

RESOURCES, DATA RESOLUTION AND  
SMALL MAMMAL RANGE DYNAMICS

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**Detailed revisions made to 'Resources, data resolution and small mammal range dynamics ' in response to general (a) and minor comments (b), included in Examiner 1 and 2 reports.**

<b>E</b>	<b>Comment</b>	<b>Response</b>	<b>Pg</b>
<b>a. General comments</b>			
1	P 10. last paragraph: What does it mean that SDM should be readily generalised? Should an even more important attribute be that species models produce distribution maps that are accurate?	Reworded: '...should produce more accurate geographic maps of species distributions across its range, and over time, that can be reliably interpreted.'	11
1	P 11. last paragraph: How might the fragmentation of habitat effect occupancy predicted in a SDM?	The effects of habitat fragmentation on predicted occupancy were already highlighted in the Discussion section 'Capacity to improve model interpretation through realised niche characteristics':  'In addition, the history of vegetation clearance in the landscape may cause the reasonably dispersal limited <i>I. o. obesulus</i> , <i>R. f. grevi</i> and <i>R. l. lutreolus</i> to be absent from suitable patches due to local extinctions, or occupy suboptimal habitat. All of these dynamics lead to more complex species responses to environmental gradients (Holt et al. 2005), increased uncertainty or bias in SDM predictions.'	21
1	P 12, 26, 42, 58: More detail on techniques used to define 'absence' data.	Additional justification was added to p12, p42 and p58 in the revised thesis, but not p26 where a different dataset was used.	
1	P20. third paragraph: Most empirical investigations describe how species live and use resources with all the constraints that are imposed on them by the presence of competitors, predators, resource shifts and the like (realised niche). Although this difference is clarified in later chapters, most readers are likely to have in mind the classical Hutchinsonian niche concept rather than newer (and still debated) concepts that are assumed here.	Reworded: 'First, empirical investigations into species' resource use and life history attributes would indicate variables required for basic survival and reproduction '	20
1	P40 and 41. Table 1: Which local investigations provided the information on demographic parameters (p43)? Some of the data look a bit unusual. For example, the 8 young used per female for <i>Anechinus flavipes</i> seems low: the species usually has litters of 10-12. I was a bit surprised also that Rmax values from voles and muskrats had been substituted for values for native <i>Rattus</i> . Has Rmax not been estimated from local studies for <i>R. fuscipes</i> , <i>R. lutreolus</i> or other native species?	The core references used in compiling this table have been added to a new Appendix XII in the revised thesis.  These references should aid in conveying the balance of information incorporated into the population viability models, such as reproductive rates being set to take into account mortality in developmental stages. In the case of <i>A. f. flavipes</i> that can give birth to 8-10 young, they have on average 7.6 young (Smith 1984).  All population viability analysis models were set to support stable populations (long-term density equilibrium, with stochastic variability), with information on species ecology incorporated where available. Unfortunately, Rmax values have not been estimated for most native species, which lack long-term time-series data due to field surveys being predominantly short-term and localised. For this investigation, the values adopted from species with similar ecology were similar to estimates calculated for these species based on aspects of their biology (Table 1, p61), but since they were obtained from ongoing monitoring programs, thought to be more realistic.	
1	P 56, top: Most small mammals in arid, alpine, temperate and other environments use burrows and shelter and are nocturnal, so these traits may not be adaptations to desert life <i>per se</i> but may just be adaptive in any environment.	Reworded: 'Additional behavioural adaptations that aid species' persistence in these harsh environments, include..'	56

E	Comment	Response	Pg
1	P59, Table 1: Flooding and small and spatially explicit refugia may be extremely important to small mammal dynamics in the Channel Country IBRA region. Depending on when field sampling was carried out, animals could appear to be associated with quite different sets of climatic and-especially-environmental variables. Is it possible to define the conditions that prevailed when species' sampling was carried out and obtain better model fits by running analyses for data obtained during dry and wet periods?	<p>Unfortunately available data were obtained from different times that don't align well. However, areas most likely to be flooded and refugia were represented in the existing SDM by including: i) elevation and distance to watercourse, and ii) vegetation community mapping and soil water holding capacity</p> <p><i>A. laniger</i>, <i>D. byrnei</i> and <i>N. cervinus</i> all demonstrated a positive correlation with distance to watercourse that likely represents the dynamics of gibber plains rather than flood dynamics, while species occurrence was positively correlated with soil water holding capacity of the solum. Areas with higher soil water holding capacity are likely to indicate preferred habitat, either for shelter or ready source of food (refugia).</p> <p>The occurrence of both <i>L. forresti</i> and <i>S. macroura</i> was poorly predicted, however, the species' association with understorey was reflected in the positive correlation with shrubland and hummock grassland (Table 2: Appendix XXIV), respectively. However, it is likely the SDMs were lacking key variables, or that the areas surveyed within the Channel Country IBRA region contained sub-quality habitat for these species that is only occupied during periods of greater resource availability</p>	
1	Finally the poor model fit for <i>L. forresti</i> and <i>S. macroura</i> is almost certainly not because these species have distributional gaps in or near the Channel Country (p68, bottom); the Channel Country IBRA region is a stronghold for both species. The gap that appears in distribution maps for these species is in the Simpson-Strzelecki IBRA region, which was not modelled here.	This is an important point to clarify. This sentence has been removed.	
2	The introduction does not clearly state the aims of the thesis or provide direction for the thesis. While each chapter states the hypothesis being explored, it would have been useful to include this in the Introduction to a) tie the chapters together and b) show the thought process that the candidate went through to develop a set of cogent, related research chapters.	In the revised version, the clarity of the overall direction of the thesis has been improved by collating and representing the aims in the Introduction.	6-7
2	I found it confusing following the progression of SDMs through Chapters 1-3. Providing a general outline of the development of the SDMs in the Introduction would have made this clearer.	<p>The data used in each chapter differs. Because of this, the detailed descriptions of how the datasets were derived are left to the respective methods sections, including figures to illustrate points where possible.</p> <p>Given the thesis structure, I have not included a summary in the Introduction. However, the overall clarity of the role and differences between each chapter has been improved in the revised thesis by summarising aims in the Introduction and the merger of tables into Appendix IV</p>	
2	There are multiple versions of the table describing landscape variables applicable to Chapters 1-3.	No merged into a single appendix (Appendix IV)	
<b>b. Minor comments</b>			
1	P11 and 57, bottom: <i>N. cervinus</i> does eat a lot of seed, but it has been (tentatively) classified as an omnivore. See Murray et al. 1999 Wildlife Research 26: 421-437.	<p><i>N. cervinus</i> has been classified a granivore on the basis of its diet consisting of up to 95% seed, some plant material and &lt;5% invertebrates (Watts 1970). The evidence used to support omnivores diet in Murray et al. 1999 is based on <i>N. alexis</i>, a species that consumes a broader range of items (Murray and Dickman 1994a: 1994b). Given this, I have left <i>N. cervinus</i> being summarised as a 'granivore', as it is this aspect of its ecology that I was interested in exploring in SDMs and relative to the other species.</p>	

E	Comment	Response	Pg
1	P3 (117), 4 (18), 43, 72 (L12), 85: replace effect, effected, or effecting with affect, affected, affecting.	Fixed	
1	P4, L5: A range shift reflects species maintaining its niche by tracking suitable climatic or environmental conditions.	Fixed: '... tracking suitable climatic or environmental conditions may become increasingly difficult ...'	4
1	P5, point v: Australia does not have a majority of the World's marsupials (Aust 157, Sth America and New Guinea 172)	Reworded: 'Approximately 85 % of Australian mammals are endemic to the continent, including many of the world's marsupials and monotremes (Steffen <i>et al.</i> 2009).'	5
1	P12, last line: replace measured with measures.	Fixed	
1	P14, first line: Check spelling of imperial.	Fixed	
1	P24, line 13: insert on, between effect and the.	Fixed	
1	P39, L19: delete in.	Fixed	
1	P39, bottom line: insert fine between relatively and environmental.	Fixed	
1	P52, L8: replace influences with influence.	Fixed	
1	P68, two lines from bottom: replace there with these	Fixed	
1	P68: bottom paragraph: a couple of references are made to Kotler and Brown 1988 and to Shenbrot <i>et al.</i> 1999 suggesting that these authors have worked on Australian native mammals. However, they have not, so attributing specific observations on <i>N. cervinus</i> and other native species to these authors is not correct.	Reworded to clarify these citations support the advantages associated with bipedal gait. ' <i>N. cervinus</i> builds deep burrows, and has a bipedal gait that enables species to better exploit patchy and sparse resources and better escape predation (Kotler and Brown 1988; Shenbrot <i>et al.</i> 1999).'	67
1	P72, Abstract: Opening sentences difficult to follow	Rewritten: 'In many correlative species distribution models biotic factors are excluded as interactions that have a secondary influence on species' occurrence via the <i>realised niche</i> , irrespective of a species' ecology. Over time biotic interactions can drive natural selection and changes within the <i>fundamental niche</i> , resulting in a contemporary dependency on resource availability for survival or reproduction. Resource availability may not be closely correlated with coarse climate variables, but represent the dynamics of nutrients and water availability cascading through trophic webs...'	71
1	P74, 10 lines from the bottom: the sentence beginning 'Over evolutionary time...' makes no sense.	Rewritten: 'Where resource selection improves survival or reproductive success of a species, natural selection can lead to phylogenetic and ontogenetic adaptations, polymorphism, adaptive radiation, or divergence, changes that are directly reflected in the <i>fundamental niche</i> .'	73, 80
1	P78, L7: insert of between range and adaptations.	Fixed	
1	P82: Please explain the shading in Table 1.	Added: 'Shaded values indicate no support for the methods indicated.'	81
2	The recommendations mentioned in the introduction abstract and text haven't been identified, but trends have been.	Reworded: 'To determine whether recommendations derived from world-wide or international investigations can be applied in an Australian context...'	3
		'How suitable are world-wide recommendations for Australia's mammals?'	5
2	Justify the selection of the three climate variables have been used, and why not climatic variability.	Available spatial layers representing climatic variability in the Channel Country were highly correlated with mean values (mean Pearson's <i>r</i> for MT 0.85, RS 0.98), and when used in place of mean variables, produced similar results (i.e. within 1.6% DE for all species models, excluding the <i>N. cervinus</i> climate-only model that increased by 3.8% DE using climate variables, but was insufficient to outperform the climate-and-landscape model). Overall, while local rainfall events drive resource pulses vital for the long-term	

E	Comment	Response	Pg
		<p>persistence of species in the region, the climate in this region is highly variable (Morton et al. 2011), and broad-scale climate patterns are yet to be accurately predicted.</p> <p>This information has been added to Appendix IV.</p>	
2	<p>Chap 2. Table 1. p29: Shouldn't the root zone water holding capacity read that a value of 0 was applied to polygons where &gt; 50% of the area had moderate to very low capacity? It is currently written as &lt;50%.</p>	Fixed	
2	<p>Chap 3. p39: word missing between relatively and environmental.</p>	Fixed	
2	<p>P51. The first sentence of the discussion needs rewording.</p>	<p>Reworded: 'This investigation detected a number of scale-dependent inconsistencies that related small changes in a landscape populated by fewer, more isolated populations with greater estimated rates of decline in the number of individuals and range shift (when detected) using coarse-scale environmental information.'</p>	50

#### References not cited in the thesis

Murray BR, Dickman CR (1994a) Granivory and microhabitat use in Australian desert rodents, are seeds important? *Oecologia* 99:216-225

Murray BR, Dickman CR (1994b) Food preferences and seed selection in two species of Australian desert rodents. *Wildlife Research* 21:647-655.

## Abstract

Extensive range shift and mass extinctions resulting from climate change are predicted to impact all biodiversity on the basis of species distribution models of wide-spread and data-rich taxa (i.e. vascular plants, terrestrial invertebrates, birds). Cases that both support and contradict these predictions have been observed in empirical and modelling investigations that continue to under-represent small mammal species (Introduction). Given small mammals are primary or higher order consumers and often dispersal limited, incorporating resource gradients that define the *fundamental niche* may be vital for generating accurate estimates of range shift. This idea was investigated through the influence of coarse to fine resolution, landscape- and quadrat-scale data on the range dynamics of four temperate- and five arid-zone small mammals.

This investigation determined:

- i. Landscape-scale edaphic and biotic factors improved model fit, robustness and transferability for five species, especially arid species, via improved discrimination of unsuitable habitat (specificity) or suitable habitat for a wet-heath specialist (*Rattus lutreolus lutreolus*; Chapters 1 & 4)
- ii. Quadrat-scale biotic factors improved model fit for three species; a dense understorey preferring species (*Isoodon obesulus obesulus*), granivore (*Notomys cervinus*) and insectivore (*Sminthopsis macroura*; Chapters 2 & 4),
- iii. Coarse or fine resolution environmental data were more strongly correlated with the occurrence of different species across variables, reflecting the known ecology of these species (Chapters 2 & 4), and
- iv. Fine resolution environmental data directly affected the spatial representation of available habitat in a coupled niche-population model, resulting in smaller shifts being detected for a greater number of species (Chapter 3).

Biotic interactions can drive adaptations that can lead to species becoming dependent on resource availability for survival or reproduction (Chapter 5). Complex ecosystem dynamics can make it difficult to distinguish resource partitioning caused by specialist adaptations (*fundamental niche*) from contemporary interactions (*realised niche*). In this investigation, evidence of biotic environmental variables defining the *fundamental niche* was provided by improved model transferability: representing direct (e.g. suitable habitat - *R. l. lutreolus*) or indirect influences on species' occurrence (e.g. rainfall via food availability on *I. o. obesulus*, *N. cervinus* and *Dasyuroides byrnei*). In addition to better representing resources, fine-scale environmental data affected the spatial configuration of available habitat, leading to smaller estimates of range shift. Hence, it is vital to consider species-environment relationships and conceptualise direct or proximal variables in order to construct robust SDMs. Improving this practice will also identify key relationships that influence community dynamics and require further empirical research (Chapter 5).

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*Co-authors*- Tom Prowse, Stephen Gregory, Michael Watts, Steve Delean and Damien Fordham.

*Manuscript reviewers*- Mark Hutchinson, Charley Krebs, Stephen Gregory, Donna Harris, Bill Breed, Barry Fox, Sonia Croft, Robert Brandle, Bert Harris, Salvador Herrando-Pérez, Sharn Lucas, journal editors and reviewers (e.g. Joseph Merritt, Journal of Mammalogy).

Data used under licence agreement were sourced from the Biological Databases of SA (Dept. of Environment and Natural Resources, SA), Atlas of Victorian Wildlife (Dept. of Sustainability and Environment, Vic), Atlas of NSW Data (Dept. of Environment and Climate Change), Wildnet database (Dept. of Environment and Resource Management, Qld), NT Atlas and Spatial Databases (Dept. of Natural Resources, Environment, The Arts and Sport, NT).

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## Declaration

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\* Haby, N.A., Delean, S. & Brook, B.W. 2011. Specialist resources are key to improving small mammal distribution models. *Austral Ecology* 37, 216-226.



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30 Apr 2012

Date