effectively absent from these areas. Larger trees and denser, more uneven aged stands provide multiple benefits including: a) a higher foliage biomass per tree; b) the provision of suitable forks for sleeping; c) the provision of scaffolding that provides easier access to terminal branches and outer foliage of understory trees; d) lower levels of toxins (FPCs) in some larger trees (Marsh *et al.* 2013); e) increased shade; and f) reduced risk of predation. Smith and Andrews (1997) hypothesized that dense, complex forest structure improved koala density by enabling more efficient koala foraging and movement from tree to tree. Because of their large size koalas, unlike the much smaller Greater Gliders, are unable to support themselves on small outer branches and must break them off or pull them down from a larger branch to feed. Larger trees provide scaffolding for koalas to access young leaves on the growing tips and small outer branches of younger trees, especially shade tolerant Tallowwoods and Grey Gums emerging from below the upper canopy. A high stocking or density of large trees also enables koalas to move from tree to tree by leaping, instead of coming to the ground, which carries an increased risk of predation by wild dogs which were abundant in Pine Creek State Forest. This is the only koala habitat in Australia in which the senior author has observed koalas leaping from tree to tree while feeding and moving. This behaviour has also been witnessed in Bongil Bongil National Park by Martin Smith (unpublished observations). Structurally dense and older forest stands also typically carry a larger foliage biomass which means that daily energy requirements can be satisfied in a smaller overall area.

None of the preceding findings are consistent with the NRC (2021,2022) conclusions that current native forestry regulations that permit the use of high intensity logging enable koalas to maintain their density 5–10 years after heavy harvesting. We have previously established that the findings of Law *et al* (2022b) apply to only male koalas and not female koalas, but we also consider it likely that these findings for male koalas are partially an artefact of sampling problems associated with use of remotely deployed acoustic recorders. Because of their large area of coverage (up to 38 ha) and long recording duration, there is a high likelihood that acoustic monitors failed to detect real declines in male koala density after logging due to detection of calls from koalas sheltering in unlogged filter strips and corridors retained within logged areas and calls from dispersing or displaced male koalas simply moving through logged forest in search of new habitat. Furthermore, in their study Law *et al.* (2022b) equated logging intensity with m3/ha. of wood volume removed (from compartment history records), but this is not an accurate or rigorous measure of harvesting intensity because it does not record wood volume before and after harvesting or the volume of non-commercial tree stems felled and left on the forest floor. A high wood volume may be removed by a low intensity harvesting operation in a highly productive forest and low wood volume may be removed by a high intensity operation in a low productivity forest with a high proportion of culled, non-commercial species like Forest Oak and Grey Gum. Smith and Andrews (1997) examined relationships between recorded (compartment) logging intensity and forest structure in Pine Creek State Forest and found no correlation between recorded logging intensity and existing forest structure. The only reliable way to measure logging intensity is to report stand structure (the number of tree stems in incremental size classes) before and after logging. It is extremely unlikely that high intensity logging, such as that undertaken in Pine Creek State Forest in recent years and shown in Figure 3, would have no impact on male koala density 5-12 years on because 12 year old trees are too small for climbing, resting and avoiding predators, the diversity of tree species is too low to sustain a diverse gut microbiome, and the biomass of foliage is insufficient to sustain a normal koala population density.

Law *et al.* (2022b) also claimed support for their findings from studies which found high koala densities in *E. globulus* plantations in Victoria (Ashman *et al.* 2020). However, these plantations represent an unnatural predator free environment dominated by a known preferred koala food tree grown from stock of unknown genetic provenance that is likely to have been selected for growth and which may not have the capacity for chemical defense found in *E. globulus* in natural forests with a long history of koala browsing. The occurrence of koalas in these Victorian plantations provides no proof that koalas will inhabit planted regrowth forests regenerating after intensive clear-felling in forests of northern NSW. Law *et al.* (2022b) also claimed that "*current evidence suggests regulated harvesting with environmental protections could be compatible with koala conservation. For example, a radio-tracking study in the Pilliga forests of New South Wales (Kavanagh et al. 2007) found that koalas tolerate selective harvesting of shelter trees, at least in the short term (i.e 6 months after harvesting*." Reliance on this reference to support current intensive logging practices in NSW forests could be considered disingenuous and misleading. The Kavanagh *et al.* (2007) study was carried out in a far western region where timber harvesting is highly selective, very low intensity and not representative of timber harvesting methods in the great majority of state forests within the koalas known range. The Pilliga Forests comprise a mixture of softwood (Cypress Pines) and hardwoods (*Eucalyptus* spp.) and harvesting removed only larger *Callitris glaucophylla*, which was not a preferred food tree of the koala in this study, and comprised only about a quarter of stand basal area. A finding that cypress logging had no measurable impact on koalas is therefore both unsurprising and unremarkable. Male koalas have been reported to utilize 7 year planted *Eucalyptus camaldulensis* of unknown provenance in the Gunnedah region of NSW but only in proximity to remnant natural forest (Kavanagh and Stanton (2012) and in a region where dingos are now absent. Law *et al.* (2022b) also claim that "*in tall hinterland forests of north-east NSW, a regional survey (Kavanagh et al.1995) mostly recorded koalas in regrowth forest (< 30 years old), though the rate of detection was low and confounded with low elevation*". This statement is also misleading. Hinterland forests of northeast NSW have until recently been selectively harvested at low intensity by removing only large sawlogs of merchantable tree species (due to lack of woodchip markets for smaller stems and species not suitable for sawlogs), and not by high intensity clear-felling for woodchip like that undertaken in southern NSW and Victoria. Kavanagh *et al.* (1995) did not measure actual logging intensity and forest structure in their survey sites but assumed that forests with a compartment history of several logging cycles had been "intensively" logged. Most forest in the Pine Creek area has been frequently logged on multiple occasions but harvesting prior to the mid 1990's removed only a few large, sound stems in each cycle and left forest structure in many areas complex, mature and uneven-aged. The highest quality Koala habitats mapped as zone 4 and 5 in this study would have been classified as "intensively logged" in the study of Kavanagh et al 1995. This forest cannot be reasonably described as <30 year regrowth. Also, as previously reported by Smith (2004) logging intensity was confounded with elevation in the study of Kavanagh *et al.* (1995) and the positive correlation between increased koala occurrence and logging intensity is likely to be an artefact of higher koala densities at lower elevations where logging cycles have been more frequent (but not necessarily more intense). Law *et al.* (2022) further claim, incorrectly, that the studies of Smith (2004) on koala density in the Pine Creek State Forest support their findings. Smith (2004) stated that "*Koala scats and vegetation in their home range are also correlated positively with the number of selective harvesting events*" but it cannot be concluded from this statement that koalas tolerate modern day high intensity clear-fell logging. Smith (2004) found that koalas were more abundant in forests subject to multiple low intensity events that created a complex uneven-aged structure. These events mostly included culling (felling or ringbarking) of large old dead, defective (crooked or piped) and living senescent trees and unmerchantable tree species in addition to selective removal of large sawlogs. This type of selective logging is no longer practiced in Pine Creek State Forest and cannot be equated with modern high intensity clear-fell logging which is more akin to land clearing and conversion of native forest to plantation (as shown in Figure 3). Smith *et al.* (2004) found a significant negative correlation between koala abundance and harvesting intensity as measured by the number of logged stumps/hectare in survey sites, and a significant positive correlation between the abundance of koala scats and the predominance of tree stems in larger size classes (> 50 cm dbh). Results of the current study confirm that koala density increases more than 10-fold along a gradient of increasing mapped habitat quality (zones 1-5), increasing forest age, and increasing structural complexity (as shown in photographs in Figure 2) in the study area. Habitat quality zoning effectively represents a gradient of increasing time since logging, decreasing logging intensity and increasing tree diversity and abundance of preferred food tree species (including *Allocasuarina*). The highest quality koala habitat includes forests characterized by a high density of trees across all size classes that have only been lightly selectively logged to remove large and old senescent trees, and that have a high diversity of locally preferred food trees tree species and an abundance of preferred koala food trees. The lowest quality habitat is characterized by young (20-35 year) structurally uniform trees often of a single, less preferred species regenerating after clear-fell harvesting and replanting (Figure 2). This is an artificial habitat generated by logging that does not sustain breeding female koalas and is likely to be a sink habitat (where mortality exceeds reproduction) for transient male and non-reproductive female koalas surplus to the resident breeding population. These findings indicate that continuation and expansion of high intensity logging across the remaining parts of Pine Creek State Forest available for wood production has the potential to eliminate koalas from logged areas, destroy corridor links between remnant koala habitat in Bongil Bongil National Park and nearby upland conservation areas, and reduce the quality and integrity of koala habitat in the surrounding region including the proposed Great Koala National Park.

CONCLUSIONS

This study shows that male and female koalas are distributed quite differently within forest habitats and that koala habitat modelling, mapping and impact assessment based solely on monitoring of male koala calls, without additional consideration of female distribution and abundance, produces erroneous results that are misleading and unsuitable for koala conservation and management. Environmental determinants of koala habitat differ between the sexes, are more complex than hitherto considered and cannot be adequately described by the abundance of a limited number of so called primary and secondary koala food trees, or by models that predict koala distribution and abundance as a function of limited number of mapped GIS layers. Male and female koalas are sexually segregated in forest habitat with males more widespread and abundant in low quality, intensively (clear-fell) logged forest which may be considered sink habitat where mortality exceeds reproduction, and breeding females are more abundant and largely confined to lightly selectively logged forest with a complex uneven-age structure and a greater diversity and abundance of locally preferred koala food trees. The findings of previous koala habitat modeling and logging impact studies which concluded that koalas are not impacted by intensive (clear-fell) logging, based on the use of remotely deployed acoustic monitors to measure (male) koala abundance, incorrectly assumed that male calling is indicative of female breeding success and should consequently be disregarded as incorrect and unreliable. The results of this study show that breeding female koalas are absent from uniform aged regrowth forests that regenerate after clear-fell harvesting and re-planting for periods of up to 35 years and are likely to remain absent from forests that are re-cut on short rotations or that retain a reduced floristic diversity and simplified structure. Lists of so called Primary and Secondary koala food trees are unsuitable for predicting and modelling koala habitat, distribution and abundance. Koala diets are highly variable, regionally or locally unique, and generally include the full range of available eucalyptus and many non-eucalyptus tree species. Dietary preferences are determined by the outcome of long-term, local plant-folivore interactions and the capacity of local food tree species to increase leaf toxicity in response to over-browsing. Koalas typically change food trees daily, despite the risk of predation when coming to the ground to move between trees, and seldom feed on the same tree twice within long periods of observation. This behaviour is consistent with a need to minimize or prevent induced increases in toxicity in new leaf growth on preferred food trees. It is hypothesized that high levels of natural (selected) and induced toxicity in the foliage of preferred koala food trees limits the overall rate of leaf consumption by koalas to about 1-2 % of annual leaf production and maintains koala densities at relatively stable levels of about 0.3 koalas per hectare or 3 hectares per koala in optimal forest habitat. Large home ranges, complex mature forest structure, a high diversity of food tree species and a diverse gut microbiome are essential to allow female koalas to rotate food trees, minimize induced toxicity and select individual leaves with an above average dry matter and nitrogen digestibility, sufficient to satisfy the requirements of breeding and lactation, with minimal risk of predation. Abnormally high koala population densities in woodlands and open forests (> 0.6/ha) are largely limited to areas where koalas have been introduced or re-introduced to plantations or natural areas where aboriginal hunters and dingos were historically present but are now absent and where food trees have not been selected for resistance to koala browsing pressure. Prior to European settlement the major stronghold of the koala is likely to have been tall wet forests in the low to mid elevation foothills and ranges rather than woodlands and dry open forests of the western slopes and coastal floodplains. Remnant mid to low elevation tall wet forests, especially in northeast NSW where the climate is mild and extensive wildfire is rare, can be considered core areas for koala conservation where cessation of timber harvesting and increased reservation is a priority (as proposed in the Great Koala National Park). Increased reservation of stable koala populations in networks of fire and drought refuge areas linked by corridors can be considered of critical importance for long term koala conservation in general, to facilitate recovery from periodic wildfire, drought and logging events throughout its geographic range. Future studies of koala habitat need to consider differences between the sexes and a wider range of predictor variables including forest productivity, forest structure, the diversity and abundance of locally important food tree species, the effects of site variation on toxicity of local tree species, the capacity of local koala gut microbiomes to counter leaf toxicity, long term koala population stability and historical koala browsing pressure, and the risk of disturbance (from wildfire, drought/warming, logging, clearing, and predation).

ACKNOWLEDGEMENTS & CONTRIBUTIONS

Data analysis, interpretation and report preparation for this study was undertaken by Andrew Smith following a request from John Pile to statistically analyse koala monitoring data collected in Pine Creek State Forest between 1996 and 1999. These data were voluntarily collected by John Pile and John Murray using a method developed in discussion with the senior author in 1996/97 and endorsed by a Scientific Working Group (including the senior author) appointed by the NSW Government to advise on koala management. Grid based koala habitat mapping in the study area was carried out by John Pile and John Murray (engineering surveyors) on behalf of the Coffs Harbour Pine Creek koala Support Group in 1997 under contract to the NSW Government for the purpose of preparing a koala Plan of Management (SFNSW 2000). John Pile also assisted in undertaking radiotracking studies of koalas in the study area overseen by Australian Museum Business Services. Andrew Smith is currently retired, has no employment or funding affiliations and undertook this work on a voluntary basis. Long term koala monitoring data for Bongil Bongil National Park collected by volunteers (including both authors) and coordinated by NSW National Parks and Wildlife Service (North Coffs Coast Area) were made available to facilitate interpretation of Pine Creek State Forest monitoring data. Dan Lunney and Martin Smith provided helpful comments on the draft manuscript. This report has been submitted for publication and the published version may vary after taking into account feedback from referees.

REFERENCES

Allen B.L., Carmelito, E., amos, M., Goullllet, M., Allen, L.R., Speed J., gentle m., and Leung L.R. 2016. Diet of dingoes and other wild dogs in peri-urban areas of north-eastern Australia. *Science. Report.* **6**, 23028; https://doi: 10.1038/srep23028 (2016).

AMBS 2011. Investigation of the impact of roads on Koalas. Australian Museum Business Services. Draft Report

Andrews, S.P., Gration, G., Quin, D. & Smith, A.P. 1995. Description and Assessment of Forestry Impacts on Fauna of the Urbenville Forestry Management Area. Report prepared by Austeco Pty Ltd for State Forests of NSW, Pennant Hills.

Ashman, K., Rendall, A., Symonds, M., Whisson, D. 2020. Understanding the role of plantations in the abundance of an arboreal folivore. *Landscape Urban Planning.* 193:103684. https://doi: 10.1016/j.landurbplan.2019.103684

Baur, G. N. 1965 Forest types of New South Wales. Forestry Commission of NSW Research Note No. 17. FCNSW Sydney.

Brice, K. L., Trivedi, P., Jeffries, T. C., Blyton, M. D. J., Mitchell, C., Singh, B. K. 2019. The koala (*Phascolarctos cinereus*) faecal microbiome differs with diet in a wild population. *PeerJ* **7**:e6534. https://doi: 10.7717/peerj.6534,

Blyton, M. D. J., Soo, R. M., Whisson, D., Marsh, K. J., Pascoe, J., Le Pla, M. 2019. Faecal inoculations alter the gastrointestinal microbiome and allow dietary expansion in a wild specialist herbivore, the koala. *Animal Microbiome.* **1**:6. doi: 10.1186/s42523-019-0008-0, PMID.

Blyton, M. D. J., Pascoe, J., Hynes, e., Soo, R. M., Hugenholtz, P., and Moore, B.D. 2023 The koala gut microbiome is largely unaffected by host translocation but rather influences host diet. *Frontiers Microbiology*, **14** - 2023 https://doi.org/10.3389/fmicb.2023.1085090

Borzak, C.L., Potts, B.M., Barry, K.M., Pinkard, E.A., and O'Reilly-Wapstra, J.M. 2016 Genetic stability of physiological responses to defoliation in a eucalypt and altered chemical defence in regrowth foliage. *Tree Physiology* **37**, 220–235. https://doi:10.1093/treephys/tpw101

Caughley, G. 1977 Analysis of vertebrate populations. John Wiley and Sons.

Committee of the South Gippsland Pioneer's Association 1920. The land of the Lyre Bird a story of settlement in the great forest of South Gippsland. Gordon and Gotch Australia.

Cristescu, R. H., Ellis, W., de Villers, D., Lee, K., Woosnam-Merchez, O., Frere, C. H., Banks, P. B., Dique, D., Hodgkinson, S., Carrick, H., Carter, D., Smith, P., & Carrick, F. 2011. North Stradbroke Island: An Island ark for Queensland's koala population? *Proceedings of the Royal Society of Queensland*, **117**: 309–334.

Cristescu, R. H., Foley E., Markula, A., Jackson, G., Jones, D., and Frere, C. 2015 Accuracy and efficiency of detection dogs: a powerful new tool for koala conservation and management. *Scientific Reports* 5: 8349. https://doi: 10.1038/srep08349

Close, R., Ward S., and Phalen, D. 2017 A dangerous idea: that Koala densities can be low without the populations being in danger. *Australian Zoologist* **38** (3): 272-280.

Crowther, M.S. , Lunney, D., Lemon, J., Stalenberg, E., Wheeler, R., Madani, G., Ross, K.A. and Ellis, M. 2014 Climate-mediated habitat selection in an arboreal folivore. *Ecography* **37**: 336–343.

DAWE 2022, National Recovery plan for the Koala: Phascolarctos cinereus (combined populations of Queensland, New South Wales and the Australian Capital Territory). Department of Agriculture, Water and the Environment, Canberra.

DECC 2008. NSW recovery plan for the koala (*Phascolarctos cinereus*). Department of Environment and Climate Change, Sydney, NSW. (The department is now DPIE NSW).

DeGabriel, J.L., Moore, B.D., Shipley, L.A., Krockenberger, A.K., Wallis, I.R., Johnson, C.N., Foley, W.J. 2009 Inter-population differences in the tolerance of a marsupial folivore to plant secondary metabolites. *Oecologia* **161**:539–548. https://doi. org/ 10. 1007/ s00442- 009- 1407-9

DELWP 2020 Victoria's bushfire emergency: biodiversity response and recovery. Department of Environment Land, Water and Planning, Victorian state Government.

Department of Planning and Environment 2022 NSW Koala Strategy. Towards a doubling of the number of koalas in new South Wales by 2050. NSW Government.

Eberhard, I. H. 1978. Ecology of the koala, *Phascolarctos cinereus* (Goldfuss) Marsupialia: Phascolarctidae, in Australia. In 'The Ecology of Arboreal Folivores'. (Ed. G. G. Montgomery.) 315–327. Surrey Beatty: Sydney.

Ellis, W. A. H., Melzer, A., Green, B., Newgrain, K., Hindell, M. A., and Carrick, F. N. 1995. Seasonal variation in water flux, field metabolic rate and food consumption of free-ranging koalas (*Phascolarctos cinereus*). *Australian Journal of Zoology* **43**, 59–68.

Ellis, W., Hale, P., Carrick, C., Hasegawa, M., Nielsen, M., and Esser, D. 2001. Aspects of the ecology of koalas at Blair Athol Coal Mine. In 'Proceedings of the Emerald Conference on the Research and Management of Non-urban Koala Populations, 2–4 July 1997'. (Eds A. Melzer and D. Lamb.) 127–138.

Ellis, W., Hale, P., and Carrick, F. 2002a Breeding dynamics of koalas in open woodlands. *Wildlife Research,* **29**, pp.19-25.

Ellis, W., Melzer, A., Carrick, F.N. and Hasegawa, M. 2002b Tree use, diet and home range of the koala (Phascolarctos cinereus) at Blair Athol, central Queensland, *Wildlife Research,* **29** (3), pp.303-311.

Ellis, W. A, Melzer, A, Bercovitch, F.B. 2009 Spatiotemporal dynamics of habitat use by koalas: the checkerboard model. Behavioural Ecology and Sociobiology **63**:1181–1188.

Ellis, W, Bercovitch, F., FitzGibbon, S., Roe P., Wimmer, J., Melzer, A., and Wilson, R. 2011 Koala bellows and their association with the spatial dynamics of free-ranging koalas. *Behavioural Ecology* **22**: 372-377

Ellis M. V., Rhind S.G., Smith M., and Lunney D. 2016 Changes in the distribution of reports of the koala (*Phascolarctos cinereus*) after 16 years of local conservation initiatives at Gunnedah, north-west New South Wales, Australia. *Pacific Conservation Biology* http://dx.doi.org/10.1071/PC16004

Elms, F. P. 1920 animal bird and insect life in the scrub. Pp 48-55 in Committee of the South Gippsland Pioneer's Association (1920). The land of the Lyre Bird a story of settlement in the great forest of South Gippsland. Gordon and Gotch Australia.

EPA 2016 Koala Habitat Mapping pilot: NSW State Forests. Environment Protection Authority, 59 Goulburn Street, Sydney NSW 2000.

Eyre, T. and Smith, A. P. 1997 Floristic and structural preferences of yellow-bellied gliders (Petaurus australis) and selective logging impacts in southeast Queensland. *Forest Ecology and Management* **98**, pp 281-295.

Ferrier, S. and Smith, A. P. 1990 Using geographic information systems for biological survey design, analysis and extrapolation. *Australian Biologist* **3**, 105-116.

Fife, D. N., Nambiar, E.K.S., and Saur, E. 2008 Retranslocation of foliar nutrients in evergreen tree species planted in a Mediterranean environment. *Tree Physiology* **28**, 187–196.

Florence, R., Melzer, A., and Smith, A.P. 1997 Recommendations for management of koalas in Pine Creek State Forest and the formulation of a koala plan of management. A report on the Scientific Working Party Workshops. Koala Research Centre University of Central Queensland.

Foley W., Kehl. J.C., Nagy K.A., Kaplan, I. R., and Boorsboom, A.C. 1990 Energy and Water Metabolism in Free-living Greater Gliders, *Petauroides volans.* Australian Journal of Zoology, 38, 1-9.

Gherlenda, A.N., Moore, B.D., Haigh, A.M. Johnson, S.N., and Rielgler, M. 2016 Insect herbivory in a mature *Eucalyptus* woodland canopy depends on leaf phenology but not CO2 enrichment. *BMC Ecol.* ***16**:47.* DOI 10.1186/s12898-016-0102-z

Goldingay, R. L.., McHugh, D., and Parkyn, J. L. 2022 Multiyear monitoring of threatened iconic arboreal mammals in a mid-elevation conservation reserve in eastern Australia, *Ecology and Evolution*. **12**: e8935. https://doi.org/10.1002/ece3.8935DOI: 10.1002/ece3.8935

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

Gordon, G., McGreevy, D. G., and Lawrie, B. C. 1990. Koala population turnover and male social organisation. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) 189–192 Surrey Beatty: Sydney.

Grig A.H., and Mulligan D.R. 1999 Litterfall from two eucalyptus woodlands in central Queensland. Australian Journal of Ecology **24**: 662-664.

Hagens, S.V., Rendall, a. R., and Whisson D. A. 2018 Passive acoustic surveys for predicting species' distribution: optimising detection probability. *Plos One* https://doi.org/10.1371/journal.pone.0199396.

Heil M., and Ton J. 2008 Long-distance signalling in plant defence. *Trends in Plant Science* **13** No.6 264-272.

Henry, S. R. 1985. The diet and socioecology of gliding possums in southern Victoria. Ph.D. Thesis, Monash University, Melbourne.

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.

Hindell, M.A., Lee, A.K. 1988 Tree use by individual koalas in a natural forest. *Australian Wildlife Research* **15**, 1-7.

Hynes, E. F., Whisson, D. A., Di Stefano, J. 2021. Response of an arboreal species to plantation harvest. *Forest Ecology and Management.* **490**:119092. doi: 10.1016/j.foreco.2021.119092

Jiang, A. Z., Murray, P., Phillips, C., Tribe, A., and Ellis, W. 2022 Movement of Free-Ranging Koalas in Response to Male Vocalisation Playbacks. *Animals* **12**, 287. doi.org/10.3390/ani12030287

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**: 285-99.

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

Kavanagh, R. P., Stanton, M. A. & Brassil, T. E. 2007 Koalas continue to occupy their previous home-ranges after selective logging in *Callitris–Eucalyptus* forest. *Wildlife Research.* **34**, 94–107. doi. org/ 10. 1071/ WR061 26

Kavanagh R. and Stanton M.A. 2012 Koalas use young *Eucalyptus* plantations in an agricultural landscape on the Liverpool Plains, New South Wales *Ecological Restoration and Management* **3** 297-305

Krockenberger A. K. 1993 Energetics and nutrition during lactation in the koala Phascolarctos cinereus. Ph.D thesis. University of Sydney.

Law, B., Caccamo, G. and Brassili, T. 2015 A spatially explicit predictive model of the distribution of the koala *Phascolarctos cinereus* in north-eastern NSW. NSW Department of Primary Industries.

Law, B.1, Gonsalves, L.1, Bilney, R.2, Peterie, J.2, Pietsch, R.3, Roe, P.4 and Truskinger, A. 2020
Using Passive Acoustic Recording and Automated Call Identification to Survey Koalas in the Southern Forests of New South Wales. *Australian Zoologist* ***40*** *(3)* 477-86
Law, B., Caccamo, G., Roe, P., Truskinger, A., Brassil, T., Gonsalves, L., McConville, A. and Stanton, M. 2017. Development and field validation of a regional, management-scale habitat model: A koala *Phascolarctos cinereus* case study. *Ecology and Evolution*, **7**(18): 7475-7489. https://doi.org/10.1002/ece3.3300

Law, B. S., Brassil, T., Gonsalves, L., Roe, P., Truskinger, A. and McConville, A. 2018. Passive acoustics and sound recognition provide new insights on status and resilience of an iconic endangered marsupial (koala *Phascolarctos cinereus*) to timber harvesting. *PLOS ONE* **13**: e0205075. https://doi.org/10.1371/journal.pone.0205075

Law, B., Gonsalves, L., Burgar, J., Brassil, T., Kerr, I., Wilmott, L., Madden, K., Smith, M., Mella, V., Crowther, M., Krockenberger, M., Rus, A., Pietsch, R., Truskinger, A., Eichinski, P., & Roe, P. 2022a. Validation of Spatial Count Models to Estimate koala Phascolarctos cinereus Density from Acoustic Arrays. NSW Primary Industries. *Wildlife Research*, **49**(5):438-448. https://doi.org/10.1071/WR21072

Law, B., Gonsalves, L., Burgar, J., Brassil, T., Kerr, I., O'Loughlin C.O., Eichinski, P., & Roe, P. 2022b Regulated timber harvesting does not reduce koala density in north-east forests of New South Wales. Nature portfolio Scientific Reports **12** 3968 https://doi.org/10.1038/s41598-022-08013-6

Lee, A. K. and Carrick, F. N. 1989 Phascolarctidae. Pp 740-754 in the *Fauna of Australia* **1B**. Australian Biological Resources Study Canberra. AGPS Canberra.

Lumsden, L.F., Nelson, J.L., Todd, C.R., Scroggie, M.P., McNabb, E.G., Raadik, T.A., Smith, S.J., Acevedo, S., Cheers, G., Jemison, M.L. & Nicol, M.D. 2013. A New Strategic Approach to Biodiversity Management – Research Component. Arthur Rylah Institute for Environmental Research.

Lunney, D. 1987 The effects of logging fire and drought on possums, and gliders near Bega NSW. *Australian Wildlife Research* **14**, pp 263-74.

Lunney, D., and Leary, T. 1988 The impact on native mammals of land-use changes and exotic species in the Bega district, New South Wales, since settlement. *Australian Journal of Ecology* **13** (1) pp67-92

Lunney, D., Matthews, A., Moon, C., and Ferrier, S. 2000. Incorporating habitat mapping into practical koala conservation on private lands. *Conservation Biology* **14**, 669–680. https://doi:10.1046/j.1523-1739.2000. 99386.x

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**, pp 567–575. https://doi:10.1016/j.biocon. 2004.03.029

Lunney, D., and Moon, C. 2012 An ecological history of Australia's forests and fauna (1770-2010), in *World Environmental History*, [Eds Mauro Agnoletti, Elizabeth Johann and Simone Neri Serneri], in *Encyclopedia of Life Support Systems (EOLSS),* Developed under the Auspices of the UNESCO, Eolss Publishers, Oxford, UK,

Lunney, D., Stalenberg, E., Santika, T., Rhodes, J.R., 2014. Extinction in Eden: identifying the role of climate change in the decline of the koala in south-eastern NSW. *Wildlife Research* **41**, 22–34

Lunney, D., Predavec, M., Miller, I., Shannon, I., Fisher, M., Moon, C., Matthews, A., Turbill J., and Rhodes, J.R. 2015 Interpreting patterns of population change in koalas from long-term datasets in Coffs Harbour on the north coast of New South Wales. *Australian Mammalogy* **38**(1) 29-43 https://doi.org/10.1071/AM15019

Lunney, D., Moon, C., Sonawane, I., Predavec, M., and Rhodes, J. R. 2022. Factors that drive koala roadkill - an analysis across multiple scales in New South Wales, Australia. *Australian Mammalogy*. **44**(3) 328-337. https://doi:10.1071/AM21040

MacGregor, C. M. 1997 Records of tree species in the diet of koalas in Pine Creek State Forest. Report to state Forests of NSW Coffs Harbour. University of New England.

Marsh, K.J., Moore, B.D., Wallis, I.R. and Foley, W.J. 2013 Continuous monitoring of feeding by koalas highlights diurnal differences in tree preferences. *Wildlife Research*, 2013, **40**, 639–646. doi.org/10.1071/WR13104

Marsh, K.J, Saraf, I. Hocart, C.H., Youngentob, K.N., Singh, I.P., Foley, W.J. 2019 Occurrence and distribution of unsubstituted B-ring flavanones in *Eucalyptus* foliage. *Phytochemistry* **160**:31–39. https://doi. org/ 10. 1016/j. phyto chem. 2019. 01. 005

Marsh, K. J., Blyton, M. D., Foley, W. J., Moore, B. D. 2021. Fundamental dietary specialisation explains differential use of resources within a koala population. *Oecologia* **196**, 795–803. https://doi: 10.1007/s00442-021-04962-3

Martin, R. W. 1985. Over browsing, and a decline of a population of the koala *Phascolarctos cinereus*) in Victoria. III. Population dynamics. *Australian Wildlife Research* **12**, 377–385.

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.

Masters P., Duka, t., Berris s., and Moss G. 2004 Koalas on Kangaroo Island: from introduction to pest status in less than a century. *Wildlife Research* **31(3) 267 – 272.**

Matthews, A., Lunney, D., Gresser, S., and Maitz, W. 2007. Tree use by koalas (*Phascolarctos cinereus*) after fire in remnant coastal forest. *Wildlife Research* **34**, 84–93. https://doi:10.1071/WR06075

Matthews, A., Lunney, D., Gresser, S. Maitz, W. 2016 Movement patterns of koalas in remnant forest after fire. *Aust. Mammal.* **38**, 91–104. https:// doi. org/ 10. 1071/ AM140 10 (2016).

McAlpine, C.A., Rhodes I.R., Bowen, M.E., Lunney, D., Callaghan, J.G., Mitchell, D.L. and Possingham, H.P. 2008 Can multiscale models of species' distribution be generalized from region to region? A case study of the koala. *Journal of Applied Ecology* **45**, 558–567.https://doi: 10.1111/j.1365-2664.2007.01431.x

McAlpine, C.A., Preece, H., Peterson, A. 2015. Review of the National Koala Conservation and Management Strategy 2009–2014. Unpublished report to the Australian Department of Environment.

McAlpine, C., Lunney, D., Melzer, A., Menkhorst, P., Phillips, S., Phalen, D., Ellis, W., Foley, W., Baxter, G., de Villiers, D., Kavanagh, R., Adams-Hosking, C., Todd, C., Whisson, D., Molsher, R., Walter, M., Lawler, I., and Close, R. 2015 Conserving koalas: A review of the contrasting regional trends, outlooks and policy challenges. *Biological Conservation* **192**: 226-236

Menkhorst, P. W. 1995. Koala *Phascolarctos cinereus* (Goldfuss 1817). In 'Mammals of Victoria: Distribution, Ecology and Conservation'. Ed. P. W. Menkhorst. pp. 85–88. Oxford University Press: Melbourne, Vic., Australia.

Menkhorst, P. 2008. 'Hunted, marooned, re-introduced, and contracepted: A history of koala management in Victoria' in D Lunney, L Munn and W Meikle (eds), *Phascolarctos cinereus* (Koala) Conservation Advice Threatened Species Scientific Committee 37 Too Close for Comfort: Contentious Issues in Human-wildlife Encounters, Royal Zoological Society of NSW, Mosman, NSW.,73-92.

Menkhorst, P. 2009 Blandowskis' mammals: clues to a lost world. *Proceedings of the Royal Society of Victoria*: 61-89

Menkhorst, P., Ramsey, D., O'Brien, T., Hynes, E., and Whisson D. 2019 Survival and movements of koalas translocated from an over-abundant population. *Wildlife Research* **46**: 557–565, https://doi.org/10.1071/WR19090

Milford, H.B. 1999 Soil landscapes of the Coffs Harbour 1:100,000 sheet. Department of Land and Water Conservation Sydney.

Mitchell, D. l., Soto-Berelov, M., Langford, W.T., and Jones, S. D. 2021 Factors confounding koala habitat mapping at multiple decision making scales. *Ecological Restoration and Management* **22** (2) pp 171-82 https://doi: 10.1111/emr.12468

Mitchell, P. J. 1989. The social organisation of koalas. Ph.D. Thesis,Monash University, Melbourne.

Mitchell, P. 1990*a*. 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.)

Mitchel,l P. 1990*b*. Social behaviour and communication of koalas. In 'Biology of the Koala'. (Eds A. K. Lee, K. A. Handasyde and G. D. Sanson.) pp. 151–170. (Surrey Beatty: Sydney.)

Moore B.D., and Foley W.J. 2000 A review of feeding and diet selection in koalas (*Phascolarctos cinereus*). *Australian Journal of Zoology*, **48**, 317–333.

Moore B. D., Wallis I. R., Wood J. T., Foley W. J. 2004 Foliar nutrition, site quality, and temperature influence foliar chemistry of tallowwood (*Eucalyptus microcorys*). *Ecological Monographs* **74**: 553-568. https://doi: 10.1890/03-4038.

Moore, B.D., and Foley, W.J. 2005 Tree use by koalas in a chemically complex landscape. Nature 435:488–490

Predavec, M. 2015 Modification of the preliminary map of the likelihood of koalas within NSW. Internal report. Office of Environment and Heritage, NSW Government.

Nagy, K,A., Martin, R.,W. 1985 Field metabolic rate, water flux, food consumption and time budget of koalas, *Phascolarctos cinereus* (Marsupialia: Phascolarctidae) in Victoria. *Australian Journal of Zoology* **33**:655–665

Newman and Partners 1997 A brief history of forest management at Pine Creek. Unpublished report to state Forests of NSW.

NRC 2021 Koala response to harvesting in NSW north coast state forests Final report. Natural Resources Commission of NSW.

NRC 2022 Koala response to harvesting in NSW north coast state forests Final report (updated). Natural Resources Commission of NSW.

OEH 2018 *A review of koala tree use across New South Wales,* Sydney, NSW, Australia. Available at https://www.environment.nsw.gov.au/research-and-publications/publications-search/a-review-of-Koala-tree-use-across-new-south-wales

Osawa, R. 1992. Tannin-protein complex-degrading enterobacteria isolated from the alimentary tracts of koalas and a selective medium for their enumeration. *Appl. Environ. Microbiol.* **58**, 1754–1759. https://doi: 10.1128/aem.58.5.1754-1759.1992

Osawa, R., Blanshard, W.H., and O'Callaghan, P.G. O. 1993 Microbial studies of intestinal microflora of the koala, Phascolarctos cinereus ci. 11 Pap, a special maternal faeces consumed by juvenile koalas. *Australian Journal of Zoology* **41**, 611-20

Phillips, S. and Callaghan, J. 2000 Tree species preferences of koalas (Phascolarctos cinereus) in the Campbelltown area south-west of Sydney, New South Wales. *Wildlife Research* **27**, 509–516.

Predavec, M., Lunney, D., Shannon, I., Scotts, D., Turbill, J., and Faulkner, B. 2015 Mapping the likelihood of koalas across New South Wales for use in private native forestry: developing a simple species distribution model that deals with opportunistic data. *Australian Mammalogy* **37**(2) 182-193.

Radford Miller S. L. 2012. *Aspects of the ecology of the koala,* Phascolarctos cinereus, *in a tall coastal production forest in north eastern New South Wales*. Doctoral dissertation. Southern Cross University.

Recher, H., Rohan-Jones, W., and Smith, P. 1980 Effects of the Eden woodchip industry on terrestrial vertebrates with recommendations for management. Forestry Commission of NSW Research Note 42. Sydney

Short, J, and Smith, A. P. 1994 Mammal decline and recovery in Australia. *J. Mammal* **75** (2) 31: 288-297.

Sluiter A.,F., Close R.L. and Ward S.J., 2002. Koala feeding and roosting trees in the Campbelltown area of New South Wales. *Australian Mammalogy* **23**: 173-175.

Smith A.P. 1982. Leadbeaters possum and its management. In 'Species at Risk: Research in Australia'. (Ed. R. H. Groves and W. D. L. Ride.) pp. 129-47. Australian Academy of Science: Canberra.

Smith, A. P. 1997 Koalas in the Pine Creek Study Area: Conservation significance and recommendations for management. Austeco Environmental Consultants, Armidale, NSW.

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* (ed. Lunney D), pp. 591-611. Royal Zoological Society of New South Wales, Mosman, NSW Australia.

Smith, A, 2010. Effects of proposed logging on populations of the Greater Glider (Petauroides volans) and Yellow-bellied Glider (Petaurus australis) in Four Coupes at Brown Mountain, East Gippsland, Victoria. Report to the Supreme Court of Victoria Proceedings No. 8547 of 2009.

Smith, A. P. 2015 Preliminary Review of Crown and Private Native Forestry Koala Habitat Mapping Projects. Report to the Environment Protection Authority, Setscan Pty Ltd., Currumbin Qld.

Smith, A. P. 2019 Effects of past logging on 58 coupes located in the Central Highlands Regional Forest Agreement Area in Victoria on the Greater Glider (Petauroides volans) A report to the Federal Court of Australia Proceeding VID 1228/2017

Smith, A. P. **2020** Review of CIFOA mitigation conditions for timber harvesting in burnt landscapes. A report to the NSW Environment Protection Authority. Setscan Pty Ltd. https://www.epa.nsw.gov.au/-/media/epa/corporate-site/resources/forestry/review-of-cifoa-mitigation-conditions-for-timber-harvesting-in-burnt-landscapes.spleezs

Smith A. P. 2021 Impact of Logging and Wildfire on the Greater Glider. Second Report to the Supreme Court of Victoria Proceeding S ECI 2020 00373. Setscan Pty Ltd, Currumbin Qld.

Smith A.P. Lindenmeyer, D., and Suckling G. 1985. The Ecology and Management of Leadbeater's Possum. A research report to World Wildlife Fund Australia for Project 51. University of New England Armidale NSW

Smith, A. P. and Lindenmayer, D. l988. Tree hollow requirements of Leadbeater's Possum and other arboreal marsupials in logged Mountain Ash Forests. *Australian Wildlife Research* **15**: 347-62

Smith, A. P., Moore, D. M. and Andrews, S. A. 1992 Proposed forestry operations in the Glen Innes Management Area. Fauna Impact Statement Supplement to the Environmental Impact Statement Report. Forestry Commission of NSW. 98 pp.

Smith, A. P., Andrews, S. A. and Moore, D. M. 1994 Terrestrial fauna of the Grafton and Casino State Forest Management Areas, description and assessment of forestry impacts. Grafton-Casino Management Area EIS Supporting Document No 1. State Forests of NSW, 136 pp.

Smith A.P., Andrews S. A., Gration G., Quin, D., and Sullivan. B. 1995 Description and assessment of forestry impacts on fauna of the Urunga-Coffs Harbour Management Area EIS. Supporting Document No 4. Coffs Harbour and Urunga Forest Management Area. Environmental Impact Statement. State Forests of NSW. State Forests of NSW, Sydney.

Smith A. P. and Quin, D. 1996 Patterns and causes of extinction and decline in Australian Conilurine Rodents. *Biological Conservation.* **77** 243-267.

Smith, A.P. and Andrews, S. 1997 koala Habitat, Abundance and Distribution in the Pine Creek Study Area. Report to State Forests of NSW, North East Region, Coffs Harbour, NSW. Setscan Pty Ltd Armidale NSW.

Smith, A.P., Horning, N. and Moore, D. 1997 Regional biodiversity planning and lemur conservation with GIS in western Madagascar. *Conservation Biology* **11** (2): 498-512.

Smith, A. P., Watson, G., and Murray, M. 2002 Fauna habitat modelling and wildlife linkages in Wyong Shire. Report to Wyong Shire Council, Wyong. Setscan Pty Ltd. Currumbin Qld.

Smith M. 1922 Koalas and land use in Gunnedah Shire**.** A report on the Bearcare project. NSW National Parks and wildlife Service. Hurstville NSW.

Sullivan, B. J., Norris, W. M., and Baxter, G. S. 2003. Low-density koala (*Phascolarctos cinereus*) populations in the mulgalands of south-west Queensland. II. Distribution and diet. *Wildlife Research* **30,** 331–338. https://doi:10.1071/WR00032

State Forests of NSW 2000 Koala management plan Pine Creek State Forest. State Forests of NSW North East Region.

Strahan, R. 1978 what is a koala? In *The Koala: Proceedings of the Taronga Symposium*. T.J. Bergin ed., Zoological Parks Board of NSW, Sydney, pp3-19.

Thompson, J. 2006 The comparative ecology and population dynamics of koalas in the koala coast region of Southeast Queensland. Ph.D thesis, University of Queensland St. Lucia.

Tucker, G., Melzer, A., and Ellis, W. 2007 The development of habitat selection by subadult koalas. *Australian Journal of Zoology* **55**, 285-289.

VicForests 2019 Greater Glider Conservation Strategy. Version 2. VicForests, Victorian State Government.

Warneke, R.M., 1978. The status of the koala in Victoria. In *The Koala: Proceedings of the Taronga Symposium*. T.J. Bergin ed., Zoological Parks Board of NSW, Sydney, 109-114.

Watson, G., Elks, G., and Smith, A. P. 1999 Vegetation report for Guy Fawkes River National Park for use in fire and resource Management. Report to NSW National Parks and Wildlife Service. Austeco Environmental Consultants, Armidale.

Wallis R. L. 2013 Koalas *Phascolarctos cinereus* in Framlingham Forest, south-west Victoria: introduction, translocation and the effects of a bushfire. *Victorian Naturalist* **130** (1) pp 37-40

Whisson, D., and Shimmin, G. 2006 Managing an Overabundant Koala Population for Conservation of Riparian Habitats on Kangaroo Island, South Australia. Proc. 22nd Vertebr. Pest Conf. (R. M. Timm and J. M. O'Brien, Eds.) Published at Univ. of Calif., Davis. Pp. 23-28.

Whisson, D. A., Dixon, V., Taylor, M. L., Melzer, A. 2016. Failure to respond to food resource decline has catastrophic consequences for koalas in a high-density population in southern Australia. *PLoS One* **11**:e0144348. https://doi: 10.1371/journal.pone.0144348, PMID:

Whisson, D. and Ashman, K.R. 2020 When an iconic native animal is overabundant: The koala in southern Australia. *Conservation Science and Practice* **2**:e188. https://doi: 10.1111/csp2.188

Woinarski, J. C., Burbidge, A. A., & Harrison, P. L. 2015. Ongoing unravelling of a continental fauna: decline and extinction of Australian mammals since European settlement. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 4531–4540. https://doi.org/10.1073/pnas.14173 01112

Woodward, W., Ellis, W. A., Carrick, F. N., Tanizaki, M., Bowen, D., and Smith, P. 2008. Koalas on North Stradbroke Island: diet, tree use and reconstructed landscapes. *Wildlife Research* **35**, 606–611. https://doi:10.1071/ WR07172