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Running head: Spatial patterns in koala habitat quality

Title: PALATABILITY MAPPING: A KOALA’S EYE VIEW OF SPATIAL VARIATION IN HABITAT QUALITY

BEN D. MOORE\textsuperscript{1,2}
Evolution, Ecology and Genetics, Research School of Biology, Australian National University, Canberra, ACT 0200, Australia.

IVAN R. LAWLER\textsuperscript{3}
School of Earth and Environmental Sciences, James Cook University of North Queensland, Douglas, Queensland 4811, Australia.

IAN R. WALLIS
Evolution, Ecology and Genetics, Research School of Biology, Australian National University, Canberra, ACT 0200, Australia.

COLIN M. BEALE\textsuperscript{4}
Ecology Group, Macaulay Land Use Research Institute, Aberdeen AB15 8QH, United Kingdom.

WILLIAM J. FOLEY
Evolution, Ecology and Genetics, Research School of Biology, Australian National University, Canberra, ACT 0200, Australia.

\textsuperscript{1} Current address: Ecology Group, Macaulay Land Use Research Institute, Aberdeen AB15 8QH, United Kingdom
\textsuperscript{2} email: b.moore@macaulay.ac.uk
\textsuperscript{3} Current address: Department of the Environment, Water, Heritage and the Arts GPO Box 787, Canberra ACT 2601, Australia
\textsuperscript{4} Current address: Department of Biology (Area 18), PO Box 373, University of York, YO10 5YW
Abstract:

Ecologists trying to understand the value of habitat to animals must first describe the value of resources contained in the habitat to animals and second, they must describe spatial variation in resource quality at a resolution relevant to individual animal foraging. We addressed these issues in a study of koalas in a *Eucalyptus* woodland. We measured beneficial and deterrent chemical characteristics as well as the palatability of trees using a near infrared spectroscopic model based on direct feeding experiments. Tree use by koalas was influenced by tree size and foliar quality but was also context-dependent: trees were more likely to be visited if they were surrounded by small, unpalatable trees or by large, palatable trees. Spatial autocorrelation analysis and several mapping approaches demonstrated that foliar quality is spatially structured in the woodland at a scale relevant to foraging decisions by koalas and that the spatial structure is an important component of habitat quality.

Keywords: NIRS; associational defence; formylated phloroglucinol compounds; spatial autocorrelation; plant secondary metabolites; habitat quality; patch use; *Phascolarctos cinereus*, generalized additive mixed modelling.
Introduction

A fundamental aspect of animal habitat quality is the quality and amount of food available. To understand this, ecologists need to be able to describe variation in food quality at scales that are relevant to foraging individuals through to scales that are relevant to populations and species (Searle et al. 2007). A concept closely linked to food quality is palatability, an emergent property resulting from a complex series of interactions. Palatability must be deduced from herbivores’ feeding behavior, which is a product of the herbivores’ current nutritional state, their past experiences (if any) with the food, and their perceptions of the tradeoff between any detrimental qualities of the food (e.g., plant secondary metabolites, PSMs) against the food’s positive nutritional qualities (Bryant et al. 1991; Provenza et al. 1998). Feeding studies with captive animals can often reveal animals’ preferences from among a limited range of foods (Hjältén et al. 2004; Schreiber & Swihart 2009), or identify factors such as PSMs which cause them to reject some foods (Bryant et al. 1983; Lawler et al. 1999), but they are not necessarily useful for predicting foraging behavior by wild animals that are faced with more complex choices and tradeoffs while foraging in heterogeneous environments.

The defensive and nutritional chemistry of many, if not most, plant populations is highly variable (Lawler et al. 2000) and that this variation is often spatially structured (Covelo & Gallardo 2004; Andrew et al. 2007). Spatial hotspots of highly palatable or highly unpalatable plants are ecologically important, because the likelihood of a plant being eaten is a product not only of its own characteristics but also of the context in which it occurs (Feng et al. 2009). Plants experience associational defense or associational resistance when they benefit from reduced herbivory because of their association with neighbouring plants and associational susceptibility if the association is detrimental (Atsatt & O'Dowd 1976, Barbosa et al. 2009). A plant can experience associational resistance from unpalatable neighboring plants when herbivores make foraging decisions at the scale of a patch of plants, or by association with palatable neighbors if they act as attractant-decoys when herbivores forage at an individual-
plant scale (Bergvall et al. 2006). Whether such associational effects occur, and whether spatial patches of trees of similar palatability are of any significance to foraging herbivores thus depends upon the scale of the herbivore’s foraging movements (Milchunas & Noy-Meir 2002).

A recent meta-analysis shows that although both associational resistance and susceptibility occur in plant-mammal interactions, the former is more likely (Barbosa et al. 2009). Few studies have looked for these effects in continuous, natural plant associations, because the environment has seldom been described at the spatial resolution required. However, any discussion of spatial context in plant-herbivore interactions should explicitly consider heterogeneity of plant associations.

In this study, we aimed to comprehensively describe the spatial distribution of foliar chemistry and palatability in a patch of *Phascolarctos cinereus* Goldfuss (koala) habitat large enough to include multiple koala home ranges. The koala is a highly specialised arboreal folivore which feeds almost exclusively on *Eucalyptus* L'Hérit. species (Martin & Handasyde 1999). Therefore, individual trees represent an unambiguous and discrete unit of habitat selection. Describing the habitat in such detail makes possible the investigation of spatial dependence in foliar palatability and an assessment of whether spatial dependence and spatial context influence the use of trees by koalas.

To achieve this goal, we used near infrared reflectance spectroscopy (NIRS) (Foley et al. 1998). In NIRS, statistical calibrations are established between near infrared spectra and qualitative or quantitative attributes of organic samples such as tree leaves. Because it is correlative, NIRS is ideal for predicting emergent properties of plant material, such as palatability or digestibility of foods (McIlwee et al. 2001; DeGabriel et al. 2008) or rates of decomposition (Stolter et al. 2006) and it does not require *a priori* knowledge of the underlying chemistry. In this study, we used NIRS to develop an empirical calibration for palatability of foliage to koalas (i.e., voluntary dry matter intake of *Eucalyptus* foliage).
Tree use and diet choice by koalas have previously been linked, with various degrees of support, to tree size and species and to foliar concentrations of nitrogen, phosphorous, potassium, fibre, volatile terpenes, soluble sugars and leaf moisture (Moore & Foley 2000). However, the single most powerful deterrents of koala feeding are a group of lipid-soluble phenolics known as the formylated phloroglucinol compounds, or FPCs (Moore & Foley 2005; Moore et al. 2005). Thus, one testable hypothesis arising from measurement of foliage palatability was that the NIRS predictions of palatability were negatively related to concentrations of FPCs and positively related to concentrations of nitrogen. NIRS calibrations for palatability have been developed previously for greater gliders (Petauroides volans Kerr) and common ringtail possums (Pseudocheirus peregrinus Ogilby) feeding on Eucalyptus (McIlwee et al. 2001; Wallis & Foley 2003), but they have not been applied to studies of wild animals. A second hypothesis was that the use of trees by wild koalas can be predicted as well as or better by these NIRS calibrations than by combinations of individually measured chemical constituents.

Methods

Study site and species

The study site was the Koala Conservation Centre, a 7.6 ha fenced koala reserve on Phillip Island (38°28’ S, 145°13’ E), Victoria, Australia. Approximately 20 koalas foraged freely throughout the reserve, which included 5.9 ha of remnant woodland dominated by the trees Eucalyptus globulus Labill. and E. ovata Labill. and to a lesser extent by E. viminalis Labill. The eastern side of the reserve was formerly cleared pasture land that had been replanted with approximately 400 trees, which averaged 6 m in height at the time of this study (Fig. 1). All trees in the reserve were individually marked and mapped before this study commenced. In January 1997, diameters at breast height (130 cm), or DBH, were measured and foliage samples were collected (approximately 50 g wet weight) from all eucalypt trees, for a total of 376 remnant and 119 planted E. globulus, 383 remnant and 30 planted E. ovata and 161
remnant and 215 planted *E. viminalis*. Samples of clean, fully-expanded, adult foliage were
sealed in plastic bags and immediately frozen. Samples were subsequently freeze-dried and
then ground to pass a 1 mm screen using a Tecator cyclone mill prior to collection of NIR
spectra or other chemical analysis.

**Measurements of foliar palatability**

Feeding measurements were made with three different groups of six individually-housed
each occasion, six male koalas (5.1–11.25 kg) were captured using standard techniques from
trees on French Island, Victoria. In total, we determined the palatability of foliage from 50 *E.
globulus*, 29 *E. ovata* and 69 *E. viminalis* trees. Some trees were growing in the reserve, but
many were collected from within a 50 km radius of it, on Phillip Island, French Island and the
mainland. The index of foliar palatability was the mean dry mass of foliage voluntarily eaten
overnight by each of four male koalas, randomly assigned from a group of six koalas, under the
no-choice feeding protocol (described by Moore et al. 2005). Briefly, at least 3 kg (fresh
weight, including branches) of foliage from a single tree was weighed and presented to an
individual koala overnight (from 1700 - 0800 hrs). Uneaten and dropped foliage was
reweighed the following morning, and the amount eaten was calculated and corrected for
evaporative loss determined from a control branch placed outside the cage overnight. For each
measurement, a sample of the foliage fed to koalas was frozen for subsequent collection of
NIR spectra, other chemical analyses and determination of dry weight.

**Development of NIRS calibration models**

For all dried and ground foliage samples, we collected the reflectance spectrum from 400 to
2500 nm using a NIRSystems 6500 scanning spectrophotometer with spinning cup attachment
(NIRSystems, Silver Spring, Maryland, USA). Each sample was scanned twice or until the root
mean square of two scans (stored as log (1/reflectance)) was less than 3.0 × 10^-4, and the two
spectra were averaged.
In most cases, mathematical transformations (one or both of the standard normal variate (SNV)) and detrend transformations (Barnes et al. 1989) were applied to raw NIR spectra to reduce the influence of particle size. Predictive equations were then developed using modified partial least squares regression (MPLS), with cross-validation to prevent overfitting of models (Shenk & Westerhaus 1991). These regressions were performed on the first or second derivatives of the transformed spectra, using the software WinISI II, Version 1.02 (Infrasoft International). The optimum mathematical treatment was selected by minimising the standard error of cross-validation. Attempts were made to develop a universal NIRS calibration for palatability that could be applied across all three eucalypt species, in addition to combined two-species calibrations and individual single-species calibrations. To identify the best calibration, different combinations of data from each of the three experimental periods were tested.

Calibration data for total FPC concentrations were determined using the HPLC assay described by Moore et al. (2004b) and nitrogen was determined using a semimicro Kjeldahl technique. The NIRS calibrations used to measure these constituents are described in Moore and Foley (2005).

**Koala tree use data**

A community volunteer group, assisted by nature park rangers, systematically searched the reserve for at least 3 daylight hours once per month and recorded the tag numbers of all trees occupied by koalas. Between January 1993 and March 2004, 1522 such observations were recorded from *Eucalyptus* trees.

**Statistical modelling of tree use by koalas**

Generalised additive models (GAM) and generalized additive mixed models (GAMM) were used to describe koala visits to trees in the reserve. GAMs allow the consideration of multiple smooth explanatory variables, with the extension to GAMMs allowing spatially explicit models to be fitted, reducing the incidence of Type I statistical errors in spatial datasets (Lennon 2000). However, when the dataset is restricted to individual tree species, the spatial
structure of the the tree use by koalas is not completely described and estimation of the spatial
effects becomes inaccurate. Consequently, non-spatial GAMs were used to build single species
models and then combined for all species using a spatially explicit GAMM. All GAM and
GAMM models were implemented using the R package “mgcv” (Wood 2006, 2008).
Modelling was carried out in three stages. Firstly, pairs of non-spatial GAM models, with
Poisson errors and a log-link were fitted to koala data for individual tree species, with tree size
(DBH) and either palatability or, for comparison, total FPC and nitrogen content as covariates.
All covariates were smoothed with penalised regression splines with the maximum dimension
fixed at 4. For each of the pair of models for each species, Akaike’s Information Criterion
(AIC) was used to select a minimum adequate model.
The second stage of the analysis combined all species in a spatially explicit GAMM model,
again with Poisson errors and a log-link and including an exponential covariance model of the
residual spatial autocorrelation. Covariates were species identity, nitrogen, a species × nitrogen
interaction and smoothed DBH and FPC concentration. Predictions of individual tree use were
generated and used to determine an index of neighborhood quality for use in the third stage of
analysis. The neighborhood quality was the mean predicted number of koala visits to all trees
within a 25 m radius away from the focal tree.
The final stage of analysis was to repeat the first and second stages, but now including an
additional smooth term describing the neighborhood quality estimated in the second stage.
Goodness-of-fit was assessed using residual plots, and as there was some evidence of zero-
inflation in the GAM models, the analysis was repeated using Constrained Zero-inflated
Generalized Additive Models (COZIGAM, Liu & Chan 2008) with the zero-inflation a
function of tree size. These models showed improved fit but regression coefficients were
essentially similar and consequently those models are not reported further.

Spatial analysis of foliar characteristics
The strength and scale of spatial autocorrelation in FPC concentrations and predicted DMI were determined by calculating Moran’s $I$, an index of global spatial autocorrelation, at 10 m distance intervals from 10 m to 200 m. Values of $I$ were tested for significance against 1000 permutations, and autocorrelograms were constructed with these data. These analyses excluded planted trees as the aim was to understand spatial dependence in a natural woodland.

**Mapping**

A number of interpolated surfaces were produced to describe the phenotypic landscape within the reserve. This approach aimed to visualize spatial trends in foliar attributes of a single tree species, without regard for the size of individual trees or their contribution to the nutritional landscape facing herbivores. For this approach, the intensity $\hat{\lambda}_v(z)$ of the attribute of interest at a location $z$ in the study area $A$ was determined by

$$\hat{\lambda}_v(z) = \left\{ \frac{\sum_{i=1}^{n} y_i}{\sum_{i=1}^{n} \frac{1}{(z - z_i)^b}} \right\} \cdot \frac{1}{\sum_{i=1}^{n} \frac{1}{(z - z_i)^b}} \quad z \in A \quad \text{equation 1}$$

where $z_i (i=1, \ldots, n)$ are locations of $n$ observed trees in the circular neighborhood with radius $\tau$, $(z - z_i)$ is the Euclidean distance between $z$ and $z_i$ in meters, $y_i$ is the attribute value at $z_i$ and $b$ is a positive real number called the power constant. Interpolated surfaces were also produced to describe the density of predicted (extracted from the final GAMM using the “predict” function in R) and observed koala visits throughout the reserve using equation 2.

$$\hat{\lambda}_v(z) = \frac{1}{p_v(z)} \left\{ \sum_{i=1}^{n} k(z - z_i) y_i \right\} \quad z \in A \quad \text{equation 2}$$

The kernel, or probability density function, $k$, used to weight observations within the search radius $\tau$ was determined from 332 observations of movements by radiocollared female koalas from one tree to another within the reserve. For records to qualify, koalas must have remained under continuous direct visual observation from the moment they left the canopy of one tree until they entered another. These observations were made as part of another study (KJ Marsh...
and BD Moore, unpublished data). The term \( p_*(z) \) is an edge correction equivalent to the volume under the scaled kernel centered on \( z \) which lies inside \( A \).

**Results**

**NIRS predictions of foliar attributes**

The mean amount of foliage eaten by koalas varied considerably among individual trees of *E. globulus* (16 - 232 g DM, mean = 136.6) and *E. viminalis* (37 - 267 g DM, mean = 139.2), but less so among *E. ovata* (134 - 213 g DM, mean = 145). Mathematical treatment of spectra and descriptive statistics for NIRS calibrations of foliage palatability are described in appendix 1 in *Ecological Archives*. The models for *E. globulus* and *E. viminalis* both had \( r^2 \) values of 0.78 and had standard errors of cross validation of 33.2 and 39.4 respectively. NIRS-predicted palatability values agreed well with observed values and palatability was normally distributed for both species (Fig. 2). All attempts to develop a calibration encompassing more than one species or to predict palatability of *E. ovata* were unsuccessful.

The set of koala feeding observations used to develop the calibration for *E. globulus* (the “calibration set”) included spectra from all trees except those identified as spectral outliers (Shenk & Westerhaus 1991). For *E. viminalis*, however, calibration sets including leaf samples from feeding trials in all experimental periods produced markedly less powerful predictive equations than those produced from any of the three groups separately. The final *E. viminalis* calibration set excluded the 1998 data but included 18 trees each from 2001 and 2003.

Among remnant trees of both species, the foliage of larger trees tended to be less palatable than that of smaller trees (linear regressions: for *E. globulus*, \( \text{DMI} = 207.2 - 0.37(\text{DBH}) \); \( F_{1,374} = 22.14; P < 0.001, r^2 = 0.053 \); for *E. viminalis*, \( \text{DMI} = 170.2 - 0.54(\text{DBH}) \); \( F_{1,374} = 6.42; P = 0.01, r^2 = 0.033 \)). A multiple linear regression \( (F_{2,377} = 67.8, P < 0.001) \) explaining 26% of variation in predicted palatability for *E. viminalis* included as significant independent variables FPC concentration (effect = -4.45, \( P<0.001 \)) and nitrogen (effect = 2.77, \( P = 0.04 \)). An
equivalent regression for *E. globulus* explained 24% of variation ($F_{2,492} = 77.2, P < 0.001$; FPC
effect = -3.27, $P < 0.001$; nitrogen effect = 2.66, $P = 0.007$).

**Koala Tree Use**

Koalas were observed 895, 259 and 421 times in *E. globulus*, *E. ovata* and *E. viminalis* respectively. DBH and neighborhood quality were highly significant predictors of koala visits to both *E. globulus* and *E. viminalis* (Table 1). Below about 60 cm DBH, the larger the tree, the more likely it was to be visited by koalas, but above 60 cm, the likelihood of being visited was not related to DBH (Fig. 3).

For *E. globulus*, koala visits were positively associated with palatability (GAM 2, Table 1, Fig. 3). The explanatory power of this model was very similar to an alternative model (GAM 1) that included FPC concentration (negative association) and nitrogen (positive association); koala visits decreased below a nitrogen threshold of 12 mg/g DM (Table 1, Fig. 3). Similarly for *E. viminalis*, GAM 4 showed a positive association between koala visits and palatability and was equally satisfactory as GAM 3, which showed that koala visits decreased as foliar FPC concentration increased above about 20 mg/g DM. GAM 5 showed koala visits to *E. ovata* were explained by a positive relationship with DBH and in this case also by a negative relationship with nitrogen concentration (Table 1, Fig. 3).

Because the NIRS calibration for palatability of *E. ovata* was unsuccessful, it was not possible to include palatability in a GAMM describing visits to all three species. GAMM 1 (Table 1) reveals that after accounting for spatially autocorrelated residual error, koala visits were explained by DBH, neighborhood quality, FPC concentration, foliar nitrogen and tree species (*E. ovata* or other). Koala visits were positively associated with nitrogen for *E. viminalis* and *E. globulus*, but negatively for *E. ovata*. The smoothed term for neighborhood quality was U-shaped, indicating that a tree’s likelihood of koala visitation increased both in good neighborhoods (where neighboring trees were predicted to receive many koala visits) and in bad ones (where the opposite was true) compared to an average neighbourhood (Fig. 3).
GAMM 1 predicted that koala visits varied across a range of DBH, FPC concentrations and neighborhood quality values (Fig. 3).

Spatial autocorrelation

FPC concentrations exhibited spatial autocorrelation up to a distance of 30 m in each species (Fig. 4A), and patchy species distributions (Fig. 1) and between-species differences in foliar chemistry (Moore et al. 2004) produced much stronger spatial autocorrelation at distances of up to 150 m when all trees in the reserve were considered (Fig. 4A). In contrast to FPC concentrations, spatial autocorrelation in NIRS-predicted palatability for *E. globulus* and *E. viminalis* and in foliar nitrogen for all three species was insignificant.

Mapping

60% of female koala tree-tree movements were between trees less than 30 m apart (Fig. 4B). An interpolated surface generated using equation 1, where $\tau = 30$ m and $b = 0.4$ highlighted several hotspots of high-FPC phenotypes in the population of *E. globulus* (Fig. 5B). A comparison of two interpolated surfaces from equation 2 ($\tau = 50$ m and $k$ = the kernel shown in Fig 4B) showed that the density of koala visits predicted by GAMM1 (Fig. 5C) correctly identified several local koala hotspots and coldspots in the density of observed koala visits (Fig. 5D), however the two maps were less congruent along much of the left-hand side of the mapped area.

Discussion

We have demonstrated for the first time that NIRS predictions of plant palatability derived from feeding behavior of captive animals describe an important individual plant trait that influences foraging by wild herbivores. This technique offers a novel, herbivore-driven perspective of food and habitat quality. We successfully developed NIRS models to predict DMI of foliage by koalas for two widely used koala food species. The significant relationship between predictions made by these models and FPC and nitrogen concentrations is consistent with previous understandings of the factors influencing koala feeding preferences. The fact that
the final calibrations were influenced both by positive and negative aspects of plant quality is remarkable, particularly given the fact that statistical analysis of the feeding experiments in isolation failed to detect a relationship between nitrogen and koala feeding (Moore et al. 2005).

A great strength of the generalized additive modelling approach adopted here is that splines can be inspected to reveal the true shape of the relationship between koala visits and each significant tree attribute. For example, smooth terms fitted in GAM 1 and 3 (Fig. 3) reveal threshold effects of nitrogen and FPC concentrations respectively. Koalas apparently do not discriminate among *E. globulus* on the basis of foliar nitrogen as long as it exceeds a threshold (about 12 mg/g); below that threshold, trees can escape koala herbivory to varying degrees: the lower the foliar nitrogen, the less likely koalas are to visit.

Unexpectedly, one model suggested that koalas preferentially used *E. ovata* trees with lower, rather than higher, nitrogen concentrations. Total nitrogen is a crude index of protein availability to herbivores because protein that becomes bound to tannins is largely indigestible (DeGabriel et al. 2008), so a measure of digestible nitrogen might show a different relationship to koala tree use. It is also conceivable that an unmeasured leaf attribute, such as the cyanogenic glycoside prunasin, which has previously been reported from *E. ovata* (Gleadow et al. 2008), covaries with nitrogen concentrations and deters koalas.

The models also revealed that trees are more likely to be visited by koalas if they are growing in either a particularly poor neighborhood or a particularly good neighborhood, where the quality of the neighborhood is influenced by both the size of neighboring trees and their foliar chemistry. The observed effect is presumably the result of two processes operating simultaneously. The associational susceptibility of trees in particularly poor neighborhoods can be explained by an attractant-decoy effect (Milchunas & Noy-Meir 2002), whereby the trees attract koalas because alternatives in the immediate vicinity are poor by comparison. The
associational susceptibility of trees in high-quality neighborhoods can be explained if koalas
also make foraging decisions at a larger ‘patch’ scale resulting in a preference for ‘good’
neighborhoods. Other studies have also shown that herbivores make simultaneous foraging
decisions at multiple scales in experimental arenas (Hjältén et al. 1993; Bergman et al. 2005),
however the success of this study in describing these processes in natural, continuous
vegetation illustrates the value of this fine-scale mapping approach.
The strong neighborhood effect on tree use by koalas emphasises the importance of ‘seeing the
forest for the trees’ when considering spatial variation in habitat quality, because although trees
themselves are variable and represent habitat patches, further larger-scale patchiness in their
value to herbivores is also present. Fine-scale spatial autocorrelation was observed among FPC
concentrations of each species considered. FPC concentrations are highly heritable in
*Eucalyptus* (Andrew et al. 2005) and Andrew et al. (2007) showed in *E. melliodora* that strong
spatial autocorrelation in FPC concentrations overlaid a highly congruent spatial structure in
genetic variance. The strength and scale of autocorrelation observed in this study for FPCs are
comparable to those in *E. melliodora* and those for genetic markers in Tasmanian *E. globulus*
(Skabo et al. 1998) and are probably largely a product of isolation by distance (Heywood
1991). In addition to endogenous genetic factors however, it is also conceivable that
exogeneous factors have contributed to the observed spatial structure, either through
geographical heterogeneity in natural selection (Endler 1977; Linhart & Grant 1996) or
through environmental influences on phenotypes (Gram & Sork 2001; Brenes-Arguedas &
Coley 2005).
Mapping approaches such as the smoothed phenotypic surfaces presented here (Fig. 5) allow
the identification of phenotypic hotspots, where the intensity of the trees’ interactions with its
herbivores may differ from elsewhere. This map, along with the analysis of spatial
autocorrelation, reveals that the scale of patchiness in FPC concentrations is the same scale that
koalas forage at, as half of all observed movements by female koalas in the reserve were of
350 30 m or less. As a consequence, after many movements from tree to tree, koalas will find
351 themselves in trees of similar quality to the tree they have just left. For less mobile folivores,
352 possibly including the common ringtail possums in the reserve, which are far more sensitive to
353 variation in FPC concentrations (Lawler et al. 1998; Moore et al. 2004a), and for insects, this
354 scale of spatial structure might be a defining feature not only of the foraging landscape but also
355 of fine-scale species distribution patterns. Furthermore, although the study site at Phillip Island
356 was relatively small, flat and edaphically homogenous, across larger and more diverse areas,
357 greater intraspecific variation in the quality of trees can be expected (O'Reilly-Wapstra et al.
358 2002; Moore et al. 2004c), with correspondingly significant consequences for folivore habitat
359 quality. These observations emphasise the importance of considering animal behavior and the
360 scale of animal foraging decisions when assessing landscape condition for herbivores (Searle et
361 al. 2007).
362 It is not surprising that tree size should so strongly affect where koalas are found during the
363 day. Larger trees possess more foliage and thus represent larger feeding patches; however they
364 may also provide more shade and greater safety from perceived dangers on the ground.
365 Although it has been demonstrated on Phillip Island that the presence of a koala in a tree is a
366 reliable indicator that some feeding has occurred in the tree (B.D. Moore, K. J. Marsh,
367 unpublished data, Martin & Handasyde 1999), these data are not ideal for investigating the
368 effect of foliar quality on feeding. Koalas mostly feed at night, and particularly if koalas favor
369 relatively smaller trees for feeding, then observed diurnal visits likely provide a biased
370 snapshot of where feeding takes place. Isolated records of koala visits also ignore such
371 subtleties as variation in meal length and number of meals eaten per tree visit that characterize
372 koala feeding behavior (Marsh et al. 2007). These facts suggest that the models might
373 somewhat overestimate the importance of tree size to koalas and underestimate the importance
374 of foliar characteristics.
The map of predicted koala densities throughout the reserve is based upon model predictions of visits to individual trees, but the interpolation was directed by observed koala movement patterns. This map is one attempt to ‘scale up’ the current understanding of habitat use at one of the smallest scales possible, the individual tree, to a larger scale. However, conservation professionals and landscape ecologists generally work at scales beyond the 7 hectare reserve that we studied. For example, one previous multiscale model of koala habitat selection considered factors operating from the tree scale through the stand scale and patch scale to factors varying at a landscape scale of 100’s to 1000’s of hectares (McAlpine et al. 2008).

Reynolds (2008) has commented that two major challenges in spatial ecology are to understand the effects of landscape heterogeneity on animal movement, and to translate observations taken at small spatial and temporal scales into expected patterns at greater scales. More studies like this, that consider herbivory and associational effects in exhaustively documented, heterogeneous habitats, will help to address the first challenge; practical limitations to the extent at which habitats can be analyzed in such detail mean that ecologists need to develop new strategies to tackle the second challenge. In particular, they will need to design sampling strategies which trade off spatial scale against resolution but which describe habitats in a way meaningful to herbivores, while remaining conscious that animals can change movement patterns over time and in different habitats (Morales and Ellner 2002).

Although this is the first demonstration that NIRS can be used to predict herbivore responses to plant quality directly from NIRS spectra, the principles are applicable to the majority of plant-herbivore interactions and the technique offers a promising route to rapidly describe plant and habitat quality at a variety of scales (Foley et al. 1998). Furthermore, remote sensing techniques can already detect foliar biochemistry at the scale of individual trees and patches (Kokaly et al. 2009) making the development of high-resolution, large scale maps a worthy goal for researchers in the future. It is our hope that the approaches presented here offer a useful way forward for ecologists as they attempt to understand the way in which physical,
chemical and spatial aspects of habitat ultimately interact to determine the presence or absence
of individuals and populations of animals and the susceptibility of plants to herbivores at a
variety of scales.

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Table 1. Generalized additive models (GAM 1 - 5) separately describing koala visits to three *Eucalyptus* species at Phillip Island and a generalized additive mixed model (GAMM 1) describing visits to all three species. Smoothed terms are illustrated in Fig. 3.

<table>
<thead>
<tr>
<th>Terms</th>
<th>Estimate</th>
<th>$\chi^2$, $z$, $t$ or $F$</th>
<th>$P$</th>
<th>$r^2$</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GAM 1 - <em>E. globulus</em></strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>s(DBH)</td>
<td>-</td>
<td>489.124</td>
<td>&lt;0.001</td>
<td></td>
<td>0.32</td>
</tr>
<tr>
<td>s(neighborhood)</td>
<td>-</td>
<td>41.603</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>s(FPC)</td>
<td>-</td>
<td>13.805</td>
<td>0.002</td>
<td></td>
<td></td>
</tr>
<tr>
<td>s(nitrogen)</td>
<td>-</td>
<td>9.925</td>
<td>0.022</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>GAM 2 - <em>E. globulus</em></strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>s(DBH)</td>
<td>-</td>
<td>535.6</td>
<td>&lt;0.001</td>
<td></td>
<td>0.33</td>
</tr>
<tr>
<td>s(neighborhood)</td>
<td>-</td>
<td>55.9</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>s(palatability)</td>
<td>-</td>
<td>20.0</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>GAM 3 - <em>E. viminalis</em></strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>s(DBH)</td>
<td>-</td>
<td>92.5</td>
<td>&lt;0.001</td>
<td></td>
<td>0.36</td>
</tr>
<tr>
<td>s(neighborhood)</td>
<td>-</td>
<td>55.5</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>s(FPC)</td>
<td>-</td>
<td>13.7</td>
<td>0.003</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>GAM 4 - <em>E. viminalis</em></strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>s(DBH)</td>
<td>-</td>
<td>106.7</td>
<td>&lt;0.001</td>
<td></td>
<td>0.35</td>
</tr>
<tr>
<td>s(neighborhood)</td>
<td>-</td>
<td>48.9</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>s(palatability)</td>
<td>-</td>
<td>16.7</td>
<td>&lt;0.001</td>
<td></td>
<td></td>
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</tbody>
</table>
### GAM 5 - *E. ovata*

<table>
<thead>
<tr>
<th>Term</th>
<th>Value</th>
<th>SE</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>s(DBH)</td>
<td>-</td>
<td>203.9</td>
<td>&lt;0.001</td>
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<tr>
<td>nitrogen</td>
<td>-0.12</td>
<td>-3.2</td>
<td>0.002</td>
</tr>
</tbody>
</table>

### GAMM 1 - all species

<table>
<thead>
<tr>
<th>Term</th>
<th>Value</th>
<th>SE</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>s(DBH)</td>
<td>-</td>
<td>144.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>s(neighborhood)</td>
<td>-</td>
<td>6.0</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>s(FPC)</td>
<td>-</td>
<td>5.4</td>
<td>0.003</td>
</tr>
<tr>
<td>nitrogen</td>
<td>0.06</td>
<td>3.013</td>
<td>0.003</td>
</tr>
<tr>
<td>species: <em>E. ovata</em></td>
<td>1.98</td>
<td>2.392</td>
<td>0.017</td>
</tr>
<tr>
<td>nitrogen × species: <em>E. ovata</em></td>
<td>-0.15</td>
<td>-2.808</td>
<td>0.005</td>
</tr>
</tbody>
</table>

*s(…) denotes smooth terms*

†For GAMs, $\chi^2$ statistics describe parametric terms and z statistics describe smooth terms; for the GAMM, $t$ statistics describe parametric terms and $F$ statistics describe smooth terms.
**Figure Captions**

**FIG. 1.** Spatial distribution of *Eucalyptus globulus*, *E. ovata* and *E. viminalis* trees in the study area. The fenced area is divided into 4 regions indicated by solid lines: The largest region contains only remnant trees and the three smaller areas on the lower and right-hand edges contain only planted trees.

**FIG. 2.** Palatability (dry matter intake, g) of foliage to koalas, predicted by near-infrared spectroscopic calibrations plotted against mean (n = 4) observed palatability to captive koalas for (a) *E. globulus* and (b) *E. viminalis*. Solid lines indicate ordinary least squares linear regressions and dashed lines show a 1:1 relationship. Parts (c) and (d) are histograms showing the distributions of NIRS-predicted palatability of *E. globulus* (n = 495) and *E. viminalis* (n = 380). Solid lines indicate scaled kernel density estimates and dashed lines indicate scaled normal distributions.

**FIG. 3.** Smooth terms included in generalized additive models 1 & 2 (*E. globulus*), 3 & 4 (*E. viminalis*) and 5 (*E. ovata*) and generalized additive mixed model 1 (all species), described in the text and in table 1. Each row corresponds to one model, shaded regions show 95% confidence interval around smooth.

**FIG. 4(a).** Autocorrelograms showing spatial autocorrelation (Moran’s I) of FPC concentrations at 10 m intervals in *E. globulus*, *E. ovata*, *E. viminalis* and all species together. Shaded regions indicate a 95% confidence interval determined from 1000 permutations, filled circles indicate values that differ significantly from the expected value of I given a lack of autocorrelation, which is indicated by the gray horizontal line. (b) Gaussian kernel density estimate (solid line) and corresponding cumulative density function (dashed line) of observed
tree-to-tree movements by female koalas at Phillip Island (n = 332). For the kernel density estimate, the estimated density at distances of less than 9 m was increased to match the maximum density value.

FIG. 5. (a) Map of remnant *E. globulus* trees. Size of circles shows relative dbh of trees, shade of gray indicates foliar FPC concentrations as indicated in key. Gray outline delimits extent of remnant woodland. (b) Interpolated surface generated using equation 1, illustrating mean FPC concentrations of *E. globulus* in a search radius of 30 m with a power constant of 0.4. Koala density maps generated using equation 2 with a maximum search radius (τ) of 50 m (c) from the predictions of GAMM 1 and (d) from observed koala tree use; shading indicates relative koala densities from high (dark shading) to low (light).
E. globulus
E. ovata
E. viminalis
(a) Moran's I

- E. globulus
- E. ovata
- E. viminalis
- All species

(b) Koala movements

Kernel density estimate

Cumulative density (%)