

# Out on a limb: habitat use of a specialist folivore, the koala, at the edge of its range in a modified semi-arid landscape

Andrew G. Smith · Clive A. McAlpine ·  
Jonathan R. Rhodes · Daniel Lunney ·  
Leonie Seabrook · Greg Baxter

Received: 13 July 2012 / Accepted: 3 January 2013 / Published online: 12 January 2013  
© Springer Science+Business Media Dordrecht 2013

**Abstract** Habitat loss and natural catastrophes reduce the resources available to animals. Species can persist if they have access to additional resources and habitats through the processes of landscape complementation and supplementation. In arid and semi-arid ecosystems, where productivity is limited by precipitation, the impact of landscape change and prolonged drought is severe on specialist species whose range boundaries are limited by aridity. We examined the pattern of occurrence by a specialist arboreal folivore, the koala, at the periphery of its biogeographic range, in a semi-arid rangeland landscape. We used hierarchical mixed modelling to examine the effect of landscape change on koala populations and their habitat use during and after a

prolonged drought. We found that the tree species and the distance of a site from water courses were the most important determinants for koala presence in these landscapes. Koalas were predominantly detected in riverine habitat along the water courses, which are primary habitat and provide refugia in times of drought and extreme heat. There was a strong positive effect from the interaction between the amount of primary and secondary habitat in the landscape, although individually, the amount of each of these habitats was not important. This shows koalas will persist in more intact landscapes. There was no difference in habitat use between dry and wet years, but we consider that it can take several wet seasons for koalas to expand into habitats away from water courses.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10980-013-9846-4) contains supplementary material, which is available to authorized users.

A. G. Smith (✉) · C. A. McAlpine · J. R. Rhodes ·  
L. Seabrook · G. Baxter  
Landscape Ecology and Conservation Group, School of  
Geography, Planning & Environmental Management, The  
University of Queensland, Brisbane, QLD 4072, Australia  
e-mail: andrew.g.smith@uq.edu.au

D. Lunney  
Office of the Environment and Heritage, PO Box 1967,  
Hurstville, NSW 2220, Australia

D. Lunney  
School of Biological Sciences and Biotechnology,  
Murdoch University, Murdoch, WA 6150, Australia

**Keywords** Landscape change · Resource use ·  
Landscape supplementation · Refugia ·  
Climate extremes · Drought

## Introduction

Landscape change results in habitat loss and fragmentation, which limits the availability of habitat and resources, and reduces landscape connectivity (Mönkkönen and Reunanen 1999). Habitat loss from clearing of native vegetation is the principal driver of species' extinctions, making it the key threat to global biodiversity (Fahrig 2001; Pereira et al. 2004).

Catastrophic natural processes, such as storms, floods, droughts and wildfires, also impact populations (Sabo and Post 2008), compounding anthropogenic landscape change. As a result, conserving biodiversity in human-modified landscapes is a major challenge, especially when there is a high degree of environmental stochasticity (Fischer and Lindenmayer 2007). Understanding how a species uses resources at multiple scales in human-modified landscapes with high environmental variability requires knowledge of how a species interacts with resource patterns in space and time (Murray et al. 2008; Bergman et al. 2012).

Landscape change alters habitat heterogeneity, which can modify a species' access to essential resources, according to the processes of landscape complementation and supplementation (Dunning et al. 1992). Landscape complementation allows a species to access non-substitutable resources from different habitat elements, while landscape supplementation allows a species to supplement principal resources with substitute resources from different habitats (Dunning et al. 1992). These processes can have positive effects on a species' persistence and are often linked to source-sink dynamics (Pulliam 1988; Dunning et al. 1992). Source habitats have abundant resources, or resources that are of high-quality, enabling a population to increase because reproduction exceeds mortality (Pulliam 1988). Conversely, sink habitats have fewer, or lower quality resources than surrounding source habitats, and consequently mortality exceeds reproduction (Pulliam 1988). Landscape complementation and supplementation allow populations to maintain their presence in marginal sink habitat if a species can access resources in surrounding habitat and matrix areas (Dunning et al. 1992). However, populations in sink habitats are more susceptible to catastrophic environmental variation and anthropogenic modifications to habitat (Kawecki 2008). Consequently, further reductions in the quality of sink habitats through environmental stochasticity or anthropogenic modifications can convert them into non-habitat.

Reduction in habitat quality can cause declines in populations at the periphery of a species' biogeographic range, where suitable habitat might exist beyond the range boundaries, but a number of factors restrict access to that habitat, including restrictions on dispersal (immigration and emigration), predation and competition, and the population size (Gaston 2009). One factor limiting a species' distribution is a climate

that does not exceed physiological tolerances, or reduce availability of resources, known as the 'climatic envelope' (Nix 1986). Extreme weather also has potential to impact on species at their range edges (Parmesan et al. 2000) and reduce the quality of refugia, in which individuals of a population can persist in extreme conditions (Byrne 2008).

Drought is an extreme climatic event, characterised by prolonged periods of dry weather, in contrast to aridity, where the climate is in a permanently dry state (Mpelasoka et al. 2008). Severe drought causes extensive dieback of plants, including deep-rooted trees (Fensham and Holman 1999; Rice et al. 2004). This reduces the quantity and quality of resources available to animals, resulting in nutritional and physiological stress (Martínez-Mota et al. 2007). Increased frequencies of extreme weather events, including drought, heatwaves and heavy rainfall, are predicted effects of climate change (Smith 2011). Many species will not adapt to the rapid shifts in environmental conditions (e.g., Courtland 2008), increasing the risk of range contractions driven by local extinctions at the range boundary (Channell and Lomolino 2000).

The koala (*Phascolarctos cinereus*) provides an ideal case study of how a species on the edge of its range is influenced by landscape change and climatic variation. Koalas are arboreal, folivorous marsupials that select from a sub-set of *Eucalyptus* spp., where individual tree selection depends on tree size and structure, and chemistry and water content of leaves (Moore and Foley 2000; Moore et al. 2004). Despite their specialist requirements, koalas range over 30 bioregions across eastern Australia, from moist coastal to dry semi-arid regions. Habitat use by koalas is influenced by processes at a hierarchy of scales, which vary regionally (McAlpine et al. 2008; Rhodes et al. 2008) and declines follow from habitat destruction and fragmentation (McAlpine et al. 2006a, 2008; Rhodes et al. 2006).

Extreme climatic events, in particular drought or prolonged high temperatures, limit the koala's range (Adams-Hosking et al. 2011; Seabrook et al. 2011). In semi-arid Queensland and New South Wales, heatwaves led to population declines near the edge of the species' biogeographic range (Gordon et al. 1988; Lunney et al. 2012). Climate change projections predict hotter and drier climates, with the koala's range predicted to contract east and south to more mesic regions (Adams-Hosking et al. 2011). Identifying how koalas use human-modified landscapes during

droughts will allow us to assess their habitat needs for survival at the edge of their range in a changing climate.

We examined the pattern of occurrence of koalas in a semi-arid rangeland landscape at the edge of their range that was subject to human landscape change and extreme drought, followed by wet conditions. We hypothesised that koala occurrence would depend on ecological factors at multiple scales, including the species and condition of trees at the tree scale, the distance from the creek at the site scale, and the quality and area of habitat at the home-range and landscape scales. We assumed that processes of landscape complementation or landscape supplementation would be necessary for koalas to continue to persist in semi-arid landscapes and that this would be linked to source/sink dynamics. We applied a hierarchical mixed modelling approach to test the importance of the landscape context, the distance of habitat to creeks at the site scale, and the species and condition of individual trees. Our research was conducted during and immediately following a severe drought, enabling us to examine habitat use by koalas during a dry and wet period. Consequently, our approach includes both spatial and temporal scales in the study design.

## Methods

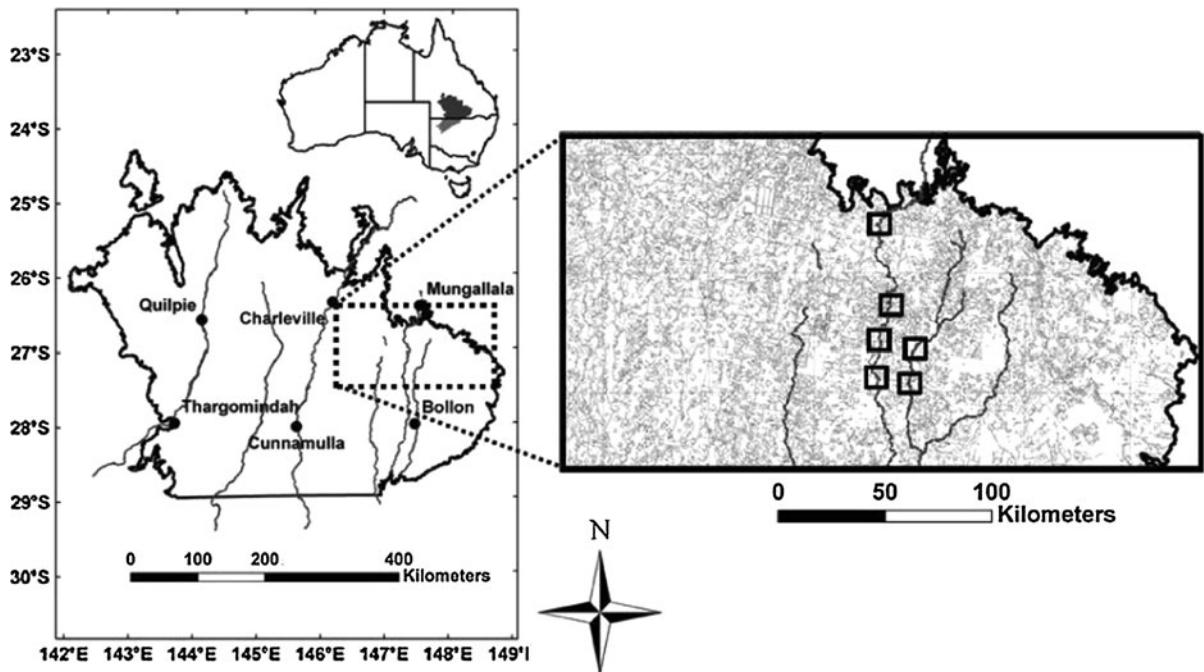
### Study region

The semi-arid Mulgalands Bioregion of Queensland covers an area of 192,036 km<sup>2</sup> (Thackway and Cresswell 1995) and is dominated by flat to undulating plains intersected by an extensive north–south drainage system (Fig. 1). The climate is hot and dry, with aridity increasing from the north-east, with an average annual rainfall of 460 mm, to the south-west, with an average rainfall of 285 mm (Bureau of Meteorology 2011). The hottest daily temperatures exceed 40 °C and the annual mean maximum temperature is approximately 28 °C (Bureau of Meteorology 2011). The soils include fertile alluvial clays on the floodplains and drainage lines, with infertile red earths on the hills and low ranges (Sattler and Williams 1999). Our study was concentrated along the ephemeral Mungallala and Wallam Creek systems in the east of the region. The first sampling year (2009) was during a severe drought, where water in the creeks was limited

to intermittent semi-permanent and permanent water holes. Flooding occurred at the beginning of the second sampling year (2010), where record daily rainfalls over 150 mm were recorded and the Mungallala and Wallam Creeks rose to their highest recorded heights, leading to severe flooding (Bureau of Meteorology 2011). Koalas are concentrated in the riparian habitats in the higher rainfall zone in the east (Sullivan et al. 2004). Vegetation is mainly woodland dominated by poplar box (*Eucalyptus populnea*) or mulga (*Acacia aneura*), which is intersected by continuous strips of riparian vegetation dominated by river red gum (*E. camaldulensis*). Widespread habitat conversion to cattle pasture, and frequent severe drought, are the major threatening processes for koalas in the region (Seabrook et al. 2011). Approximately 30 % of native vegetation cover has been cleared (Sullivan et al. 2004) with the clearing rate of vegetation in 2008–2009 at approximately 0.39 % or 24,717 ha (Department of Environment and Resource Management 2010).

### Survey design and explanatory variables

The Mungallala and Wallam Creeks occur in some of the region's most modified landscapes. We selected a priori four spatial scales that we deemed to be most ecologically relevant: the tree (individual tree); the site ( $\leq 1$  ha); the home-range ( $\sim 300$  ha); and the landscape (100 km<sup>2</sup>). Trees provide food and shelter and are the primary resource unit of koala management (Matthews et al. 2007). The site is where animals interact with resources on a daily basis (Murray et al. 2008) and comprises multiple trees. Koalas have distinct home-ranges, and in dry landscapes these range from 1 to  $>100$  ha (Kavanagh et al. 2007: Pilliga Scrub, NSW) and  $<10$  to  $>250$  ha (Ellis et al. 2002: Blair Athol, Qld). With no prior knowledge of koala home-ranges in the Mulgalands Bioregion, we sampled at a resolution of 300 ha, the maximum recorded home-range for koalas in dry landscapes (Ellis et al. 2002). We defined a landscape as a 10  $\times$  10 km (100 km<sup>2</sup>) area, because it would contain sufficient habitat for a sub-population of koalas, based on known maximum dispersal distances (Dique et al. 2003). We compared koala habitat use and requirements during a drought and the exceptionally wet year that followed. The sampling design was hierarchical, with finer scales nested within larger scales.



**Fig. 1** The location of the study region and survey landscapes

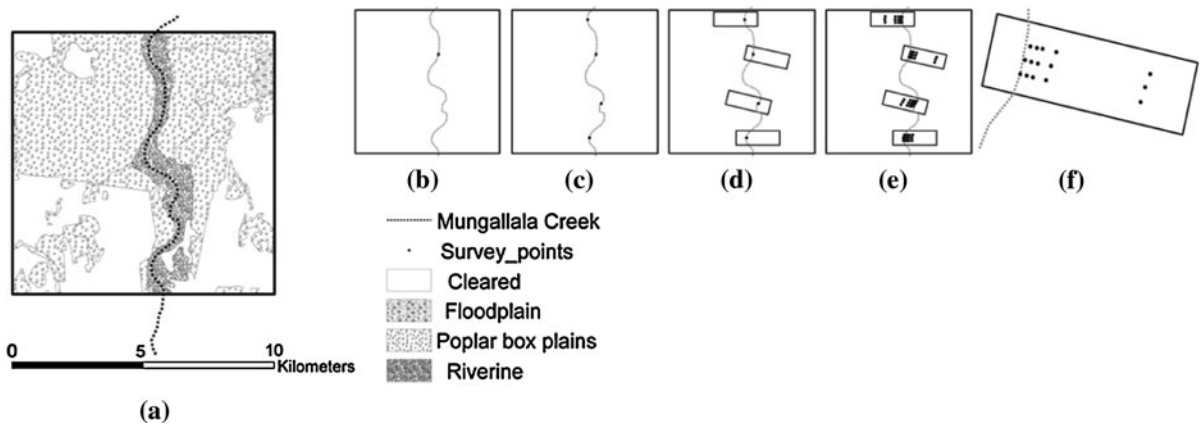
Using ArcMap (ESRI ArcGis Version 9.3), we randomly identified 39 non-contiguous landscapes along the two creeks. The area of each habitat was obtained using Regional Ecosystem mapping Version 5 (Queensland Herbarium 2005). We applied a stratified selection process to select a subset of 18 possible landscapes, where the landscapes were sorted into groups with similar values for the amount of cleared land, and then one landscape of each area value was selected at random. At the time of analysis, the Regional Ecosystem mapping Version 6.0b (Queensland Herbarium 2009) was available and used for quantifying the landscape scale habitat, because it was representative of vegetation in the field at the time of surveying.

We quantified the area of primary riverine vegetation and the secondary woodlands vegetation within each landscape. Riverine vegetation is dominated by river red gum occurring in linear patches along watercourses, and is primary habitat for koalas in the Mulgalands (Sullivan et al. 2003b) and is refugia habitat in times of drought (Gordon et al. 1988). Poplar box and/or mulga woodland communities are analogous to the plains vegetation described by Sullivan

et al. (2003b) and are secondary habitat because they rarely contain koalas. We did not consider landscape configuration metrics, such as patch isolation because previous multiple-scale studies on koalas have found that the area of primary habitat is the most important landscape attribute influencing koala occupancy (McAlpine et al. 2006a; Rhodes et al. 2006).

Within each landscape, we generated four 300 ha rectangular sampling blocks by randomly selecting a single location along the creek, then selecting three more locations at a distance >2,000 m from each other, placing the centre of the end of each block on the creek at the selected location (Fig. 2). Consequently, each block was positioned perpendicular to the creek line, with two blocks on each side of the creek. This design allowed for the detection of koalas on both sides of the creek. We also calculated the area of riverine and woodlands vegetation within each 300 ha block.

Each sampling block contained five sampling sites: one in riparian vegetation directly adjacent to the creek; three at random intervals between the creek and 500 m from the creek; and the fifth site at a random interval between 500 and 2,000 m from the creek



**Fig. 2** Graphical summary of survey design. Site selection sequence: **a** An empty landscape, **b** random selection of a plot on the creek within each landscape, **c** three more plots selected along the creek at distances  $\geq 2,000$  m apart, **d** four 300 ha sampling blocks were then placed on the four sites, with two blocks located on each side of the creek, **e** an additional two

(Fig. 2). This design followed from pilot surveys which showed that koalas were restricted to the riverine vegetation, although Sullivan et al. (2003a, 2004) found that koalas utilise a wide range of habitats other than riverine communities. By placing sites on and off creeks, we aimed to capture any variation in off-creek use in each landscape. We used the distance from the creek and the proportion of *E. camaldulensis* as site scale explanatory variables.

To control for fine scale variation and improve the detectability of koalas, each site contained three survey plots arranged parallel to the creek and at a distance of 200 m apart. Survey plots consisted of 30 neighbouring trees with a diameter at breast height  $>10$  cm (DBH: 130 cm above ground level). A central tree was selected and its location recorded using a GPS (Garmin Legend HCx). Sample sites allowed for detecting koala faecal pellets on and away from the creeks, while plots controlled for fine scale variation within a site and improved detectability. Each tree species was identified, and its height and its condition recorded, attributes important for selecting trees by koalas in semi-arid landscapes (Smith et al. 2013). Tree height was measured using a laser range finder with inclinometer (Laser Technology TruPulse 360). Tree condition was based on two categories: good condition if the canopy had a healthy crown or minor dieback; and poor condition if the canopy had several major branches dead, substantial epicormic

plots were placed on either side of the original plot at 200 m intervals, making up a site, and then four more sites were selected parallel to the creek within each block, **f** each block had a site consisting of three plots located on the creek, with three additional sites between the creek and 500 m, and an additional site located at a random interval between 500 and 2000 m

growth, or the tree was nearly dead with peeling bark and foliage restricted to basal shoots (Table 1). The response variable was the presence or absence of koala faecal pellets under each tree using a basal pellet search described in Smith et al. (2013).

#### Seasonal variation

To test for differences in koala occurrence post-drought, we repeated the 2009 surveys using the same plot/site locations in the wet year. Record flooding occurred in early March 2010 and we conducted surveys from June to October, which allowed at least three months for koala pellets to accumulate under trees.

#### Statistical modelling

Continuous variables were standardised to a mean of 0 and a standard deviation of 1, which converts contrasting absolute values of variables to a single scale (Zuur et al. 2007). Pairwise tests for collinearity of the standardised data were conducted using a Spearman correlation matrix. We used univariate general linear modelling to test the relative importance of pairs of variables with a correlation coefficient value  $\geq \pm 0.5$ . The variable with the higher AIC value was then removed from the analysis. We applied a log + 1 transformation to the “Distance from creek”

**Table 1** The explanatory variables used in the modelling of koala occurrence

Scale	Explanatory variable	Description
Tree	Tree species	Identification of each tree to a species level for <i>Eucalyptus camaldulensis</i> , <i>E. melanophloia</i> , <i>E. populnea</i> or as a non-eucalypt
	Tree condition	Two categories of canopy health dependent on the amount of dieback, where: 1 = good condition (none to some minor branches dead, slight shedding of bark or basal growth) 2 = poor condition (several major branches dead, severe shedding of bark or foliage restricted to basal growth)
Site (30 trees, $\leq 1$ ha)	Distance from creek	The distance in metres of the centre of the site from the nearest watercourse
Home-range ( $\sim 300$ ha)	Area of woodland in block	The area in hectares of the woodland habitat within each 300 ha sampling block
Landscape (100 km <sup>2</sup> )	Area of riverine in landscape	The area in hectares of the primary riverine habitat within each landscape
	Area of woodland in landscape	The area in hectares of the secondary woodland habitat with each landscape
	Interaction between riverine and woodland in landscape	The interaction between the areas of the riverine and woodland habitats
Temporal (seasonal variation)	Season	Two categories 1 = drought (2009) 2 = wet (2010)

to reduce the errors when fitting the models due to majority of koala faecal pellet presences occurring on the creek (distance = 0). We were also interested in the possibility of an interaction between the amount of primary and secondary habitat, and we included the interaction as a variable in our modelling. All analyses were carried out using the R statistical program (Version 2.13, R Development Core Team 2011).

We developed 256 alternative models, which included all linear combinations of the remaining eight variables. Using the lme4 package (Bates et al. 2011), we applied a mixed logistic regression model using all model combinations with random intercepts on grouping factors “plot”, “site”, “block” and “landscape”. The random intercept models account for variation at these hierarchical groupings (Zuur et al. 2009). The models took the following general form:

$$\ln\left(\frac{p_{ijklm}}{1 - p_{ijklm}}\right) = \alpha + \beta'X_{ijklm} + \gamma'_{ijklm} \quad (1)$$

where  $p_{ijklm}$  is the probability of a koala pellet being present in tree  $i$  of plot  $j$  nested in site  $k$  nested in block  $l$  nested in landscape  $m$ ;  $\alpha$  is the intercept;  $\beta$  is the vector of coefficients;  $X_{ijklm}$  is the vector of explanatory variables for tree  $i$  of plot  $j$  nested in site  $k$  nested in block

$l$  nested in landscape  $m$ ;  $\gamma_{ijklm}$  is the normally distributed random intercept for plot  $j$  nested in site  $k$  nested in block  $l$  nested in landscape  $m$ , with mean zero.

Models were ranked by AIC values and the Akaike weight for each model was calculated (Burnham and Anderson 2002). Model averaging was applied to determine the average parameter estimates and unconditional variance for each variable in the model (Burnham and Anderson 2002). We then ranked each variable according to its relative importance by using the sum of Akaike weights ( $\Sigma w_i$ ), where the variables with large weight values are more important than variables with smaller weight values (Burnham and Anderson 2002). Quantile–quantile plots (Landwehr et al. 1984) were used to assess model adequacy. This involved simulating model residuals 1000 times and plotting the predicted residuals on the  $x$ -axis against the fitted residuals on the  $y$ -axis, where a linear relationship indicates a good model fit (Landwehr et al. 1984; Rhodes et al. 2009). To test for spatial autocorrelation among model residuals, we created spline correlograms using the ncf package in R (Bjørnstad 2009). Spline correlograms display the spatial correlation using a smoothed spline with 95 % confidence intervals calculated by bootstrapping

(Bjørnstad and Falck 2001). Splines that are flat and centred on zero demonstrate spatial randomness, (i.e., the data are spatially independent), while splines that are not flat with 95 % confidence intervals that do not encapsulate zero show spatial autocorrelation (Bjørnstad and Falck 2001).

## Results

A total of 7949 trees were surveyed in 265 plots in 2009, and 8418 trees were surveyed in 281 plots in 2010. The discrepancy in number of trees sampled was due to flooding that cut the first season short. Koala faecal pellets were present in 52 plots in the first season and 49 plots in the second season. Tests for correlations identified the following variables to be important: tree species, tree condition, distance from creek, area of woodland community at the home-range scale, area of riverine community and area of woodland community at the landscape scale. The tree scale tree height, site scale proportion of *E. camaldulensis*, and the home-range scale variable of area of riverine vegetation within blocks were excluded from analysis due to high correlations. We included the remaining variables, along with season.

Estimates of the relative importance of each variable showed that the Tree species and distance from creek were the most important for the presence of koala faecal pellets (Fig. 3). Tree Condition and the interaction between area of riverine and area of woodland were of secondary importance (Fig. 3). Area of woodland at the home-range scale, season, and the landscape scale variables of area of woodland and area riverine were less important.

The model average parameter estimates (Fig. 4) showed that *E. camaldulensis* was the most important variable explaining the presence of koalas, with a strong positive value. The distance from creek had a strong negative effect, while the interaction using the two landscape scale variables of area of riverine and area of woodland had a strong positive effect. The other variables had weak parameter effects.

The quantile–quantile plot (Appendix 1—supplementary material) of our most parsimonious model showed that the simulated residual points lie close to the 1:1 line and occurred within the simulated 95 % confidence interval, identifying a good model fit. Similarly, the spline correlogram produced for the fitted

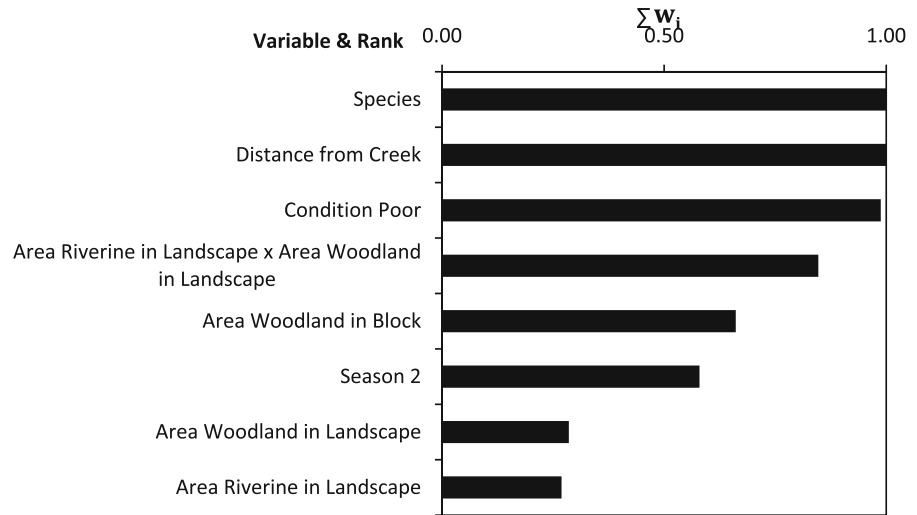
residuals of our most parsimonious model showed no spatial structure, indicating there was minimal spatial autocorrelation (Appendix 2—supplementary material).

## Discussion

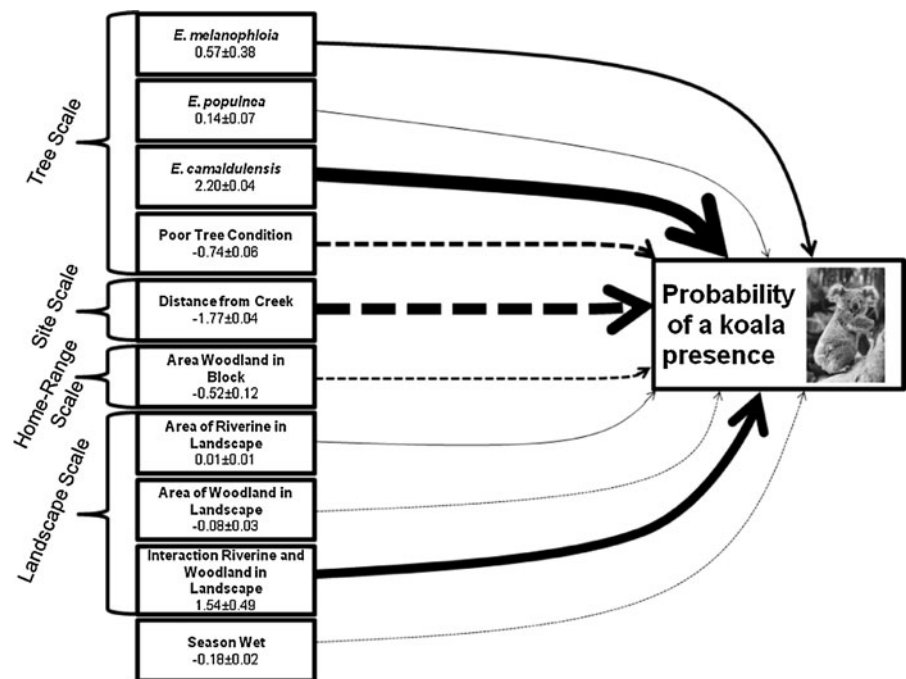
At the finest scale of resource selection, we found that koalas predominantly utilise the river red gum, which only occurs on drainage lines in riverine habitats. We rarely found koala pellets away from the creek. Riverine vegetation is critical refugia habitat in times of drought and is the source habitat for koala populations post-drought. This supports the findings of Gordon et al. (1988) who showed that koalas could survive in the riverine habitat during extreme heat events, and that in times of abundance, koalas would most likely move into surrounding marginal habitat. Sullivan et al. (2004) estimated that over half of the koalas in the Mulgaland's occurred in habitats away from the creeks. Seabrook et al. (2011) found that drought had significantly reduced the numbers of koalas throughout the region and that populations were restricted to riverine habitat. This suggests that the woodland habitats away from the creek are sink habitats, particularly during drought.

There was a strong positive interaction between the area of riverine and woodland habitat, although individually, these variables did not contribute strongly to the model. This result shows that koalas are more likely to occur in a landscape that has greater amounts of both riverine and woodland habitat, a reflection of the process of landscape supplementation (Dunning et al. 1992). In landscapes where the primary habitat is limited by habitat loss and fragmentation, secondary or matrix habitats can assist in landscape supplementation, which is important for gaining additional resources or facilitating movement (Dunning et al. 1992; Ricketts 2001; Prugh et al. 2008). A parallel example can be seen in howler monkeys (*Alouatta palliate mexicana*), an arboreal specialist, which persisted in patches nested within agricultural landscapes by supplementing their diets with high quality fruit and flowers outside their home habitat patches (Asensio et al. 2009). In our study, the presence of koalas in secondary habitat away from the creeks was rare, but did occasionally occur immediately adjacent to the creek (also see Seabrook et al. 2011; Smith et al. 2013), so even in times of drought it

**Fig. 3** The relative importance of the variables that explain the presence of koalas in the semi-arid Mulgalands bioregion, using the model averaging approach, where variables are ranked in order of the sum of the Akaike weights ( $\sum w_i$ ) for each variable



**Fig. 4** Path diagram showing the model averaged parameter estimate and unconditional variance of each explanatory variable used in all combinations of the mixed-effects logistic regression models used to model the presence and absence of koalas at four spatial scales (*Tree, Site, Home-Range and Landscape*). *Unbroken lines* represent positive effects and *dashed lines* are negative effects. The *thickness of the line* is weighted by the parameter average estimates for each variable



can be presumed to provide additional resources. Further evidence for use of secondary habitat by koalas in the Mulgalands Bioregion was provided by Davies et al. (unpublished manuscript), where satellite telemetry showed koalas spend approximately 20 % of their time in secondary habitat.

Our results did not show a change in the use of riverine and non-use of woodland habitat immediately following the drought. We attribute this finding to the view that it was too soon for koalas to move away from the creek. In our interpretation, secondary habitat is not only required

for additional habitat by koala populations when conditions favour growth, but also that the probability of finding koalas in more intact landscape is higher.

**Resource and habitat quality**

Resource and habitat quality is a key factor for the persistence of populations (Thomas et al. 2001; Kawecki 2008). Specialist species are particularly sensitive to resource and habitat quality because they have less choice of resources and habitats than



generalists (Bender and Fahrig 2005). Specialists are more likely to respond to sharp edges between habitats than generalists (Holland et al. 2009), and persistence will be reduced if landscape connectivity is compromised (e.g. Newell 1999). For arboreal animals, habitat quality is linked to the structure of woody cover (Emmons and Gentry 1983) and folivores depend on the foliar chemistry of those trees (Moore and Foley 2000). In arid and semi-arid habitats, the quality of woody cover depends on rainfall, land use, the density of vegetation (Fensham et al. 2005) and landscape structure (Debus et al. 2009), while the leaf chemistry, and therefore resource quality, changes spatially across landscapes, limiting folivores to a subset of food trees (Moore et al. 2010; Smith et al. 2013).

We demonstrated that the koala, a specialist arboreal folivore, was highly selective of the resources available at fine scales. In semi-arid regions, koalas prefer river red gum (Sullivan et al. 2003a; Seabrook et al. 2011; Smith et al. 2013). Consequently, in semi-arid landscapes where resource and habitat quality vary considerably, primary riparian habitat provides key resources and critically important refugia habitat for koalas, especially during drought.

Due to the importance of river red gums for koalas at the tree scale, the lack of importance of the area of riverine vegetation was unexpected. This suggests that koalas will occur in the landscape as long as there is riverine habitat with river red gum, irrespective of the habitat's extent. However, arboreal species are more sensitive to area of habitat than ground-dwelling species (Prugh et al. 2008), so there may be a threshold for the amount of riverine vegetation, below which koalas would decline. McAlpine et al. (2006b) and Rhodes et al. (2008) found that area of habitat for koalas was important for their persistence. Furthermore, while many species can traverse, and even acquire resources from, the matrix (Ricketts 2001; Franklin and Lindenmayer 2009), a specialist such as the koala could potentially become more restricted by landscape change than a generalist (Holland et al. 2009).

Implications for management of arboreal species or species in marginal habitat at the edge of their range

Despite the individual tree being the conspicuous unit of management and conservation for arboreal and/or folivorous species, they are sensitive to the amount of

habitat at greater scales (e.g. McAlpine et al. 2006b). While the amount of individual habitat types might not influence the persistence of a species, a synergistic interaction may take place between habitats, where a species might be able to complement and supplement their resources by occasionally accessing other habitats. The interactive effects between habitat loss and climate change are predicted to have an even greater impact on extinction of species than either process on its own (Mantyka-Pringle et al. 2012). Extreme weather can adversely impact vegetation (e.g. Fensham and Holman 1999; Breshears et al. 2005) and animals (e.g. Gordon et al. 1988; Welbergen et al. 2008). Therefore, the identification and protection of refugia for a species is critical for its conservation, such as for koalas in semi-arid regions.

In the Mulgalands, the riparian zones that contain riverine vegetation are presently protected from mechanical clearing, but vegetation clearing away from watercourse is permitted for thinning, clearing for encroachment and fodder harvesting (Department of Environment and Resource Management 2009). Using buffer zones to protect all native woody vegetation away from creeks is one solution to protect secondary habitats, but a quantitative analysis of extinction thresholds relating to secondary habitat, which defines the minimum amount of habitat a population requires to persist, would be required before a definitive buffer could be determined.

## Conclusion

The persistence of animals in human-modified landscapes and/or landscapes subject to natural catastrophes is a challenge for conservation management. For specialist species, conservation cannot simply focus on saving habitat at one scale, such as protecting preferred tree species, but it must also consider the area of habitats that the species uses, including those habitat that are sub-optimal for persistence, such as sinks. Despite a low frequency of use, marginal habitat may contribute to a species' survival, because it contains additional resources that complement or supplement resources in the primary source habitats. Furthermore, species at the edge of their biogeographic range may be more vulnerable to extreme weather from climate change, and refugia habitats must be identified and protected. Our findings show

that the presence of koalas in the semi-arid Mulga-lands bioregion not only depends on river red gums along creek lines, but also on the extent of riverine and woodland habitats at the landscape scale. Protection of habitat on and away from drainage lines is therefore critical for the persistence of koalas in the face of predicted extreme weather events from climate change in modified agricultural landscapes.

**Acknowledgments** We thank the Australian Research Council, the Australian Koala Foundation and South West NRM who funded this study (ARC Linkage Project 0882090). The surveys would not have been possible without the permission from the graziers to survey on their land and we are extremely grateful to them for this and for being hospitable to the field staff. We thank a number of volunteers who helped conduct field surveys. We also thank Lorenzo Cattarino, for helping with R scripts. Finally, we are grateful to two anonymous reviewers and coordinating journal editor who helped us improve the manuscript.

## References

- Adams-Hosking C, Grantham HS, Rhodes JR, McAlpine C, Moss PT (2011) Modelling climate-change-induced shifts in the distribution of the koala. *Wildlife Res* 38:122–130
- Asensio N, Arroyo-Rodríguez V, Dunn JC, Cristóbal-Azkarate J (2009) Conservation value of landscape supplementation for howler monkeys living in forest patches. *Biotropica* 41(6):768–773
- Bates D, Maechler M, Bolker B (2011) lme4: linear mixed-effects models using Eigen and Eigen. R package version 0.999375-42. <http://CRAN.R-project.org/package=lme4>. Accessed 29 Oct 2011
- Bender DJ, Fahrig L (2005) Matrix structure obscures the relationship between interpatch movement and patch size and isolation. *Ecology* 86(4):1023–1033
- Bergman K-O, Jansson N, Claesson K, Palmer MW, Milberg P (2012) How much and at what scale? Multiscale analyses as decision support for conservation of saproxylic oak beetles. *Forest Ecol Manag* 265:133–141
- Bjørnstad ON (2009) ncf: spatial nonparametric covariance functions. 1.1-3. <http://CRAN.R-project.org/package=ncf>. Accessed 11 May 2011
- Bjørnstad ON, Falck W (2001) Nonparametric spatial covariance functions: estimation and testing. *Environ Ecol Stat* 8:53–70
- Breshears DD, Cobb NS, Rich PM et al (2005) Regional vegetation die-off in response to global-change-type drought. *Proc Natl Acad Sci USA* 102(42):15144–15148
- Bureau of Meteorology (2011) Australian Government. <http://www.bom.gov.au>. Accessed 14 Aug 2011 and 22 Oct 2012
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Byrne M (2008) Evidence for multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography. *Quat Sci Rev* 27:2576–2585
- Channell R, Lomolino MV (2000) Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *J Biogeogr* 27:169–179
- Courtland R (2008) Polar bear numbers set to fall. *Nature* 453(7194):432–433
- Davies N, McAlpine C, Seabrook L, Bradley A, Baxter G, and Lunney D Home range sizes and resource use at the edge of a species' range: case study of koalas in south-western Queensland. Unpublished manuscript
- Debus VJ, House APN, Taylor DW, Swift SA (2009) Landscape structure influences tree density patterns in fragmented woodlands in semi-arid eastern Australia. *Austral Ecol* 34(6):621–635
- Department of Environment and Resource Management (2009) Regional Vegetation Management Code for Western Bioregions—version 2. Queensland Government
- Department of Environment and Resource Management (2010) Land cover change in Queensland 2008–2009: a Statewide Landcover and Trees Study (SLATS) report, 2011 Department of Environment and Resources Management, Brisbane
- Dique DS, Thompson J, Preece HJ, de Villiers DL, Carrick FN (2003) Dispersal patterns in a regional koala population in south-east Queensland. *Wildl Res* 30:281–290
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65(1):169–175
- Ellis WAH, Melzer A, Carrick FN, Hasegawa M (2002) Tree use, diet and home range of the koala (*Phascolarctos cinereus*) at Blair Athol, central Queensland. *Wildl Res* 29:303–311
- Emmons LH, Gentry AH (1983) Tropical forest structure and the distribution of gliding and prehensile-tailed vertebrates. *Am Nat* 121(4):513–524
- Fahrig L (2001) How much habitat is enough? *Biol Conserv* 100:65–74
- Fensham RJ, Holman JE (1999) Temporal and spatial patterns in drought-related tree dieback in Australian savanna. *J Appl Ecol* 36:1035–1050
- Fensham RJ, Fairfax RJ, Archer SR (2005) Rainfall, land use and woody vegetation cover change in semi-arid Australian savanna. *J Ecol* 93:596–606
- Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. *Global Ecol Biogeogr* 16:265–280
- Franklin JF, Lindenmayer DB (2009) Importance of matrix habitats in maintaining biological diversity. *Proc Natl Acad Sci USA* 106(2):349–350
- Gaston KJ (2009) Geographic range limits: achieving synthesis. *Proc R Soc B* 276:1395–1406
- Gordon G, Brown AS, Pulsford T (1988) A koala (*Phascolarctos cinereus* Goldfuss) population crash during drought and heatwave conditions in south-western Queensland. *Aust J Ecol* 13:451–461
- Holland EP, Aegerter JN, Dytham C (2009) Comparing resource representations and choosing scale in heterogeneous landscapes. *Landscape Ecol* 24:213–227

- Kavanagh RP, Stanton MA, Brassil TE (2007) Koalas continue to occupy their previous home-ranges after selective logging in *Callitris-Eucalyptus* forest. *Wildl Res* 34:94–107
- Kawecki TJ (2008) Adaptation to marginal habitats. *Annu Rev Ecol Evol Syst* 39:321–342
- Landwehr JM, Pregibon D, Shoemaker AC (1984) Graphical methods for assessing logistic regression models. *J Am Stat Assoc* 79(385):61–71
- Lunney D, Crowther MS, Wallis I et al (2012) Koalas and climate change: a case study on the Liverpool Plains, north-west New South Wales. In: Lunney D, Hutchings P (eds) *Wildlife & climate change: towards robust conservation strategies for Australian fauna*. Royal Zoological Society of New South Wales, Mosman, pp 150–168
- Mantyka-Pringle CS, Martin TG, Rhodes JR (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biol* 18(4):1239–1252
- Martínez-Mota R, Valdespino C, Sánchez-Ramos MA, Serio-Silva JC (2007) Effects of forest fragmentation on the physiological stress response of black howler monkeys. *Anim Conserv* 10(3):374–379
- Matthews A, Lunney D, Gresser S, Maitz W (2007) Tree use by koalas (*Phascolarctos cinereus*) after fire in remnant coastal forest. *Wildl Res* 34:84–93
- McAlpine CA, Bowen ME, Callaghan JG et al (2006a) Testing alternative models for the conservation of koalas in fragmented rural–urban landscapes. *Austral Ecol* 31:529–544
- McAlpine CA, Rhodes JR, Callaghan JG et al (2006b) The importance of forest area and configuration relative to local habitat factors for conserving forest mammals: a case study of koalas in Queensland, Australia. *Biol Conserv* 132:153–165
- McAlpine CA, Rhodes JR, Bowen ME et al (2008) Can multi-scale models of species' distribution be generalized from region to region? A case study of the koala. *J Appl Ecol* 45(2):558–567
- Mönkkönen M, Reunanen P (1999) On critical thresholds in landscape connectivity: a management perspective. *Oikos* 84(2):302–305
- Moore BD, Foley WJ (2000) A review of feeding and diet selection in koalas (*Phascolarctos cinereus*). *Aust J Zool* 48:317–333
- Moore BD, Wallis IR, Marsh KJ, Foley WJ (2004) The role of nutrition in the conservation of the marsupial folivores of eucalypt forests. In: Lunney D (ed) *Conservation of Australia's forest fauna*. Royal Zoological Society of New South Wales, Sydney
- Moore BD, Lawler IR, Wallis IR, Beale CM, Foley WJ (2010) Palatability mapping: a koala's eye view of spatial variation in habitat quality. *Ecology* 91(11):3165–3176
- Mpelasoka F, Hennessy K, Jones R, Bates B (2008) Comparison of suitable drought indices for climate change impacts assessment over Australia towards resource management. *Int J Climatol* 28:1283–1292
- Murray JV, Low Choy S, McAlpine CA, Possingham HP, Goldizen AW (2008) The importance of ecological scale for wildlife conservation in naturally fragmented environments: a case study of the brush-tailed rock-wallaby (*Petrogale penicillata*). *Biol Conserv* 141:7–22
- Newell GR (1999) Responses of Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*) to loss of habitat within a tropical rainforest fragment. *Biol Conserv* 91:181–189
- Nix H (1986) A biogeographic analysis of Australian elapid snakes. In: Longmore R (ed) *Atlas of elapid snakes of Australia*. Bureau of Flora and Fauna, Australian Flora and Fauna Series Number 7. Australian Government Publishing Service, Canberra, pp 4–15
- Parmesan C, Root TL, Willig MR (2000) Impacts of extreme weather and climate on terrestrial biota. *Bull Am Meteorol Soc* 81(3):443–450
- Pereira HM, Daily GC, Roughgarden J (2004) A framework for assessing the relative vulnerability of species to land-use change. *Ecol Appl* 14(3):730–742
- Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. *Proc Natl Acad Sci USA* 105(52):20770–20775
- Pulliam HR (1988) Sources, sinks, and population regulation. *Am Nat* 132(5):652–661
- Queensland Herbarium (2005) *Vegetation Communities and regional ecosystems survey and mapping version 5.0*. Environmental Protection Agency, Brisbane
- Queensland Herbarium (2009) *Vegetation communities and regional ecosystems survey and mapping version 6.0b*. Department of Environment and Resource Management, Brisbane
- R Development Core Team (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>. Accessed 11 May 2011
- Rhodes JR, Wiegand T, McAlpine CA et al (2006) Modeling species' distributions to improve conservation in semiurban landscapes: koala case study. *Conserv Biol* 20(2):449–459
- Rhodes JR, Callaghan JG, McAlpine CA et al (2008) Regional variation in habitat-occupancy thresholds: a warning for conservation planning. *J Appl Ecol* 45(2):549–557
- Rhodes JR, McAlpine CA, Zuur AF, Smith GM, Ieno EN (2009) GLMM applied on the spatial distribution of koalas in a fragmented landscape. In: Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (eds) *Mixed effects models and extensions in ecology with R., statistics for biology and health*. Springer, New York, pp 469–492
- Rice KJ, Matzner SL, Byer W, Brown JR (2004) Patterns of tree dieback in Queensland, Australia: the importance of drought stress and the role of resistance to cavitation. *Oecologia* 139:190–198
- Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. *Am Nat* 158(1):87–99
- Sabo JL, Post DM (2008) Quantifying periodic, stochastic, and catastrophic environmental variation. *Ecol Monogr* 78(1):19–40
- Sattler P, Williams R (1999) *The conservation status of Queensland's bioregional ecosystems*. Environmental Protection Agency, Brisbane
- Seabrook L, McAlpine C, Baxter G, Rhodes J, Bradley A, Lunney D (2011) Drought-driven change in wildlife distribution and numbers: a case study of koalas in south west Queensland. *Wildl Res* 38:509–524

- Smith MD (2011) The ecological role of climate extremes: current understanding and future prospects. *J Ecol* 99: 651–655
- Smith AG, McAlpine C, Rhodes JR et al (2013) At what spatial scales does resource selection vary? A case study of koalas in a semi-arid region. *Austral Ecol*. <http://onlinelibrary.wiley.com/doi/10.1111/j.1442-9993.2012.02396.x/abstract>
- Sullivan BJ, Baxter GS, Lisle AT (2003a) Low-density koala (*Phascolarctos cinereus*) populations in the mulgalands of south-west Queensland. III. Broad-scale patterns of habitat use. *Wildl Res* 30:583–591
- Sullivan BJ, Norris WM, Baxter GS (2003b) Low-density koala (*Phascolarctos cinereus*) populations in the mulgalands of south-west Queensland II. Distribution and diet. *Wildl Res* 30:331–338
- Sullivan BJ, Baxter GS, Lisle AT, Pahl L, Norris WM (2004) Low-density koala (*Phascolarctos cinereus*) populations in the mulgalands of south-west Queensland. IV. Abundance and conservation status. *Wildl Res* 31:19–29
- Thackway R, Cresswell ID (1995) An interim biogeographic regionalisation for Australia: a framework for establishing the national system of reserves, version 4.0. Nature Conservation Agency, Canberra
- Thomas JA, Bourn NAD, Clarke RT et al (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proc R Soc B* 268:1791–1796
- Welbergen JA, Klose SM, Markus N, Eby P (2008) Climate change and the effects of temperature extremes on Australian flying-foxes. *Proc R Soc B* 275:419–425
- Zuur AF, Ieno EN, Smith GM (eds) (2007) *Analysing ecological data*. Springer, New York
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (eds) (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York