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Risks in extrapolating habitat preferences over the geographical range of threatened taxa: a case study of the quokka (*Setonix brachyurus*) in the southern forests of Western Australia

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Abstract

Context. Extrapolation of knowledge for threatened taxa between parts of their range that are disconnected and/or ecologically diverse can result in significant sources of error that undermine the effectiveness of conservation efforts.

Aims. We investigated the risks associated with extrapolation of ecological information across environmental gradients, using the quokka (*Setonix brachyurus*) as a case study. Information documented in the northern part of its range is currently used to manage this species across its range in south-western Australia. We examined the suitability of this approach by developing a habitat suitability model (HSM) for the quokka in the southernmost areas of its range and comparing this with existing knowledge for the species.

Methods. We surveyed 327 sites, representative of a range of ecotypes, for presence/absence of quokkas. Occupancy models were applied to select a subset of habitat variables that best predicted occupancy patterns.

Key results. Occupancy patterns were influenced by complex vegetation structure, low levels of woody debris and habitat patchiness. HSMs developed for quokkas in the north could not predict occupancy patterns in the south. Significant fragmentation of subpopulations was observed due to patchiness in the availability of suitable habitat.

Conclusions. The choice of predictor variables in HSMs that are not transferrable between regions could contribute to inappropriate management of habitat for quokkas and an increased risk of local extinctions. In addition, failure to consider processes that affect preferred habitat variables could contribute to the segregation of habitat patches and intervening distances that are too great for successful dispersal, immigration and recolonisation processes.

Implications. The extrapolation of HSMs between geographical areas can increase the risk of outcomes that are detrimental to the conservation of threatened species. Where such extrapolation is necessary, actions guided by the HSMs should be implemented in a management framework that can detect adverse effects, allow for inclusion of new ecological information and explicitly consider the limitations and assumptions of this approach. In addition, perceptions of habitat fragmentation need to include processes such as fire regimes and feral animals that affect the availability and connectivity of habitat and have the potential to adversely affect population viability.

Additional keywords: habitat occupancy, fragmentation, metapopulation, threatened species, vegetation structure, fire regime.

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Introduction

Effective strategies for the conservation of threatened species require knowledge of factors driving occupancy and survival (Moilanen and Hanski 1998). Species distribution models (SDMs) and habitat suitability models (HSMs) are increasingly being used to determine the ecological requirements of single species, to predict their occupancy and to support conservation planning and impact-evaluation processes (Guisan and Zimmermann 2000; Guisan *et al.* 2006; Real *et al.* 2009;

Acevedo *et al.* 2010). These models can provide useful ecological insight and strong predictive capability where ecologically relevant data with high resolution are used (e.g. Lindenmayer *et al.* 1999; Osborne *et al.* 2001). However, there are many examples where the models fail, due to coarse resolution data or broadly applied high resolution data from a single region (e.g. Constible *et al.* 2010; Murray *et al.* 2011; Heinänen *et al.* 2012; Williams-Tripp *et al.* 2012; Young *et al.* 2012). In these instances, geographical extrapolation of the models results in poor predictive performance.

Sources of error associated with such extrapolation are particularly important for threatened species that occur in discrete and highly variable locations.

One serious consequence arising from such extrapolation is an inability to adequately manage habitat for threatened species due to the lack of transferability of HSMs between geographical regions. The management of the threatened and widely distributed Canadian toad *Bufo hemiophrys* (Constible *et al.* 2010) provides such an example. In the prairies, the species is closely associated with low land aquatic habitats and so timber harvesting activities in this region are not required to protect upland areas. However, in the boreal forests in the northern parts of its distribution, the species spends more than 30% of its time in upland habitats. Here, failure to protect these upland areas from timber harvesting activities will result in loss of critical habitat and an increased risk of local extinctions (Constible *et al.* 2010).

A species potentially affected by the risk of extrapolating knowledge over its geographical range is the quokka (*Setonix brachyurus*), a monogeneric, monospecific wallaby listed as vulnerable by the IUCN (IUCN 2013). The quokka is restricted to south-western Australia and two near-shore islands (White 1952; Storr 1964; Maxwell *et al.* 1996; Sinclair 1998). On the mainland of Western Australia, quokkas occur in three areas: the northern jarrah (*Eucalyptus marginata*) forest, which runs from north of Perth to Collie; disjunct reserves around Albany on the south coast; and the southern forests between Nannup and Denmark (Sinclair 1998; de Tores *et al.* 2008; DEC 2013).

The important habitat features driving occupancy of quokkas in the southern forest are largely unknown. In the absence of knowledge, quokkas in the southern forest have been managed using information documented for quokkas in the northern jarrah forest, where populations are vulnerable to predation by feral animals and favour habitats with a dense understorey and a mix of early seral stage and long unburnt vegetation (Christensen and Kimber 1975; Hayward *et al.* 2005; Hayward *et al.* 2007).

Although these habitat features are expected to also apply to quokkas in the southern forest, there is little or no empirical evidence to substantiate this, and it is unclear how appropriate it is to extrapolate what is known of this species in the north to its management in the south. The southern forests are more mesic, the climate more temperate and the near-ground vegetation generally denser, more extensive and contiguous than in the northern forests. Preliminary DNA analysis of quokkas from Rottnest Island, the northern jarrah forest and the southern forest suggests that animals in the southern population are more likely to move between habitat patches in a functioning metapopulation (P. Spencer, unpubl. data). If this is the case, the southern forest quokkas may be vulnerable to processes that increase the distance between suitable habitat patches.

In the present study, we developed an HSM for the quokka in the southernmost areas of its range, identifying specific habitat features that can be used to predict its occupancy across multiple ecotypes in this region. We aimed to investigate the appropriateness of extrapolating what is known from the northern jarrah forest to quokkas in the southern forests and the potential effect of factors such as fire regimes and feral animals on the connectivity of suitable habitat.

Methods

Study area

This study was carried out in the forests between Manjimup and Walpole in south-western Australia (Fig. 1), an area dominated by open and closed heaths, tall forests, wetlands and creek systems. About 65% of the area is national park vested in the Conservation Commission for the purpose of conservation, much of which has been designated as such since 2004 (Kile 2013).

In total, 327 sites were randomly selected from a map (approximate aggregated area of 1308 ha) and were representative of a range of forest, woodland, heath and wetland ecotypes. Each

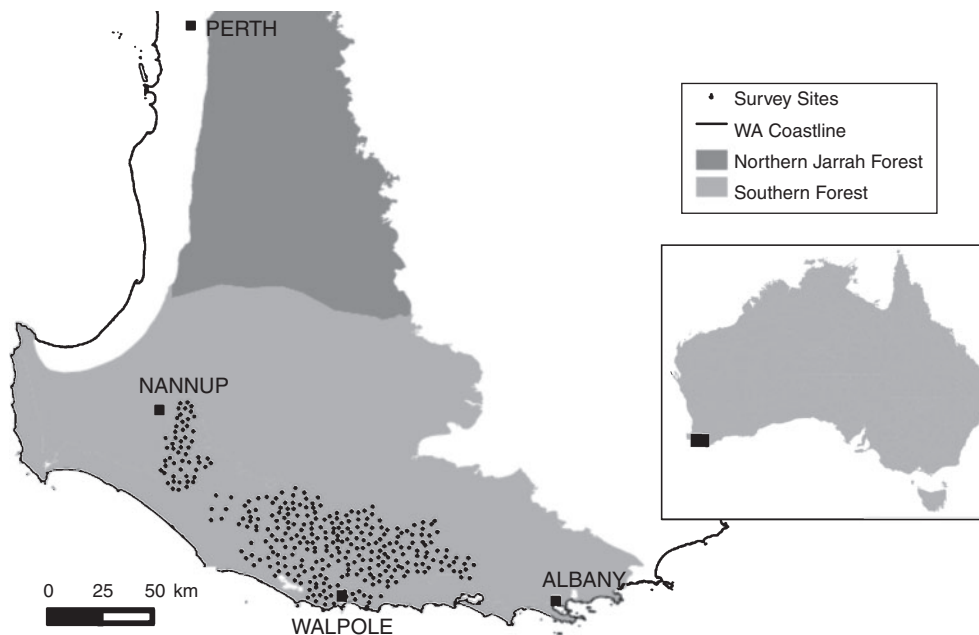


Fig. 1. Location of survey sites for the quokka within the southern forest of Western Australia.

site was surveyed for presence or absence of quokkas three times during a single summer-autumn period (Fig. 1). Presence was determined by walking two 1 km transects and recording the occurrence of fresh faecal pellets (Hayward *et al.* 2005b; Bain *et al.* 2014). All surveys were completed by trained observers to reduce potential errors in differentiating faecal pellets produced by quokkas from those of the western brush wallaby (*Macropus irma*) (Triggs 1996; Hayward *et al.* 2005b).

A series of habitat attributes were recorded at 20 random points along each transect including: landform; understorey; midstorey and overstorey height; canopy and understorey cover; horizontal density; vegetation structure; vegetation type; understorey diversity; leaf litter depth; depth and density of woody debris; vegetation age (time since last fire); season of the last fire event; distance to an alternative vegetation age; number of different vegetation ages within 1 km; adjacent vegetation age (years); distance to private land; distance to creek line; presence of pigs; presence of predators; presence of competitors; and dryness of habitat (see Table 1 for a detailed explanation of these habitat attributes and their measures). The multiple sample points were

averaged for each site to reduce variability caused by short-term changes in the spatial distribution of individuals.

Data analysis

Habitat models were developed to discriminate between locations where quokkas were present and those where they were absent. To reduce the number of variables to a suitable level, we used the procedure of Hosmer and Lemeshow (2000) with a stricter cut-off of $P > 0.10$, to enable a reduction in variables to nine or fewer. This procedure included all of the variables we considered likely to be important for site occupancy.

We maximised the model likelihood for the observed set of data to obtain parameter estimates for detection probabilities (p) and occupancy rate (ψ) using program MARK. We modelled p as either constant or as a function of sampling session (time). We modelled ψ as either constant, or as a function of the remaining habitat variables. Temporally replicated transects were treated as occasions. Models met the assumptions outlined in MacKenzie *et al.* (2002). Parametric bootstrap and Pearson Chi-Square goodness-of-fit tests were used to assess the fit of the

Table 1. Variables initially considered for use in a predictive model of habitat suitability for the quokka, in the southern forests of Western Australia

Variable	Description
Landform	Categorical classification into moist creek, dry creek, wet creek, heath, mid slope or ridge.
Understorey, midstorey and overstorey height	Average height of vegetation from the ground to the lowest vegetation layer, middle vegetation layer and tallest vegetation layer respectively (m).
Canopy and understorey cover	Average percentage of ground covered by the crown foliage and understorey foliage (%) respectively. Measured using digital cover estimation techniques (Macfarlane <i>et al.</i> 2000, Macfarlane <i>et al.</i> 2007).
Horizontal density	Density of understorey vegetation measured using a modified digital cover estimation technique, involving use of a white sheet 2m from the photographer and an image of the intervening vegetation taken horizontally.
Vegetation structure	Number of vegetation layers including ground cover, understorey, multiple midstorey layers and overstorey.
Vegetation type	A categorical classification of dominant vegetation type within the habitat.
Understorey diversity	Number of species contributing to the understorey.
Leaf litter depth	Depth of the surface leaf litter layer (mm). Leaf litter includes dead leaves, fine twigs and bark on the forest floor (Gould <i>et al.</i> 2007).
Depth of woody debris	Depth of the near-surface woody debris on the forest floor above the leaf litter (m). Consists of suspended leaves, twigs, branches and bark from the understorey, midstorey and overstorey vegetation.
Density of woody debris	Density of the layer of near-surface woody debris on the forest floor above the leaf litter. Categorical judgement of density: none, sparse, medium or dense.
Vegetation age	Time since the vegetation was last burnt in a prescribed burn or bush fire (years).
Season of fire	Season in which the habitat was last burnt: spring, summer or autumn.
Distance to alternative vegetation age	Shortest distance to nearest vegetation age different to that within the habitat being surveyed (m); determined using GIS and DPAW vegetation age mapping data.
Number of different vegetation ages within 1km	Number of different vegetation ages within 1km; determined using GIS and DPAW vegetation age mapping data
Alternative vegetation age	Nearest vegetation age different to that within the habitat being surveyed (years)
Distance to private land	Average distance to nearest private property (km); measured using ArcGIS 9.1 mapping software (ESRI 2006)
Distance to creek line	Average distance to nearest creek line (m); measured using ArcGIS 9.1 mapping software (ESRI 2006)
Presence of pigs	Categorical assessment of current presence or absence based on surveys for faecal material, diggings and detections by remote sensor camera traps undertaken concurrently and using the same protocols as the occupancy surveys for quokkas
Presence of predators	Categorical assessment of the presence or absence of feral predators such as foxes and cats based on surveys for faecal material, diggings and detections by remote sensor camera traps undertaken concurrently and using the same protocols as the occupancy surveys for quokkas
Presence of competitors	Categorical assessment of presence or absence of other herbivores such as kangaroos, wallabies, bandicoots and rabbits based on surveys for faecal pellets, diggings and shelters undertaken concurrently and using the same protocols as the occupancy surveys for quokkas.
Dryness of habitat	Subjective judgement of dry or moist based on the soil and leaf litter moisture.

occupancy models to our data (MacKenzie and Bailey 2004). We used Akaike's Information Criterion (AIC) with a small sample size correction (AICc) for model selection and considered models with delta AICc values < 2 to have strong support (Burnham and Anderson 2002). In addition, we calculated cumulative AICc weights to evaluate strength of evidence for each model.

Results

Quokkas were detected at 88 of the 327 sites surveyed, yielding a model-generated occupancy of 0.22 (naïve occupancy 0.27), and occurred in discrete patches with distances between 12 and 40 km separating occupied habitat (Fig. 2).

Occupied sites included a range of forest, woodland and wetland ecotypes but the most commonly occupied sites consisted of jarrah, marri (*Corymbia calophylla*), karri (*Eucalyptus diversicolor*) or tingle (*Eucalyptus guilfoylei* or *Eucalyptus jacksonia*) forest habitats with a sedge-dominated understorey (Table 2).

Of the 24 measured habitat variables, 17 were excluded from further analysis on the basis of univariate logistic regression models and included: (1) vegetation age; (2) height of woody debris; (3) distance to private land; (4) number of different vegetation ages within 1 km; (5) adjacent vegetation age (years); (6) distance to creek line; (7) height of understorey; (8) leaf litter depth; (9) understorey diversity; (10) horizontal density; (11) height of overstorey; (12) canopy cover; (13) presence of pigs; (14) presence of predators; (15) season of fire; (16) landform description; and (17) presence of competitors (Table 3).

Vegetation age was expected to be a significant driver of occupancy. However, quokkas occupied habitat with vegetation ages ranging between six months and 50 years and did not show any preference for particular age categories. The high proportion of unoccupied sites associated with 0.5–10 years (Fig. 3) reflects the high proportion of this age category in the landscape.

The remaining seven variables were used as covariates in occupancy models, to help explain the differences in ψ between sites, and included: (1) height of midstorey; (2) understorey cover;

(3) vegetation structure; (4) distance to an alternative vegetation age; (5) dryness of habitat; (6) vegetation type; and (7) density of woody debris (Table 4). Our analysis highlighted an AICc weight of 0.75 for model $P(\cdot)\psi(DWD+VEGST+DISA)$, which included the density of woody debris, vegetation structure and distance to an alternative vegetation age (Table 4). Detection probability was constant across the three sampling periods for all sites and was 0.94 (SE = 0.014).

The fit of the model was considered satisfactory because the Pearson Chi-Square statistic was not significant ($P = 0.99$) and the Chi-Square value for the most parameterised model fell within the 49th percentile of the bootstrapped values. The minimal change in the maximum log-likelihood ratio following removal of certain variables from the model – height of midstorey, understorey cover, vegetation type and dryness of habitat – indicated that these variables were not contributing significantly. The removal of other variables – distance to adjacent vegetation age, density of woody debris and vegetation structure – led to large increases in the AICc value and resulted in a poorly fitting model.

The probability of occupancy of habitat by quokkas decreased with increasing density of woody debris. Habitats with a dense woody debris layer were always unoccupied and sites with a medium woody debris layer were unoccupied 75% of the time (Fig. 4). The highest occupancy rate occurred in habitats with sparse or no woody debris, with occupancy rates of 71% and 35% respectively.

The probability of a habitat being occupied by quokkas was also dependent on the structure of the vegetation and, in particular, the number of vegetation layers. Habitats with three vegetation layers or more were occupied with a probability of 86%, whereas habitats with two or fewer vegetation layers had an occupancy rate of only 6% (Fig. 5).

Habitats were occupied by quokkas if they were within 0 and 450 m of an alternative vegetation age (Fig. 6), but the age of the vegetation was not significant. Habitats greater than 450 m from an alternative vegetation age were unoccupied 100% of the time.

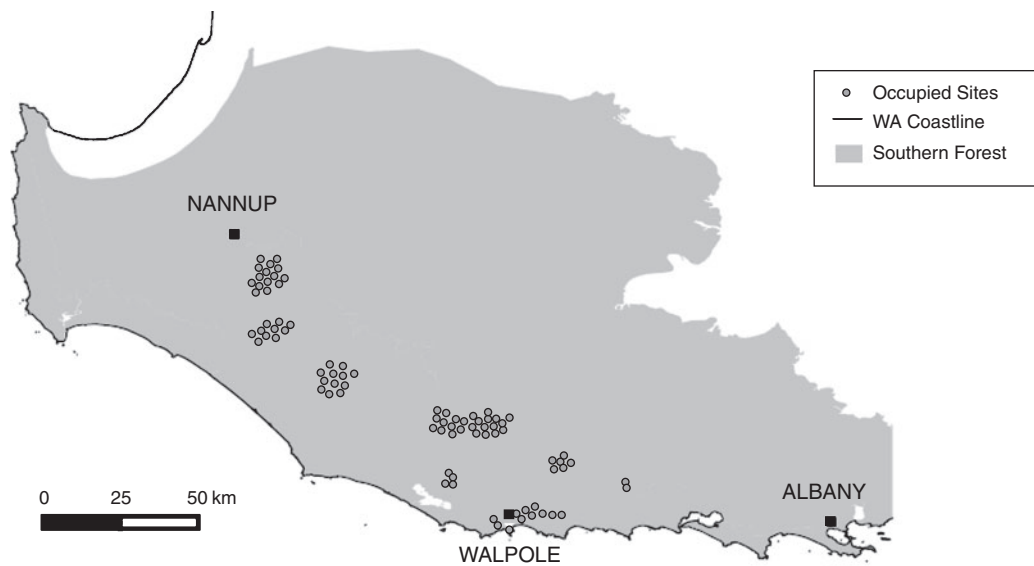


Fig. 2. Location of survey sites that were occupied by quokkas during this study.

Table 2. Vegetation types occupied by the quokka in the southern forests of Western Australia during summer and autumn

Vegetation description	No. occupied sites	No. sites surveyed
Jarrah (<i>Eucalyptus marginata</i>)/ bullich (<i>Eucalyptus megacarpa</i>) with an understorey dominated by woody species	0	11
Jarrah/ bullich with an understorey dominated by sedge species such as <i>Ghania</i> and <i>Anarthria</i>	6	14
Jarrah/ marri (<i>Corymbia calophylla</i>) / <i>Casuarina</i> forest with an understorey dominated by woody species	12	37
Jarrah/ marri/ <i>Casuarina</i> forest with an understorey dominated by <i>Lepidosperma</i> , <i>Anarthria</i> , <i>Empodisma</i> or <i>Ghania</i>	25	43
Karri (<i>Eucalyptus diversicolor</i>)/ jarrah with an understorey dominated by woody species	1	21
Karri/ jarrah forest with a sedge dominated understorey	16	29
Tingle (<i>Eucalyptus guilfoylei</i>)/ karri forest with a woody understorey	1	24
Tingle/ karri forest with a <i>Lepidosperma</i> dominated understorey	12	30
<i>Banksia</i> or <i>Casuarina</i> woodland with understorey dominated by woody species	1	16
<i>Banksia</i> or <i>Casuarina</i> woodland with understorey dominated by <i>Lepidosperma</i> , <i>Anarthria</i> or <i>Ghania</i>	2	16
<i>Taxandria</i> woodland (sometimes with karri) with a <i>Taxandria</i> / <i>Callistachyus</i> / <i>Melaleuca</i> midstorey and well developed understorey (often containing <i>Ghania</i> and <i>Lepidosperma</i>)	2	19
<i>Taxandria linearifolia</i> or <i>Melaleuca</i> thicket with an understorey dominated by <i>Ghania</i> , <i>Empodisma</i> or other sedges (no midstorey)	6	25
<i>Melaleuca</i> woodland with <i>Taxandria</i> or <i>Melaleuca</i> midstorey with an understorey dominated by heath species	4	17
Open heath dominated by <i>Anarthria</i> , <i>Dasyopogon</i> , <i>Evandra</i> with no mid or overstorey or forest vegetation with no mid or overstorey (e.g. low <i>Taxandria</i> thickets or regenerating forest)	0	25

Table 3. Variable culling process (Hosmer and Lemeshow 2000)

Habitat variables were excluded from further analysis if the *P*-value was greater than 0.1 following univariate logistic regressions

Description	Mean (\pm s.e.)		Univariate logistic regression	
	Absent	Present	-2 Log-likelihood	Sig.
Vegetation age (years)	11.5 (0.7)	11.9 (1.17)	-190.4	0.78
Depth of woody debris (m)	0.18 (0.01)	0.17 (0.01)	-190.4	0.78
Height of understorey (m)	1.1 (0.04)	1.2 (0.04)	-190.3	0.54
Leaf litter depth (m)	17.2 (1.1)	15.6 (1.3)	-190.1	0.41
Understorey diversity	4.9 (0.1)	5.2 (0.2)	-189.5	0.17
Horizontal Density (%)	76.4 (7.2)	64.6 (1.9)	-189.7	0.22
Height of overstorey	21.3 (0.8)	24.4 (1.1)	-188.8	0.14
Canopy cover (%)	80.7(12.4)	57.0 (2.1)	-189.3	0.13
Height of midstorey (m)	5.1 (0.3)	6.3 (0.3)	-185.5	0.07
Understorey cover (%)	69.4 (7.3)	52.2 (2.2)	-187.7	0.02
Vegetation structure	2.0 (0.04)	3.2 (0.05)	-143.1	<0.0
Number different vegetation ages within 1km	3.3 (0.1)	3.19 (0.2)	-190.4	0.73
Distance to alternative vegetation age (m)	595.2 (40.1)	169.4 (38.1)	-158.9	<0.0
Adjacent vegetation age (years)	11.8 (0.6)	12.1 (1.1)	-190.4	0.78
Distance to private land (km)	10.4 (0.5)	11.3 (0.8)	-190.2	0.42
Distance to creek line (m)	84.4 (7.1)	77.0 (9.5)	-190.3	0.56
Presence of pigs		Categorical	-190.4	0.97
Presence of predators		Categorical	-190.3	0.57
Season of fire		Categorical	-190.2	0.48
Landform description		Categorical	-189.7	0.24
Presence of competitors		Categorical	-189.3	0.14
Dryness of habitat		Categorical	-187.7	0.02
Vegetation type		Categorical	-187.0	0.01
Density of woody debris		Categorical	-179.9	<0.0

In habitats that were occupied by quokkas, the average distance to an alternative vegetation age was 169 m (SE = 7.43).

Discussion

Here we show that although HSMs developed for quokkas in the north may provide some predictive capability in the south, the choice of predictor variables that are not transferrable between regions could contribute to important sources of error associated with geographical extrapolation. The HSM

developed for quokkas in the northern jarrah forest is based on dense understorey, early seral stage vegetation and intensity of baiting for introduced foxes (Hayward *et al.* 2007). A dense understorey is characteristic across the landscape in the southern forest region and so is not a feature that can easily differentiate habitat patches. The southern forest contains more mesic, climatically buffered and stable ecosystems, which have a very different response to fire. It also has different patterns of growth and senescence of vegetation, which make the use of seral stages and vegetation age challenging to apply as predictors. In addition,

baiting for foxes has been applied throughout the southern forest at a consistent rate and frequency, since commencement of baiting (Burbidge et al. 1995). Consequently, the use of baiting intensity as a predictor of occupancy is meaningless in this region.

Occupancy of habitat by quokkas in the south was strongly linked to a complex vegetation structure (minimum of three layers), low densities of woody debris and habitat patchiness (between 0 and 450 m to an alternative vegetation age). In the north, density of understorey, time since fire (less than 10 years), adjacent vegetation age (greater than 25 years) and the presence of feral predators were significant drivers of habitat preference of quokkas (Christensen and Kimber 1975; Hayward et al. 2005; Hayward et al. 2007). None of these variables were found to be significant in the southern forests and if these variables were the only ones considered for the management of the species, this could negatively affect the habitat qualities that quokkas actually favour in this region.

The range of ecotypes occupied in the southern forest was more diverse than in the northern jarrah forest and many are

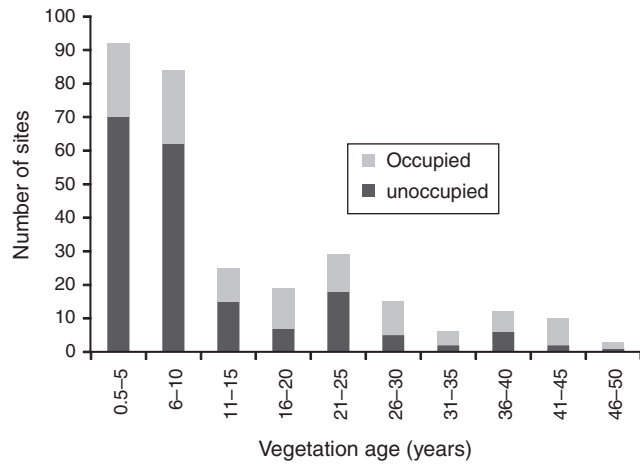


Fig. 3. The relationship between vegetation age and the number of habitats occupied by quokkas. Vegetation age relates to time since the site was last burnt (years).

associated with sites that have high levels of permanent moisture, stable productivity and relatively stable habitat features. The vegetation also tends to have a higher complexity and density, due to the high rainfall in the region and the mesic nature of the karri and tingle ecotypes, which provide an edaphic barrier to fire under some conditions (Burrows and Wardell-Johnson 2003). These systems burn relatively infrequently and vegetation age can be quite old, while still maintaining the conditions favoured by quokkas in this region. Quokkas need diurnal shelters that aid their thermoregulation (Kitchener 1981). Multiple vegetation layers achieve this by providing insulation and protection from the elements. Burning more frequently to encourage early seral stage vegetation, as is recommended for the northern forests, could reduce the structural complexity of the vegetation in these areas by removing midstorey layers (Spencer and Baxter 2006).

Similarly, managing habitats to maximise density of understorey vegetation, as is recommended for the north, could result in a dense woody debris layer in some southern forest ecotypes and thus render the habitat unsuitable. A dense woody debris layer on the forest floor suppresses new growth, smothers the understorey vegetation and substantially impedes the movement of quokkas, thus affecting food availability and safe passage through their habitat. Dense woody debris also provides poorer shelter and insulation than living vegetation, due to lower levels of shading and moisture.

One similarity between north and south is the need for a variety of seral stages to provide for dietary requirements and refuge from predators. This equates to a mosaic of young vegetation and long unburnt habitat in the northern jarrah forest (Christensen and Kimber 1975; Hayward et al. 2005; Hayward et al. 2007), less complex than that in the southern forest. Habitat patchiness is more important in the south than the age of the vegetation. The average distance to an alternative vegetation age in habitats that were occupied by quokkas was 169 m, suggesting that a relatively fine scale mosaic is required to maximise the suitability of habitat.

Surprisingly, the presence of feral predators was not found to be a significant variable in the south and this is likely due to selection of habitat by quokkas that enables their persistence in the presence of these predators. Foxes and feral cats are most

Table 4. Rankings of models^a using Akaike's Information Criterion corrected for small sample size (AICc) in program MARK to explain the occupancy rate (ψ) by quokkas and detection probability (P) in the southern forests of Western Australia^b

Occupancy and detection probability were modelled as a constant (\cdot), as a function of time (t) or as a function of habitat variables. The $\Delta AICc$ values are the difference in AICc values standardised to the model with the lowest AICc. The AICc weights are the Akaike weights associated with each model and provide the relative strength of evidence for each model. The log-likelihood (-2Log-likelihood), the number of parameters and the Pearson Chi-Square goodness of fit test statistics are also presented for each model. DWD = density of woody debris, VEGST = vegetation structure, DISA = distance to an alternative vegetation age, USCOV = understorey cover, VEGTY = vegetation type, DRY = dryness of habitat, MIDHT = height of midstorey

Model	-2Log _e L	AICc	$\Delta AICc$	AICc Weights	No. of Parameters	χ^2	P
P(\cdot) ψ (DWD VEGST DISA)	198.57	206.70	0.00	0.75	5	0.41	0.99
P(\cdot) ψ (DWD VEGST DISA USCOV)	199.09	209.28	2.58	0.21	6	1.06	0.99
P(\cdot) ψ (DWD VEGST DISA USCOV VEGTY)	182.02	213.56	6.86	0.02	19	0.6	0.99
P(\cdot) ψ (DWD VEGST DISA USCOV VEGTY DRY)	183.40	214.95	8.25	0.01	20	0.62	0.99
P(\cdot) ψ (DWD VEGST DISA USCOV VEGTY DRY MIDHT)	183.31	217.07	10.37	0.00	21	0.69	0.99
P(\cdot) ψ (DWD VEGST)	264.71	270.78	64.08	0.00	4	51.77	<0.0
P(\cdot) ψ (DWD DISA)	262.74	270.87	64.17	0.00	3	189.43	<0.0
P(\cdot) ψ (VEGST DISA)	265.80	271.87	65.18	0.00	3	12.5	0.13
P(\cdot) ψ (\cdot)	496.01	500.05	293.35	0.00	2	1.60	0.66
P(\cdot) ψ (t)	495.58	503.71	297.01	0.00	4	0.99	0.91

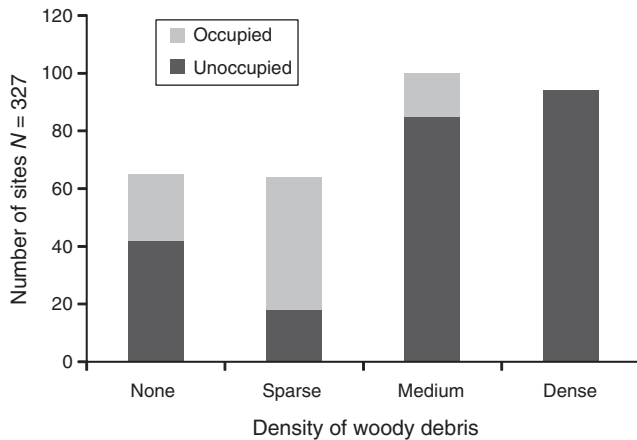


Fig. 4. The relationship between density of woody debris and the number of habitats occupied by quokkas. Woody debris consists of suspended leaves, twigs, branches and bark fallen from the understorey, as well as midstorey and overstorey vegetation.

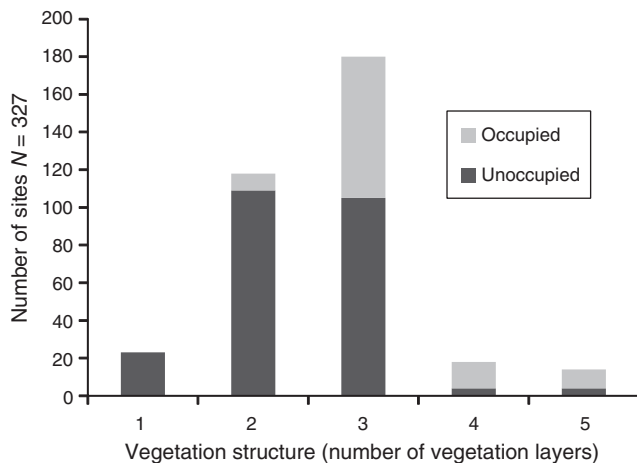


Fig. 5. The relationship between vegetation structure (number of vegetation layers) and the number of habitats occupied by quokkas.

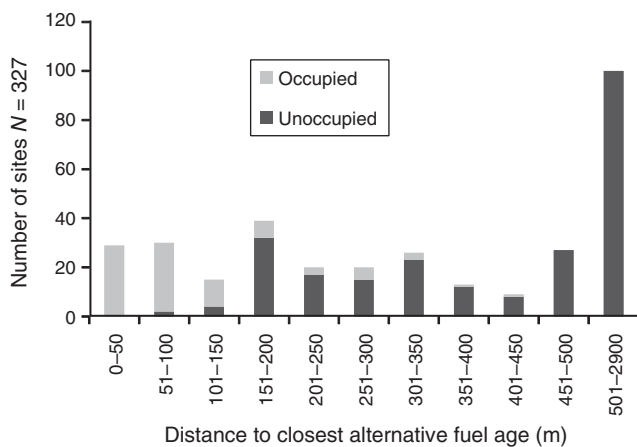


Fig. 6. The relationship between the distance to an alternative vegetation age (m) and the number of habitats occupied by quokkas.

efficient at hunting in open or easily accessible vegetation, such as walking trails or burnt ground (Saunders and McLeod 2007). The complex vegetation habitat in which quokkas primarily occur reduces the efficiency of these predators and may account for their non-significance in the models. However, both foxes and feral cats have been observed to prey on immature quokkas in the southern forest, and recruitment levels have been low in sites where quokkas occur in the presence of these predators (K. Bain, unpubl. data). Although occupancy of habitat might be unaffected by feral predators, recruitment and population demography are likely to be affected, as is the survivorship of animals moving between habitat patches. Hayward *et al.* (2007) found that the persistence of quokka populations in the northern jarrah forest was related to the control of introduced predators (foxes). The broad scale and consistent nature of baiting in the southern forest makes this variable irrelevant in this region.

Feral pigs were also not found to be significant in predicting quokka occupancy in this study; this is likely due to the way this variable was measured. Measures that adequately account for pig activity levels in the years preceding the survey are likely to be more strongly related to the quality of quokka habitat than simple contemporaneous assessments of pig presence as was used in this study. In the southern forest, feral pigs have been observed to remove seedlings and lignotubers, to disturb the soil profiles and substantially alter the density and structure of the vegetation, particularly in areas that have been recently burnt (Burnside *et al.* 2012). Although quokkas in this study occupied habitat in the presence of feral pigs, sustained feral pig activity reduced the suitability of habitat for quokkas, resulting in these areas becoming unoccupied (K. Bain, unpubl. data). The alteration of vegetation structure as a result of feral pig digging and wallowing has also been recorded in other areas of Australia (Choquenot *et al.* 1996; Hone 2002; Adams 2014).

Despite the contiguous and extensive natural vegetation system of the southern forest, quokkas occupied discrete habitat patches separated by distances of up to 40 km. The spatial availability and connectivity of suitable habitat in this landscape is influenced by fire regime and feral pig activity that alters the habitat features identified in this study as being important for quokkas. These anthropogenic processes may have already contributed to the loss of quokka subpopulations from some areas. The apparent fragmentation of subpopulations challenges our perceptions of fragmentation in natural ecosystems. The risk of anthropogenic fragmentation in this landscape – associated with fire regimes, feral animals and other disturbances such as timber harvesting – is less obvious than physical fragmentation through land clearing, but is potentially equally as detrimental.

In the southern forest, genetics (P. Spencer, unpubl. data) and movement patterns (K. Bain, unpubl. data) indicate that quokkas are still moving between habitat patches. Without active management of processes that affect vegetation structure, diversity of vegetation ages, accumulation of woody debris and feral animals (fox, cat, pig), suitable habitat patches are likely to become more segregated and intervening distances too great for successful dispersal, immigration and recolonisation processes that may be critical to the maintenance of a functioning metapopulation.

In many areas, quokkas are explicitly considered when planning fire management programs and feral animal control activities. The risks of local extinction will be significantly reduced if future management of this species takes into account the following: size and patchiness of fire, particularly within and adjacent to key riparian systems; the intensity of fire to maximise the retention of vegetation structure; and the active management of fire to avoid senescence or death of midstorey species and the associated accumulation of woody debris. Fire management regimes should consider both potential habitat and intervening non-habitat areas to maximise the availability and accessibility of suitable habitat and the functionality of the metapopulation. Management of feral pigs following fire is essential to reduce their long-term effect on the vegetation structure. The control of feral cats and foxes should also be considered to improve quokka recruitment within high priority habitats.

This study has generated knowledge of habitat important to quokkas in the southern forests and an understanding of the subtleties of fragmentation in a contiguous and natural system, which will improve our ability to protect potential habitat, to predict the outcomes of disturbance events and to minimise spatial segregation of habitat patches as a result of forest management activities. Important differences between habitats in the north and south demonstrate the risks of extrapolating knowledge between these areas. These differences, if overlooked, could lead to inappropriate management actions and local extinctions.

In this instance, the failure of the HSM between the two ecologically diverse regions was due to the selected predictors, and in particular those relating to fire and predator baiting regimes, which were not transferrable between regions due to spatial differences in ecotypes, the application of fire, the behaviour of fire and approaches to predator baiting. The HSM developed for quokkas in the north was not intended to apply to the species across its distribution and so was regionally specific in terms of its choice of predictors. The HSM developed in this study was also intended to be regionally-specific in order to investigate the appropriateness of extrapolation between the two regions. This study has identified that predictions by HSMs at a regional scale should only be transferred across geographical areas where predictor variables have been selected that are relevant to both areas and where these have been verified against local knowledge of the ecology of the study species. In addition, models that explicitly account for imperfect detection when building HSMs (such as the occupancy models used in this study) are expected to produce more accurate estimates of habitat relationships and improve predictive performance, particularly for difficult-to-detect species (Rota *et al.* 2011).

Despite the potential consequences of extrapolation of ecological knowledge, in the absence of complete information, practitioners are commonly seduced to do so regardless. This is likely to continue despite the demonstration of risks and adverse outcomes. It is therefore important that when unsubstantiated extrapolations are made they are duly acknowledged and the risks of doing so identified. It is also important that management actions influenced by these extrapolations are implemented within an active adaptive management framework that can

detect any adverse effects, test the validity of extrapolations, help fill some of the knowledge gaps and contribute to an improved approach for the future.

Another important outcome of this study is the realisation that our perception of fragmentation in natural ecosystems needs to be adjusted to include consideration of processes such as feral animals and fire. Although these processes may be less obvious than physical fragmentation through land clearing, they have the potential to contribute to the segregation of suitable habitat patches for threatened species. They can also create intervening distances that are too great for successful dispersal, immigration and recolonisation processes critical for the maintenance of a viable metapopulation.

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