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Regional variation in habitat–occupancy thresholds: a warning for conservation planning

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Summary

1. An important target for conservation planning is the minimum amount of habitat needed in a landscape to ensure the persistence of a species. Appropriate targets can be determined by identifying thresholds in the amount of habitat, below which persistence, abundance or occupancy declines rapidly. Although some studies have identified habitat thresholds, we currently have little understanding of the extent to which thresholds vary spatially. This is important for establishing whether we can apply the same planning targets across broad geographical regions.

2. We quantified habitat–occupancy relationships for the koala *Phascolarctos cinereus* (Goldfuss) in three study regions that span much of its geographical range. Standard and piecewise (broken-stick/segmented) logistic regression were used to model linear and threshold habitat–occupancy relationships. We then used an information-theoretic approach to test: (1) whether habitat–occupancy relationships were described better by threshold or linear models and (2) where threshold models were better, whether, and to what extent, threshold points varied among study regions.

3. There was substantially greater support for the threshold than the linear models across a range of habitat qualities and landscape extents. The threshold models generally predicted a rapid decline in occupancy below the threshold points.

4. Estimated threshold points varied, sometimes substantially, among study regions. This may relate to cross-regional differences in habitat quality, demographic rates, and land-use patterns. The role of habitat fragmentation is unclear.

5. *Synthesis and applications*. Variation in threshold points among study regions suggests that we should be wary of using thresholds derived in one region for setting conservation planning targets in another. Rather, we should aim to set specific targets for individual locations (and species), while acknowledging the inherent uncertainties in these targets. This has implications for our ability to make general conservation prescriptions for widely distributed species. Future research should aim to develop generic models capable of predicting threshold responses across different landscapes and life-history characteristics.

Key-words: broken-stick regression, extinction, fragmentation, habitat loss, koala, landscape ecology, logistic regression, *Phascolarctos cinereus*, piecewise regression, segmented regression

Introduction

Developing quantitative rules-of-thumb for managing biological populations is an important challenge for applied ecologists. In particular, there is great demand from conservation and landscape planners for thresholds in habitat amount, above which a species is likely to persists but below which it will not. Various authors have suggested general rules-of-thumb, such as 10–30% suitable habitat in a landscape, above which species will have a good chance of persistence (Andrén 1994; McIntyre & Hobbs 1999). These types of rules-of-thumb are used by management agencies as a guide

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for setting habitat protection targets (e.g. ANZECC/MCFFA 1997). While we know that these rules are crude and potentially misleading (Lindenmayer & Luck 2005), the need to identify thresholds is pervasive. In the absence of habitat amount targets, we are left with the unhelpful statement: 'more is better'. This problem has motivated the development of a substantial amount of theory for understanding population responses to habitat loss and identifying extinction thresholds (Lande 1987; Hanski, Moilanen & Gyllenberg 1996; With & King 1999). However, we have little understanding about the extent to which a species' response to habitat loss varies spatially in the real world. Consequently, we do not know if it is sensible to set a generalized target across a species' range or whether we must identify specific targets for specific locations.

Theory shows that extinction responses to habitat loss can be highly non-linear (Lande 1987). As habitat is lost from a landscape critical thresholds can be reached, below which further loss results in a rapid increase in extinction risk (Fahrig 2001). One mechanism for explaining these non-linear responses is that, as habitat is lost, it becomes increasingly fragmented and a threshold is eventually reached where the landscape is no longer functionally connected (With & Crist 1995). Alternatively, threshold responses may arise from habitat loss alone, independent of fragmentation, due to non-linear effects on reproduction and survival (e.g. Allee effects) and stochastic effects in small populations (Lande 1993; Stephens & Sutherland 1999).

Empirical studies that identify threshold responses to habitat loss as the point at which persistence, occupancy or abundance declines abruptly as habitat is lost show that there is substantial variation in responses (Lindenmayer, Fischer & Cunningham 2005; Denöel & Ficetola 2007; Betts, Forbes & Diamond 2007). It is generally accepted that threshold responses will vary among species with different life-history characteristics (With & King 1999; Fahrig 2001; Vance, Fahrig & Flather 2003). However, a particular species' response to habitat loss is also likely to vary spatially due to differences in landscape characteristics, such as habitat fragmentation, landscape history and land-use (Mönkkönen & Reunanen 1999). Threshold responses for a particular species may also vary spatially due to variation in demographic rates (Fahrig 2001). Understanding spatial variation in population responses to habitat loss is particularly important for widely distributed species because demographic and landscape characteristics can vary substantially across their ranges.

We addressed this issue by quantifying the extent to which threshold responses to habitat loss varied across a species' geographical range, using the koala *Phascolarctos cinereus* (Goldfuss) as a case study. The koala is a widely distributed species, extending across 30 biogeographical regions from tropical Queensland (18° S) to temperate south-east Australia (38° S). It is a forest habitat specialist and sensitive to both habitat loss and fragmentation (Melzer *et al*. 2000; McAlpine *et al*. 2006). We used data on koala presence/absence from three study regions that span its geographical range, to test: (1) whether habitat–occupancy relationships were better described by threshold or linear models and (2) where threshold models were better, whether, and to what extent, threshold points varied among study regions. To model threshold responses, we used piecewise (broken-stick/segmented) logistic regression, which provided an objective statistical method for achieving these aims.

Materials and methods

STUDY SPECIES

Koalas are arboreal folivores, feeding on a wide range of tree species from the genus *Eucalyptus*, but preferring mainly only a few species in any particular area (Hindell & Lee 1987; Phillips & Callaghan 2000; Phillips, Callaghan & Thompson 2000). Koala habitat generally consists of forest associations containing their preferred tree species, although other factors, such as tree size, water availability and nutrient status can also be important determinants of habitat quality (Moore *et al*. 2004; Matthews *et al*. 2007). Since European settlement, the koala has suffered declines in abundance and distribution due to clearing and degradation of eucalypt forests, together with historical hunting, disease, bushfire, drought and urbanization (ANZECC 1998; Melzer *et al*. 2000; Phillips 2000).

STUDY REGIONS

The study regions consisted of three local government areas: Noosa (86 800 ha) in south-east Queensland, Port Stephens (97 900 ha) on the central coast of New South Wales, and Ballarat (74 000 ha) in central western Victoria. These span much of the koala's geographical range, with Port Stephens being approximately 700 km south of Noosa and Ballarat being approximately 900 km south-west of Port Stephens. See McAlpine *et al*. (this issue) for the locations and descriptions of each study region.

HABITAT MAPPING

Koala habitat has been mapped in each study region as part of the Australian Koala Foundation's (AKF) *Koala Habitat Atlas* (Lunney *et al*. 1998; AKF unpublished data). Using data from the *Koala Habitat Atlas*, four habitat suitability classes (highly suitable, suitable, marginal and unsuitable) were mapped for each study region. See McAlpine *et al*. (this issue) for a description of the habitat mapping.

PRESENCE/ABSENCE DATA

The presence/absence data were derived from koala faecal pellet surveys conducted at sites located across the study regions during winter and spring 2001/2002 in Noosa, autumn 2002 in Port Stephens and autumn 2003 in Ballarat. Survey sites were chosen by random stratified sampling and, at each site, a single survey, based on searches for pellets under trees located at the site, was conducted to determine the presence or absence of koalas. See McAlpine *et al*. (this issue) for descriptions of the procedures used to select sites and the method for conducting pellet searches under trees.

The survey at each site was conducted using one of two alternative sampling protocols, which we differentiate by referring to sites as either 'spot assessment' or 'presence–absence' sites. The protocol used for the spot assessment sites is described by McAlpine *et al*. (this issue). For the presence–absence sites, three subsites were first

located 100 m apart, along a 200 m transect, at each site (at a few sites logistical constraints only allowed one or two subsites to be located). The location of the transect was chosen so that all three subsites were within the same vegetation type. At each subsite, pellet searches were then conducted under trees (with diameter-at-breast-height ≥ 10 cm), starting with the tree at the centre of the subsite and working outwards, until either a pellet was found or a maximum of 12 trees had been searched. For both protocols, a presence was recorded at a site if at least one pellet was found, otherwise an absence was recorded.

The data consisted of: 195 spot assessment sites and 100 presence–absence sites in Noosa (170 presences and 125 absences); 80 spot assessment sites and 126 presence–absence sites in Port Stephens (155 presences and 51 absences); and 100 spot assessment sites in Ballarat (76 presences and 24 absences). Although we combined data from surveys that used slightly different sampling protocols, the two approaches are very similar and sampling effort at each site was roughly the same, regardless of the protocol used. Therefore, combining the data was considered sound.

CONCEPTUAL MODELS

Prior to data analysis we developed three alternative conceptual models for the effect of habitat loss on the probability of occupancy. These conceptual models were then used as a basis for constructing alternative statistical models of the relationship between koala occupancy and the amount of suitable habitat. Based on the random sample hypothesis (e.g. Andrén 1994), the first model (the 'null' model) assumes that fragmentation and small population effects are not important. Under the random sample hypothesis, individuals are distributed randomly across a landscape and suitable habitat patches contain random subsamples of individuals from the broader landscape (Coleman 1981; Haila 1983). Consequently, as habitat is lost, the relationship between the proportion of habitat remaining and the proportion of the population remaining is linear and one to one (Andrén, Delin & Seiler 1997), and population density in suitable habitat remains constant. For presence/absence, provided the sizes of sampling units used to record occupancy are small relative to the total area of habitat (which is the case in our study), the probability of occupancy will remain relatively constant as habitat is lost (see Supplementary material, Appendix S1). The second model (the 'trend' model) assumes that fragmentation and/or small population effects are important and the random sample hypothesis does not hold, leading to a decline in occupancy as habitat is lost.

The random sample hypothesis may hold at high, but not at low, amounts of remaining habitat. This would occur if fragmentation and/or small population effects are only important when the amount of remaining habitat is low (e.g. Flather & Bevers 2002). In such cases, as habitat is lost, there would initially be no decline in occupancy, but there would be a decline once the amount of remaining habitat was sufficiently low. If there is a clear transition between where the random sample hypothesis holds and where it does not, then a threshold response to habitat loss would occur. This formed the basis of the third model (the 'threshold' model).

STATISTICAL ANALYSIS

Around each site we generated three circular buffers, with radii of 1000 m, 3000 m and 5000 m. Then, within each buffer, we calculated the percentage of the landscape (excluding water bodies and unmapped areas) that was: (1) highly suitable plus suitable plus marginal (HSSM) habitat; (2) highly suitable plus suitable (HSS) habitat; and (3) highly suitable (HS) habitat. Buffer sizes were chosen to encompass the range of scales at which koala dispersal occurs, ensuring that habitat amount was measured at landscape extents relevant to koalas at the population-level. Koala dispersal distances have been found generally to be in the order of 1–3 km, although can occasionally be as high as 10 km (Dique *et al.* 2003). Further, landscape extents of this size (particularly 1000 m buffers) have been found previously to be appropriate for modelling koala distributions (McAlpine *et al.* 2006). We also generated a categorical patch-scale metric for each survey site. This consisted of the habitat suitability class (highly suitable, suitable, marginal or unsuitable) of the habitat patch within which each site was located. The aim of the patch-scale metric was to capture processes occurring at the home range scale.

We then used standard and piecewise logistic regression to model the probability of koala occupancy as functions of the patch-scale habitat classes and the landscape-scale percentage habitat metrics. We considered four alternative regression models, all of which included the patch-scale habitat class, but differed in how the percentage habitat metrics were included. These models were: (1) a 'null' model – standard logistic regression (Hosmer & Lemeshow 2000) with no percentage habitat covariate; (2) a 'trend' model – standard logistic regression with a percentage habitat covariate; (3) a 'threshold (different)' (TD) model – piecewise logistic regression (Ulm 1991) with a percentage habitat covariate, but where the probability of occupancy depends only on percentage habitat below different threshold points for each study region; and (4) a 'threshold (same)' (TS) model – same as the TD model, but where all study regions have identical threshold points. These regression models were chosen as statistical representations of the three conceptual models, but with two alternative threshold models, one with a different threshold point for each study region and one with the same threshold points for all study regions.

For each percentage habitat metric we fitted (by maximum-likelihood) all four models to the data from all three study regions and calculated 95% profile-likelihood-based confidence intervals for the estimated threshold points, τ (Hilborn & Mangel 1997). Then, model comparisons were conducted to: (1) assess which of the null, trend or threshold models best described the relationships between occupancy and percentage habitat; and (2) assess whether estimated threshold points were the same, or different, among study regions. These model comparisons were conducted within an information-theoretic framework (Burnham & Anderson 2002). For each model, we calculated its Akaike's information criterion (AIC) and, for each percentage habitat metric, ranked models by their AIC values (Akaike 1973). We also calculated each model's Akaike weight and calculated evidence ratios for pairs of models. A model's Akaike weight is a measure of the probability that the model is the Kullback–Leibler best model, given a set of models (Burnham & Anderson 2002). Evidence ratios are ratios of Akaike weights for pairs of models and measure how much more likely one model is the Kullback–Leibler best model, relative to another (Burnham & Anderson 2002). Also, to gain an understanding of the support for each model within each study region, we repeated this procedure for the null, trend and threshold (TD) models for individual study regions. All models were fitted using R version 2·4·1 (http://www.r-project.org). See Supplementary material, Appendices S2, S3, and S4 for formal descriptions of the logistic regression models, the procedures used to fit them and associated R functions.

To assess model adequacy we conducted deviance-based goodness-of-fit tests for the trend, TD and TS models (Hosmer & Lemeshow 2000). Although there is some distribution theory for the

deviance and Pearson χ^2 statistics for logistic regression (Hosmer & Lemeshow 2000), it is not clear whether this extends to piecewise logistic regression. Therefore we used a parametric bootstrap approach to calculate *P*-values for the goodness-of-fit tests. From each model, we generated 1000 simulated data sets, refitted the model to each of these, and calculated the deviance for each. This provided an empirical distribution for the deviance, under the null hypothesis that the model fitted to the real data was the true model. The *P*-value for each model was then calculated as the proportion of replicates that had a deviance greater than the deviance of the model fitted to the real data (*sensu* Su & Wei 1991). We also inspected plots of the deviance contributions of individual data points to identify any highly influential data and possible reasons for any lack-of-fit (Pregibon 1981). Finally, to assess model discrimination ability, we calculated the area under the receiver operating characteristic curve (AUC) for the trend, TD and TS models (Hanley & McNeil 1982; Pearce & Ferrier 2000). The AUC is an estimate of the probability that a randomly chosen, truly occupied site is ranked correctly relative to a randomly chosen, truly unoccupied site. For each model, AUCs were calculated based on predictions from the fitted model and on predictions derived from a 'leave-one-out' cross-validation procedure (Stone 1974). The R package ROC (http://www.bioconductor.org) was used to estimate the AUCs.

Results

All models were fitted successfully to the data, except for the TD model for HS habitat for the 3000 m buffer due to convergence failure (see Supplementary material, Table S1 for comprehensive details of all model fits). For individual study regions where the threshold model could be fitted, it was the most parsimonious model in 22 of 25 cases (Table 1). Exceptions were: (1) HS habitat for the 5000 m buffer in Noosa; (2) HSS habitat for the 5000 m buffer in Port Stephens; and (3) HSS habitat for the 1000 m buffer in Ballarat. Where the threshold model was the most parsimonious, its Akaike weight ranged from 0·453 to 0·999; over 70% had Akaike weights > 0·7 and 50% had Akaike weights > 0·9 (Table 1). Therefore, in all study regions there tended to be good support for the threshold models relative to the null or trend models, particularly for HSSM habitat.

For the models fitted to the combined data from all three study regions, either the TS or TD models were always the most parsimonious, with weak relative support for the null and trend models (Table 2). One exception was for HS habitat for the 3000 m buffer. Here the TS model was only slightly more likely to be the best model than the trend model, with an evidence ratio of 1·4 (see Supplementary material, Table S1). However, for all other percentage habitat metrics, the most parsimonious threshold models had evidence ratios of at least 111·7 relative to the null or trend models (see Supplementary material, Table S1). The TD model was more parsimonious than the TS model for 6 of the 8 percentage habitat metrics where the TD model could be fitted (Table 2). Evidence ratios for the TD models relative to the TS models were 0·4, 0·4, 1·1, 3·4, 8·5, 9·8, 26·0 and 593·8 (see Supplementary material, Table S1). Therefore, while the TS model was never substantially more likely to be the best model than the TD model, in many cases the TD model was substantially more likely to be the best model than the TS model. This indicates generally greater relative support for the TD models than the TS models.

The goodness-of-fit tests did not reveal any significant lack-of-fit ($P > 0·1$) for any of the trend, TD or TS models (see Supplementary material, Table S1). Further, inspection of the deviance contributions from individual data points did not reveal any that were highly influential. Individual deviance contributions also indicated that the TD models tended to fit the data better than the trend models at low levels of percentage habitat (i.e. below the thresholds), but similarly at high levels of percentage habitat. Although less distinct, the TD models also tended to fit the data better than the TS models at low levels of percentage habitat. AUCs for the most parsimonious models were slightly less than 0·7 (see Supplementary material, Table S1), indicating poor to reasonable discrimination ability (Pearce & Ferrier 2000). The TD and TS models tended to have similar AUCs, but generally slightly higher than the trend models (see Supplementary material, Table S1). AUCs based on the cross-validation predictions had slightly lower values, but otherwise showed similar patterns (see Supplementary material, Table S1).

With one exception, predictions from the threshold models all showed rapid declines in occupancy below the threshold points, indicating general agreement with the conceptual

Table 1. Individual models for each study region, showing the most parsimonious model and its Akaike weight (in parentheses) for each percentage habitat metric

Habitat type	Buffer radius (m)	Noosa	Port Stephens	Ballarat
HSSM	1000	Threshold (0·994)	Threshold (0·499)	Threshold (0·453)
	3000	Threshold (0·994)	Threshold (0·990)	Threshold (0·908)
	5000	Threshold (0·857)	Threshold (0·996)	Threshold (0·905)
HSS	1000	Threshold (0·833)	Threshold (0·981)	Null (0·570)
	3000	Threshold (0·737)	Threshold (0·946)	Threshold (0·764)
	5000	Threshold (0·649)	Null (0·507)	Threshold (0·999)
HS	1000	Threshold (0·510)	Threshold (0·631)	Threshold (0·931)
	3000	Trend (0·901)†	Trend (0·999)†	Threshold (0·856)
	5000	Null (0·461)	Threshold (0·637)	Threshold (0·985)

HSSM = highly suitable plus suitable plus marginal habitat; HSS = highly suitable plus suitable habitat; HS = highly suitable habitat; null = null model; trend = trend model; threshold = threshold model. †Could not fit threshold model due to convergence failure.

Table 2. Overall models for each percentage habitat metric, showing Akaike weights, w, estimated threshold points, τ, and 95% confidence intervals (in parentheses)

Buffer radius (m)	Model	w_{HSSM}	w_{HSS}	w_{HS}	τ_{HSSM}	τ_{HSS}	τ_{HS}
1000	Null	0·000	0·000	0·000			
	Trend	0·000	0·001	0·007			
	TD	0·304	0·893	0·768	61·19 (52·44, 76·43)	61·47 (42·06, 87·76)	52·76 (15·55, 75·97‡)
					52·42 (8·68, 80·45)	12·94 (10·43, 42·67)	32·46 (1·00, 70·54‡)
					30·32 (3·88‡, 99·90‡)	22·20 (0·38‡, 93·01‡)	0·68 (0·20, 12·88)
	TS	0·695	0·105	0·225	58·59 (50·57, 69·59)	42·25 (31·80, 67·09)	19·21 (14·72, 31·47)
3000	Null	0·000	0·000	0·000			
	Trend	0·000	0·000	0·417			
	TD	0·963	0·517	†	45·69 (39·02, 61·98)	38·61 (26·32, 55·68)	†
					30·23 (29·29, 41·33)	36·22 (29·88, 42·30)	
					7·79 (3·15, 36·14)	17·95 (5·40, 36·71)	
	TS	0·037	0·483	0·583	41·75 (32·83, 50·06)	37·02 (29·38, 41·03)	13·12 (10·03, 37·94‡)
5000	Null	0·000	0·001	0·000			
	Trend	0·000	0·000	0·000			
	TD	0·907	0·998	0·297	55·75 (37·19, 64·10)	39·28 (25·76, 57·36)	2·63 (0·68‡, 31·20‡)
					42·50 (29·29, 49·00)	24·40 (20·12‡, 91·51‡)	11·86 (8·30, 25·91‡)
					9·01 (4·73, 36·52)	7·34 (6·78, 9·23)	8·77 (3·11, 13·70)
	TS	0·093	0·002	0·703	42·37 (29·62, 48·85)	33·99 (20·12‡, 47·62)	11·15 (8·27, 14·10)

HSSM = highly suitable plus suitable plus marginal habitat; HSS = highly suitable plus suitable habitat; HS = highly suitable habitat; null = null model; trend = trend model; TD = threshold model with a different threshold point for each study region; TS = threshold model with the same threshold points for all study regions; ‡confidence limit at minimum or maximum of data range; †could not fit model due to convergence failure. Threshold point estimates for the TD models are ordered: (1) Noosa (2) Port Stephens and (3) Ballarat.

threshold model (Figs 1, 2 and 3). The exception was for HSS habitat for the 5000 m buffer in Port Stephens, where the TD model predicted occupancy to increase below the threshold (Fig. 2e). Estimated threshold points tended to be highest in Noosa, followed by Port Stephens and then Ballarat, although there was also considerable overlap (Table 2). For example, for HSSM habitat, threshold point estimates ranged from 46–61% in Noosa, 30–52% in Port Stephens, and 8–30% in Ballarat across the different landscape extents. However, 95% confidence intervals were wide for most threshold point estimates, indicating high levels of uncertainty (Table 2).

Discussion

Conservation planners invariably require targets for species and habitats before they can make cost-effective decisions (Possingham *et al.* 2006). The task would be simplified substantially if reliable rules-of-thumb for the amount of habitat required by species could be developed based on thresholds. We found that habitat–occupancy relationships for the koala were consistently better described by threshold than linear models, but that threshold points varied, sometimes substantially, among study regions. This identifies some promise for the use of thresholds to set conservation targets, but the variation in threshold points indicates that we cannot safely transfer simple habitat targets from one region to another.

HABITAT–OCCUPANCY RELATIONSHIPS

Despite theoretical support for the existence of habitat thresholds (Hanski, Moilanan & Gyllenberg 1996; With & King 1999), empirical evidence for their existence is mixed

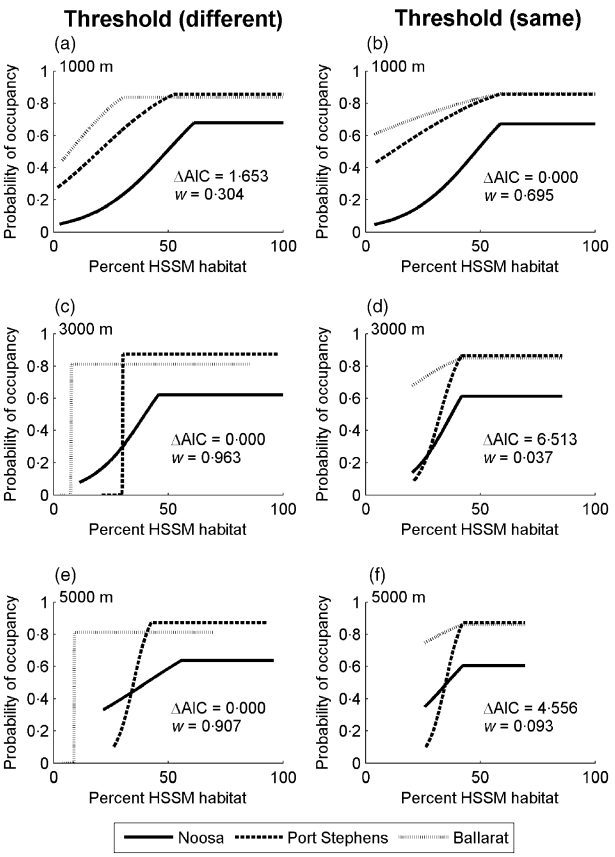

Fig. 1. Fitted threshold (different) and threshold (same) models for highly suitable plus suitable plus marginal (HSSM) habitat and the highly suitable patch-scale habitat class. (a, b) buffer radius of 1000 m (c, d) buffer radius of 3000 m and (d, e) buffer radius of 5000 m. Akaike's information criterion (AIC) differences, ΔAIC, and Akaike weights, w, for the models are also shown.

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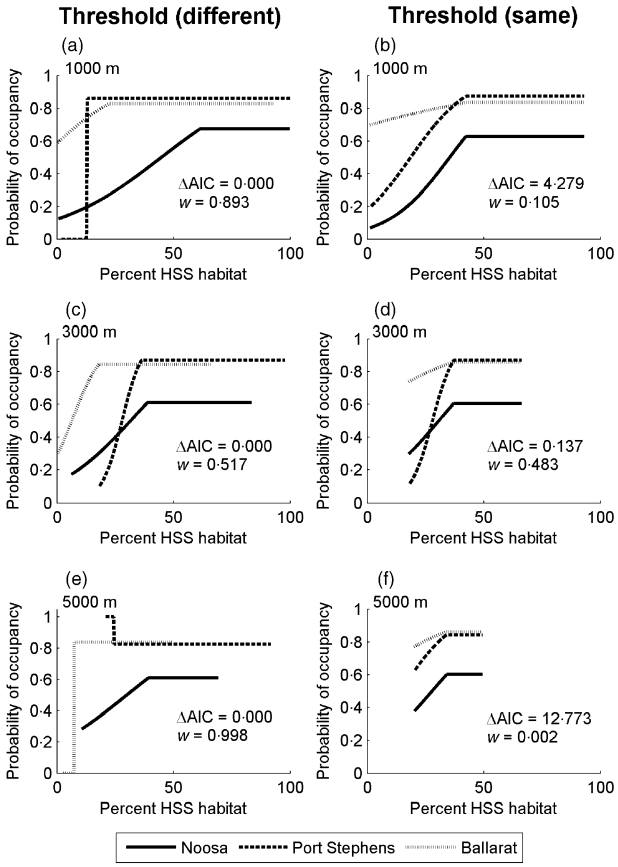

Fig. 2. Fitted threshold (different) and threshold (same) models for highly suitable plus suitable (HSS) habitat and the highly suitable patch-scale habitat class. (a, b) buffer radius of 1000 m (c, d) buffer radius of 3000 m and (d, e) buffer radius of 5000 m. Akaike's information criterion (AIC) differences, ΔAIC, and Akaike weights, *w*, for the models are also shown.

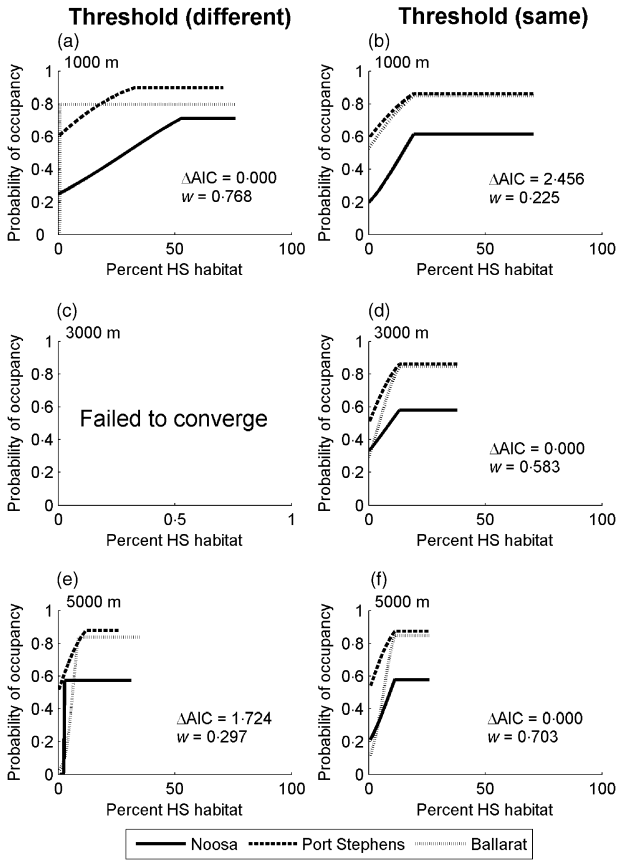

Fig. 3. Fitted threshold (different) and threshold (same) models for highly suitable (HS) habitat and the highly suitable patch-scale habitat class. (a, b) buffer radius of 1000 m (c, d) buffer radius of 3000 m and (d, e) buffer radius of 5000 m. Akaike's information criterion (AIC) differences, ΔAIC, and Akaike weights, *w*, for the models are also shown.

(Lindenmayer & Luck 2005). We did not test explicitly for the existence of threshold vs. other possible non-linear habitat–occupancy relationships. However, our finding that threshold models were more parsimonious than linear models at least suggests that declines in occupancy due to habitat loss are more rapid when the amount of remaining habitat is low than when it is high for the koala. This pattern may be a consequence of the koala's specialized habitat requirements and susceptibility to habitat fragmentation (McAlpine *et al.* 2006). Fragmentation effects could be related to the low nutritional quality of the koala's primary food sources, leading to low energy budgets for movement (Cork & Sanson 1990), and to matrix hostility, particularly in areas where roads and residential development are prevalent. Therefore, as habitat is lost, its fragmentation may eventually increase the risk of local extinction by restricting connectivity, lowering reproduction and elevating mortality (Fahrig 2003). The observed habitat–occupancy patterns could also be a consequence of stochastic extinctions in small populations due to events such as fire and disease (Melzer *et al.* 2000; Lunney *et al.* 2007). The prevalence of other small population processes, such as Allee effects, in koala populations is unclear.

Noosa generally had the highest threshold points, followed by Port Stephens and then Ballarat. Theory suggests that a key determinant of the point at which thresholds occur is reproductive output (or population growth rate), with thresholds declining as reproductive output increases (Fahrig 2001; Vance, Fahrig & Flather 2003). Evidence from a range of studies indicates that the highest koala population densities (and smallest home ranges) tend to occur in parts of Victoria and southern Australia, the lowest densities in the semi-arid forests and woodlands of inland New South Wales and Queensland and intermediate densities in the coastal forests of New South Wales and south-east Queensland (Gordon, McGreevy & Lawrie 1990; Mitchell & Martin 1990; Melzer *et al.* 2000; Dique, de Villiers & Preece 2003; Lunney *et al.* 2007). Therefore, across the koala's range, there appear to be latitudinal and longitudinal trends in density, with the highest densities found in the south and the lowest densities found in the north and west. It is interesting to note that we found occupancy probabilities in highly suitable habitat to be highest in Ballarat and Port Stephens and lowest in Noosa, which is broadly consistent with the observed latitudinal trends in density. These cross-regional differences in density are likely

to be driven by broad-scale variation in environmental variables, such as water and nutrient availability (Moore *et al.* 2004). The implications are that habitat qualities, and hence intrinsic population growth rates, are probably highest in southern parts of the koala's range and lowest in northern and western parts. This may partly explain the variation in threshold points between study regions. However, other factors that affect habitat quality, such as differences in land-use, are also likely to be important. Also, koala translocations to the Ballarat area during the 1990s (Department of Sustainability and Environment – Atlas of Victoria Wildlife unpublished data) could have artificially boosted koala densities there in the short term. Therefore, whether koala populations are in equilibrium is likely to be an important additional factor.

An alternative explanation for the variation in threshold points is that it is due to differences in habitat fragmentation among study regions. If habitat fragmentation is a key determinant of where the threshold points occur, then we would expect to see habitat thresholds occurring earliest in landscapes with the highest levels of fragmentation (Hill & Caswell 1999; Fahrig 2001). However, we observed that habitat tended to be most fragmented (as measured by patch density) in Ballarat, followed by Port Stephens and then Noosa (results not shown), and so there was an inverse relationship between fragmentation and the threshold points. In Ballarat, koalas were recorded in many areas that were highly fragmented because these also coincided with small patches of good quality habitat, containing high densities of *Eucalyptus viminalis* (a primary food tree species), on fertile soils. This led to high occupancy probabilities in good quality habitats, despite high levels of fragmentation. Therefore, the role of fragmentation is unclear, but is likely to depend on complex interactions with habitat quality, habitat selection and matrix hostility.

Across the different percentage habitat metrics, we found that the most parsimonious models were those for HSSM habitat (see Supplementary material, Table S1), suggesting that the amount of both high- and low-quality habitat is important. Low-quality habitat may perform important functions for facilitating dispersal and movement within a hostile matrix (Wiegand, Revilla & Moloney 2005). Also, across the different landscape extents, the most parsimonious models were those for the 1000 m buffer (see Supplementary material, Table S1). This is consistent with koala dispersal distances, which are typically in the 1–3 km range for males and < 2 km for females, and although longer dispersal distances do occur, they are less common (Dique *et al.* 2003). The higher support for models based on the 1000 m buffer, relative to the larger landscape extents, suggests that the spatial dynamics of koala occupancy are more influenced by typical dispersal movements than less common long-distance dispersal events.

THE MODELLING APPROACH

Piecewise regression models are becoming recognized more widely as important tools for modelling ecological relationships (Toms & Lesperance 2003). However, to date there have been few ecological applications of piecewise logistic regression, despite the widespread prevalence of presence/absence data (but see Denöel & Ficetola 2007; Betts, Forbes & Diamond 2007). A particular characteristic of our threshold models was that they made better predictions at low amounts of remaining habitat than standard linear models. This is important for conservation planning because accurate extinction risk estimates are likely to be most critical when the amount of remaining habitat is low. We found that threshold model fits were adequate, but discrimination ability (AUC < 0·7) was not particularly high. However, given the relatively simple models adopted, low discrimination ability is not surprising.

The set of different statistical models was chosen to represent a small number of alternative hypotheses about the nature of the habitat–occupancy relationships. In so doing, our aim was not to necessarily find the best statistical model, but rather to test the relative support for each hypothesis. A range of other non-linear statistical models, such as polynomial regression or generalized additive models (Hastie & Tibshirani 1990), could have been considered that may have been more parsimonious. However, threshold parameter estimates for the piecewise models were directly interpretable and this allowed us to quantify explicitly differences among the study regions. This would have been more difficult to achieve using other non-linear models that do not have directly interpretable parameters (Muggeo 2003).

A potentially important component that was missing from our models was the effect of site-scale variables. Although we found that the patch-scale habitat coefficient estimates were usually sensible, in some cases occupancy was predicted to be higher in low-quality than in high-quality patches (see Supplementary material, Table S1). A likely reason for this is within-patch variation in habitat quality that we did not account for. Within-patch variation has been shown to be an important determinant of koala occupancy at a site (McAlpine *et al.* 2006) and therefore our models may have been improved by the inclusion of site-scale variables. However, we do not consider that this would have affected the broad conclusions of the study.

FUTURE RESEARCH

An extension of our approach would be to identify whether habitat–occupancy responses vary for individual habitat classes, rather than the fairly broad, aggregated, habitat categories that we used. Although this would need to consider issues of independence between habitat thresholds, it could guide more refined conservation strategies, with different targets for different habitat qualities. More generally, an important area for future research is to seek explanations for threshold responses to habitat loss and their spatial variation. Key components of this research will be identifying whether thresholds occur in other demographic variables, such as survival or reproduction, and whether habitat amount thresholds coincide with thresholds for other landscape variables, such as habitat fragmentation. Studies designed to

identify relationships between threshold points and life-history and landscape characteristics will be important. This is entirely feasible within the modelling framework that we have presented, but would require far greater replication across landscapes and species. The 'Holy Grail' in this field of research is to derive completely generic models of habitat–occupancy relationships as functions of life-history and landscape characteristics at regional scales (e.g. MacNally, Bennett & Horrocks 2000). Generic models of this kind would be of substantial benefit to conservation planners because predictions of species- and landscape-specific threshold responses would then be feasible.

IMPLICATIONS FOR CONSERVATION PLANNING

Extinction thresholds have been advocated as a useful concept for setting generalized minimum habitat area targets for conservation planning. However, this approach has been criticized for not taking into account variability in threshold responses to habitat loss (Lindenmayer & Luck 2005). Regional variation in threshold points for the koala indicates a need to set different targets in different locations. For example, minimum targets for native forest cover of around 60% in Noosa, 50% in Port Stephens and 30% in Ballarat may be sensible for conserving koala populations. A policy of uniform targets across regions will be a risky strategy unless precautionary targets can be set at high levels everywhere, which is likely to be unrealistic. If the threshold concept is to be a practical tool for conservation planning, a concerted effort is required to understand and predict how threshold behaviour varies across different species and locations. These relationships are currently highly uncertain, and it is therefore important that this uncertainty is fully accounted for when using habitat thresholds for conservation planning. This can be achieved most effectively within a decision-theoretic framework (Possingham *et al.* 2001), which would help to ensure more prudent use of ecological thresholds.

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References

Akaike, H. (1973) Information theory as an extension of the maximum likelihood principle. *Second International Symposium on Information Theory* (eds B.N. Petrov & F. Csaki), pp. 267–281. Akadémiai Kiadó, Budapest, Hungary.

Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, **71**, 355–366.

Andrén, H., Delin, A. & Seiler, A. (1997) Population response to landscape changes depends on specialization to different landscape elements. *Oikos*, **80**, 193–196.

Australian and New Zealand Environment and Conservation Council (ANZECC) (1998) *National Koala Conservation Strategy*, Environment Australia, Canberra, Australia.

Australian and New Zealand Environment and Conservation Council/Ministerial Council on Forestry, Fisheries and Aquaculture (ANZECC/MCFFA) (1997) Nationally agreed criteria for the establishment of a comprehensive, adequate and representative reserve system for forests in Australia, Commonwealth of Australia, Canberra, Australia.

Betts, M.G., Forbes, G.J. & Diamond, A.W. (2007) Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology*, **21**, 1046–1058.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York, USA.

Coleman, B.D. (1981) On random placement and species–area relations. *Mathematical Biosciences*, **54**, 191–215.

Cork, S.J. & Sanson, G.D. (1990) Digestion and nutrition in the koala: a review. *Biology of the Koala* (eds A.K. Lee, K.A. Handasyde & G.D. Sanson), pp. 129–144. Surrey Beatty & Sons, Chipping Norton, Australia.

Denöel, M. & Ficetola, G.F. (2007) Landscape-level thresholds and newt conservation. *Ecological Applications*, **17**, 302–309.

Dique, D.S., de Villiers, D.L. & Preece, H.J. (2003) Evaluation of line-transect sampling for estimating koala abundance in the Pine Rivers Shire, south-east Queensland. *Wildlife Research*, **30**, 127–133.

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

Fahrig, L. (2001) How much habitat is enough? *Biological Conservation*, **100**, 65–74.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, **34**, 487–515.

Flather, C.H. & Bevers, M. (2002) Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *American Naturalist*, **159**, 40–56.

Gordon, G., McGreevy, D.G. & Lawrie, B.C. (1990) Koala populations in Queensland: major limiting factors. *Biology of the Koala* (eds A.K. Lee, K.A. Handasyde & G.D. Sanson), pp. 85–95. Surrey Beatty & Sons, Chipping Norton, Australia.

Haila, Y. (1983) Land birds on northern islands: a sampling metaphor for insular colonization. *Oikos*, **41**, 334–351.

Hanley, J.A. & McNeil, B.J. (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, **143**, 29–36.

Hanski, I., Moilanen, A. & Gyllenberg, M. (1996) Minimum viable metapopulation size. *American Naturalist*, **147**, 527–541.

Hastie, T.J. & Tibshirani, R.J. (1990) *Generalized Additive Models*. Chapman & Hall, London, UK.

Hilborn, R. & Mangel, M. (1997) *The Ecological Detective. Confronting Models with Data*. Princeton University Press, Princeton, NJ, USA.

Hill, M.F. & Caswell, H. (1999) Habitat fragmentation and extinction thresholds on fractal landscapes. *Ecology Letters*, **2**, 121–127.

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

Hosmer, D.W. & Lemeshow, S. (2000) *Applied Logistic Regression*, 2nd edn. John Wiley & Sons, New York, USA.

Lande, R. (1987) Extinction thresholds in demographic models of territorial populations. *American Naturalist*, **130**, 624–635.

Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist*, **142**, 911–927.

Lindenmayer, D.B., Fischer, J. & Cunningham, R.B. (2005) Native vegetation cover thresholds associated with species responses. *Biological Conservation*, **124**, 311–316.

Lindenmayer, D.B. & Luck, G. (2005) Synthesis: thresholds in conservation and management. *Biological Conservation*, **124**, 351–354.

Lunney, D., Gresser, S., O'Neil, L.E., Matthews, A. & Rhodes, J.R. (2007) The impact of fire and dogs on koalas at Port Stephens, New South Wales, using population viability analysis. *Pacific Conservation Biology*, **13**, 198–201.

Lunney, D., Phillips, S., Callaghan, J. & Coburn, D. (1998) Determining the distribution of koala habitat across a shire as a basis for conservation: a case study from Port Stephens, New South Wales. *Pacific Conservation Biology*, **4**, 186–196.

MacNally, R., Bennett, A.F. & Horrocks, G. (2000) Forecasting the impacts of habitat fragmentation. Evaluation of species-specific predictions of the impact of habitat fragmentation on birds in the box–ironbark forests of central Victoria, Australia. *Biological Conservation*, **95**, 7–29.

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

McAlpine, C.A., Rhodes, J.R., Bowen, M.E., Lunney, D., Callaghan, J.G., Mitchell, D.L. & Possingham, H.P. (2008) Can multi-scale models of a species' distribution be generalised from region to region? A case study of the koala. *Journal of Applied Ecology*, in press.

McAlpine, C.A., Rhodes, J.R., Callaghan, J.G., Bowen, M.E., Lunney, D., Mitchell, D.L., Pullar, D.V. & Possingham, H.P. (2006) The importance of forest area and configuration relative to local habitat factors for conserving forest mammals: a case study of koalas in Queensland, Australia. *Biological Conservation*, **132**, 153–165.

McIntyre, S. & Hobbs, R. (1999) A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conservation Biology*, **13**, 1282–1292.

Melzer, A., Carrick, F., Menkhorst, P., Lunney, D. & John, B.S. (2000) Overview, critical assessment, and conservation implications of koala distribution and abundance. *Conservation Biology*, **14**, 619–628.

Mitchell, P. & Martin, R. (1990) The structure and dynamics of koala populations – French Island in perspective. *Biology of the Koala* (eds A.K. Lee, K.A. Handasyde & G.D. Sanson), pp. 97–108. Surrey Beatty & Sons, Chipping Norton, Australia.

Mönkkönen, M. & Reunanen, P. (1999) On critical thresholds in landscape connectivity: a management perspective. *Oikos*, **84**, 302–305.

Moore, B.D., Wallis, I.R., Marsh, K.J. & Foley, W.J. (2004) The role of nutrition in the conservation of the marsupial folivores of eucalypt forests. *Conservation of Australia's Forest Fauna* (ed. D. Lunney), pp. 549–575. Royal Zoological Society of New South Wales, Mosman, Australia.

Muggeo, V.M.R. (2003) Estimating regression models with unknown breakpoints. *Statistics in Medicine*, **22**, 3055–3071.

Pearce, J. & Ferrier, S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. *Ecological Modelling*, **133**, 225–245.

Phillips, S.S. (2000) Population trends and the koala conservation debate. *Conservation Biology*, **14**, 650–659.

Phillips, S. & 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.

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

Possingham, H.P., Andelman, S.J., Noon, B.R., Trombulak, S. & Pulliam, H.R. (2001) Making smart conservation decisions. *Conservation Biology: Research Priorities for the Next Decade* (eds M.E. Soulé & G. Orians), pp. 225–244. Island Press, Washington, DC, USA.

Possingham, H.P., Wilson, K.A., Andelman, S.J. & Vynne, C.H. (2006) Protected areas: goals, limitations, and design. *Principles of Conservation Biology* (eds M.J. Groom, G.K. Meffe & C.R. Carroll), pp. 509–533. Sinauer Associates, Sunderland, USA.

Pregibon, D. (1981) Logistic regression diagnostics. *Annals of Statistics*, **9**, 705–724.

Stephens, P.A. & Sutherland, W.J. (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution*, **14**, 401–405.

Stone, M. (1974) Cross-validatory choice and assessment of statistical predictions. *Journal of the Royal Statistical Society, Series B, Methodological*, **36**, 111–147.

Su, J.Q. & Wei, L.J. (1991) A lack-of-fit test for the mean function in a generalized linear model. *Journal of the American Statistical Association*, **86**, 420–426.

Toms, J.D. & Lesperance, M.L. (2003) Piecewise regression: a tool for identifying ecological thresholds. *Ecology*, **84**, 2034–2041.

Ulm, K. (1991) A statistical method for assessing a threshold in epidemiological studies. *Statistics in Medicine*, **10**, 341–349.

Vance, M.D., Fahrig, L. & Flather, C.H. (2003) Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. *Ecology*, **84**, 2643–2653.

Wiegand, T., Revilla, E. & Moloney, K.A. (2005) Effect of habitat loss and fragmentation on population dynamics. *Conservation Biology*, **19**, 108–121.

With, K.A. & Crist, T.O. (1995) Critical thresholds in species' responses to landscape structure. *Ecology*, **76**, 2446–2459.

With, K.A. & King, A.W. (1999) Extinction thresholds for species in fractal landscapes. *Conservation Biology*, **13**, 314–326.

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Supplementary material

The following supplementary material is available for this article.

Appendix S1. Relationship between occupancy and percentage habitat under the random sample hypothesis.

Appendix S2. Mathematical descriptions of the logistic regression models and procedures used to fit them.

Appendix S3. Descriptions of the R functions used to fit the piecewise logistic regression models.

Appendix S4. R functions used to fit the piecewise logistic regression models.

Table S1. Fitted models, parameter estimates, and AIC values.

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