Modelling the potential range of the koala at the Last Glacial Maximum: future conservation implications

Christine Adams-Hosking[a], Patrick T. Moss[a], Jonathan R. Rhodes[a, b], Hedley S. Grantham[b] and Clive McAlpine[a, b].

[a] The University of Queensland, Landscape Ecology and Conservation Group, School of Geography, Planning, and Environmental Management, Brisbane, Qld 4072 Australia.

[b] The University of Queensland, The Ecology Centre, Brisbane, Qld 4072 Australia.

Correspondence: Christine Adams-Hosking, The University of Queensland, School of Geography, Planning, and Environmental Management, Brisbane, Qld 4072 Australia.
E-mail: c.hosking@uq.edu.au

ABSTRACT

The koala *Phascolarctos cinereus* is the only member of the once diverse marsupial family Phascolarctidae to have survived the Last Glacial Maximum. A climate envelope model for *P. cinereus* was developed to predict the range for this species at present and at the Last Glacial Maximum. The model was compared to the contemporary koala records and the known fossil records of *P. cinereus* during the Quaternary. The predicted current core range for koalas was concentrated in southeast Queensland, eastern New South Wales and eastern Victoria. At the Last Glacial Maximum their predicted core range contracted significantly to southeast Queensland and northeast New South Wales. Our findings concord with other studies that find species experienced range contractions during glacial maxima. In the context of the future conservation planning for koalas in the wild, our historical perspective demonstrates the past adaptations of koalas to changes in climate and their probable range contraction to climatic refugia. The future survival of wide-ranging specialist species, such as the koala, may depend on identifying and protecting, future climatic refugia.

Key words: Climate envelope, climatic refugia, core range, koala, *Phascolarctos cinereus,* Last Glacial Maximum.

Introduction

There has been a longstanding debate regarding the use of the theory of glacial refugia to describe current patterns of biodiversity (Willis and Whittaker 2000), but recently there is an increased interest in the importance of refugia in maintaining diversity under changing climates (Sommer and Zachos 2009). From an evolutionary perspective, the term 'refugia' refers to core habitats where organisms are able to persist during periods in which their wider geographic distribution becomes uninhabitable (Svenning *et al*. 2008; Heikkinen *et al*. 2009). However, this is a biologically complex and debated concept (e.g. Klicka and Zink 1997; Knapp and Mallet 2003). Most living organisms have experienced significant changes in their distributions due to global climatic fluctuations and particularly due to major ice ages over the past three millions years (Hewitt 2000). The Last Glacial Maximum (LGM) was estimated to have been at its maximum from at least 22-19 thousand years BP (Yokoyama *et al*. 2000). In Australia, ice-sheet cover was not extensive during the LGM and there is evidence, for example, that *Eucalyptus regnans,* was able to persist either locally during the harsh environmental conditions or by contracting to near-coastal refugia (Nevill *et al*. 2009). The identification of refugia for plant and animal species may have important implications for the conservation of biodiversity under climate change.

The modern koala *Phascolarctos cinereus* is an arboreal folivorous marsupial endemic to Australia. It currently occupies a widely distributed but fragmented range in eastern Australia (Fig. 1). The evolution of the koala family (Phascolarctidae) was driven by an adaptation to open sclerophyll forests as the continent became drier (Hocknull *et al*. 2007) and to feeding almost exclusively on the leaves of eucalypt trees. This increased dependence on eucalypts through time is demonstrated for example, in changes to koala skulls (Louys *et al*. 2009). The fossil records of Phascolarctidae reveal a unique dentition of double W-shaped blades on each molar for slicing leaf matter. There are subtle variations in the koala's dental nomenclature which enables taxonomic differentiation (Long *et al*. 2002), but the dental morphology of the modern koala is only marginally more specialised than its ancestors (Archer *et al*. 2000). The fossil records show that the distribution of koalas at times in the distant past was far wider than at present (Fig. 2) and also that *P. cinereus* is the last survivor of this once diverse family containing six genera and at least 18 species (e.g. Stirton 1957; Merrilees 1967; Archer 1972; Marshall 1973; Bartholomai 1977; Pledge 1992; Black 1999; Piper 2007; Price *et al*. 2009).

The role of humans as well as climate in determining the biogeography, evolution and extinction of faunas is an area of ongoing research, in particular the investigation of fauna-rich fossil caves to ascertain faunal responses to climate change during the Pleistocene (e.g. Hocknull 2007; Prideaux *et al*. 2007). These authors have revealed significant population fluctuations driven by glacial-interglacial cycling, but stable species composition for 500 thousand years, with the exception of the megafauna that went extinct around 70 – 50 thousand years ago (Long *et al*. 2002). Research suggests that climate change alone was unlikely to have been the principal cause of the extinction of the megafauna and although Aboriginal hunting may have been a factor in determining the distribution and abundance of *P. cinereus*, there is no doubt that populations have been significantly affected by the European occupiers of Australia for the fur trade in more recent times (e.g. Fowler 1993; Hrdina and Gordon 2004).

The modern koala's primary food source is a regionally-variable selection of, primarily, *Eucalyptus* and *Corymbia* tree species (e.g. Moore and Foley 2000; Ellis *et al*. 2002). Koala populations are currently under threat from the synergistic threats of habitat loss, disease, car collisions and dog predation in coastal regions of Queensland and New South Wales (Jackson *et al*. 1999; Dique *et al*. 2003; McAlpine *et al*. 2006; Rhodes *et al*. 2008; Lunney *et al*. 2009). For example, the abundance of koalas on the Koala Coast of southeast Queensland is estimated to have declined by 64% in a ten year period (1999-2008) (State of Queensland 2009). In western semi-arid and arid regions, koalas have been shown to experience significant local population declines during drought and heatwaves (Gordon *et al*. 1988).

Climatic refugia may have played a key role in the survival of the extant koala species during the extreme climates of the LGM. Here we examine this hypothesis through a review of the past occurrence of *P. cinereus*, and comparison of its present and predicted LGM distribution using bioclimatic modelling. We discuss the implications for the management and conservation of contemporary koala populations under future climate change.

Methods

Approach and assumptions

Bioclimatic models are useful tools for predicting the responses of organisms to climatic changes because they focus on the climatic thresholds that limit species' distributions in past and present time (Mesquita and Sousa 2009). However, it must be remembered that models are simply estimates of species' potential ranges. We used Bioclim from the ANUCLIM software package (Houlder *et al*. 1999) to develop a species profile or 'climate envelope' of the distribution of the modern koala. Bioclim has been used in a large number of studies world-wide (e.g. Manning *et al*. 2005; McKenney *et al*. 2007; Green *et al*. 2008), including palynological studies (e.g. Moss and Kershaw 2000; Gallagher *et al*. 2003). As a climate envelope model, Bioclim is independent of other variables that can influence koala presence such as habitat loss and urbanisation. Bioclim has been found, when compared to other climate envelope modelling methods, to be less prone to overprediction and therefore useful as a conservative approach (Hijmans and Graham 2006). In another comparative modelling study on 18 terrestrial taxa (insects, amphibians, reptiles, birds and mammals), Bioclim attained increasingly high concordance with other modelling methods, with increasing sample sizes (Hernandez *et al*. 2006). For this study we used a large sample size (n = 3,332).

Due to the broad temporal span of the *P. cinereus* fossil records (< 1 to 569 thousand years ago) (Price 2008), these fossil data were not considered reliable for use in our modelling. We therefore used the contemporary distribution data of *P. cinereus* with its contemporary climate envelope and then used it to predict the past distribution of this species at the LGM. Determining regional climates at the LGM is a complex task. For example, Williams *et al*. (2009) found that mean annual temperatures in tropical northern Australia ranged from 3 to 7 °C below present values and up to 8 °C lower in mainland southeast Australia, with winter rainfall reduced by at least 30 % in tropical northern Australia. We therefore assumed generalised continental-scale decreases in rainfall and temperature for the study area, which may not reflect regional variations that occurred during the LGM. This study therefore examines potential macrorefugia (Ashcroft 2010) at the LGM.

Study area and populations

We used contemporary koala distribution data from databases held by the States of Queensland, New South Wales and Victoria (Fig. 1). Koalas currently also inhabit parts of southeast South Australia (Fig. 1) where they have been re-introduced after virtual extinction (Jackson 2007), an enclosed reserve in Western Australia, and various islands around the south and east of the continent. To avoid uncertainty regarding whether such populations have been translocated or are native, we excluded these populations from the analysis and only considered areas containing natural populations. We defined 'natural' as populations that are not derived from solely translocated and/or introduced individuals.

Data and climate envelope development

Bioclim uses mathematically derived climate surfaces, estimated from mean monthly climate estimates of a network of meteorological stations across Australia, to develop the climate envelopes based on the latitude, longitude and elevation. We used the modern koala sighting records over the past 100 years. The koala sightings records were obtained from the Queensland Department of Environment and Resource Management, the New South Wales Department of Environment and Climate Change and the Victorian Department of Sustainability and Environment. Duplicate records, as well as obvious outliers indicating

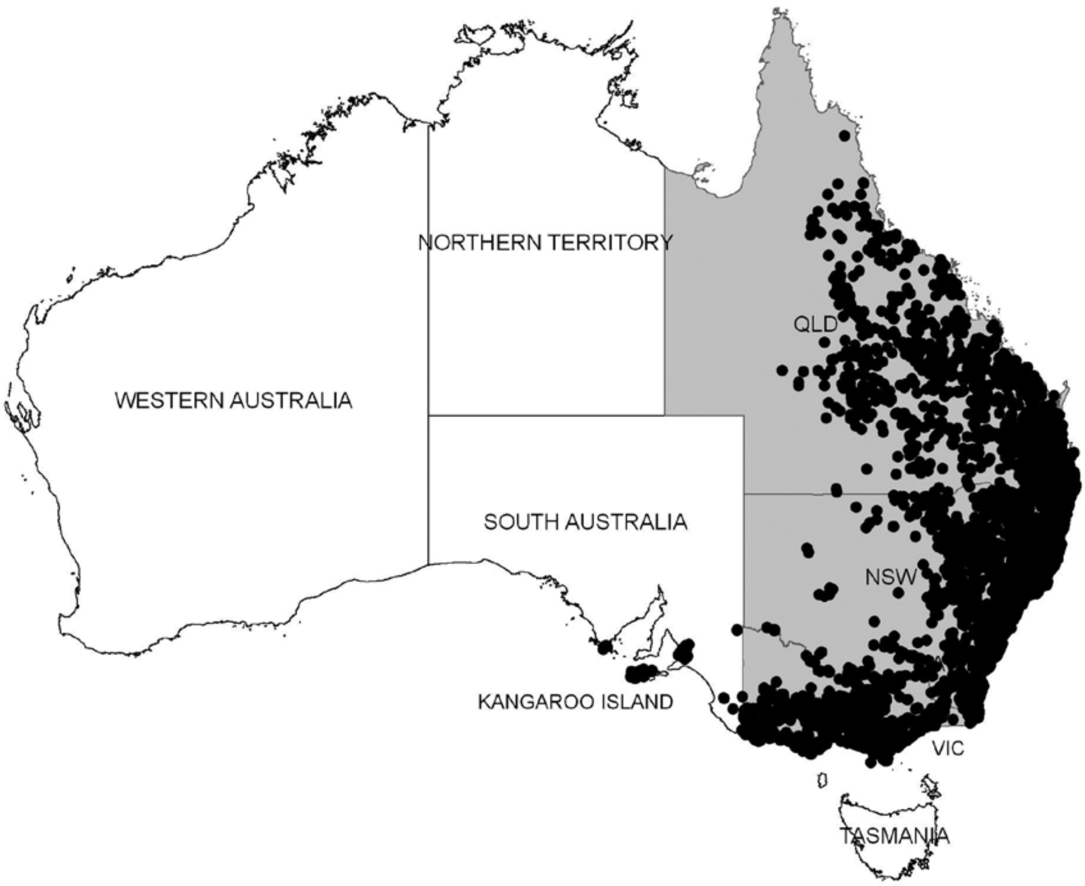

Figure 1. Modern koala range shown in black. Study area shown in grey. Koala records sourced from: Queensland Department of Environment and Resource Management, New South Wales Department of Environment and Climate Change, Victorian Department of Sustainability and Environment and South Australian Department of Environment and Natural Resources.

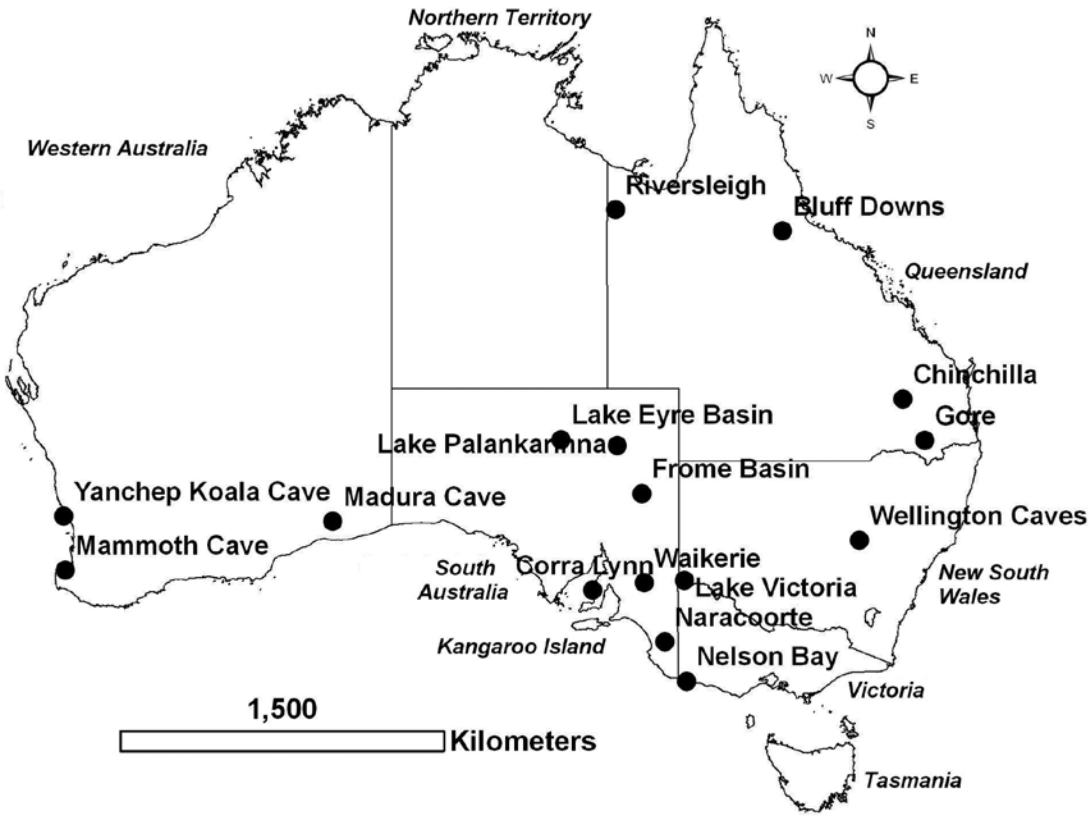

Figure 2. Published fossil sites containing relatively well-dated records of *koalas since the Late Miocene, 11-5.3 million years ago (following Price 2008).*

data entry mistakes, were removed manually by viewing the koala data points spatially. To reduce the possibility of geographical bias, such as a high density of records collected in highly populated areas, records were filtered by overlaying the occurrence records with a 10 kilometre grid and then one record was randomly selected from each grid cell (McKenney *et al.* 2007). This reduced the total number of koala records for the bioclimatic modelling from 32,029 to 3,332.

Predictions: current range of *P. cinereus*

We used Biomap, a component of Bioclim, to model the predicted current koala geographic range based on the climate envelope generated by Bioclim (temperature range -4 °C to 37.7 °C and annual precipitation 234 to 2480 mm) (Table 1). For these predictions, we calculated the entire range (1-100th percentiles) and the core range (10th - 90th percentiles). The entire range indicates locations that have bioclimatic parameters that fall within the maximum and minimum values of the climate envelope. This provides an estimate of potential koala habitats, including outliers and some may in reality not provide suitable habitat. The core range indicates the most climatically suitable locations, with points that have bioclimatic parameters that fall between the 10th and the 90th percentiles of the koala's climate envelope. However, the core range may include areas that, although optimal have, for example, been cleared for urban development or agriculture.

Although Bioclim can utilise up to 35 climatic parameters, is has been suggested that using all of these can lead to over-fitting (Beaumont *et al.* 2005). Following recommendations made by these authors, we avoided the inclusion of unnecessary climatic parameters that could place constraints on identifying climatically suitable habitat and chose a sub-set of seven key parameters based on expert opinion. These parameters were selected to represent: a) the most biologically meaningful predictors of koala distributions in terms of their thermoregulatory and nutritional needs (e.g. Moore and Foley 2000; Krockenberger 2003), and b) the most climatically influential requirements for *Eucalyptus* distribution, their primary food source (e.g. Box 1981; Hughes *et al.* 1996). These parameters were: Annual Mean Temperature; Maximum Temperature of the Warmest Period; Minimum Temperature of the Coldest Period; Annual Precipitation; Precipitation Seasonality (C of V); Precipitation of the Warmest Quarter; Precipitation of the Coldest Quarter (Table 1).

Predictions: LGM range of *P. cinereus*

It is indicated by Petherick *et al.* (2008) that the Last Glacial Maximum (LGM) in eastern Australia had two distinct cold and dry events (~ 30.8 k. cal. yr BP and 21.7 k cal. yr BP) and was particularly severe. For example, temperatures were up to 8 ° C lower than today in mainland southeast Australia with summer precipitation reduced by at least 30% (Williams *et al.* 2009). In northeast Australia temperatures were 3-7 ° C lower, with precipitation reduced to less than 50% of present values (Williams *et al.* 2009). We adjusted temperature and rainfall to generate two LGM predictions based on: 1) temperature 6 °C lower and rainfall 20% lower and 2) temperature 6 ° C lower and rainfall 40% lower. We chose regionally generalised climatic adjustments from approximate sea surface temperature (SST) reconstructions at the LGM (Turney *et al.* 2006; Van der Kaars *et al.* 2006; Barrows *et al.* 2007) and terrestrial and near-shore proxy data (Williams *et al.* 2009). We confined our predictions to the LGM due to the limitations in knowledge of the climate and the physiology of koalas at longer past time frames. We used the sub-set of seven key parameters to construct our LGM predictions.

Results

Predicted current range of *P. cinereus*

The predictions under current climate conditions (Fig. 3-a) identified a core range (10th - 90th percentiles) that falls within the modern distribution of koalas in the study area (Fig. 1). Some coastal areas were outside this core range, despite high densities of koalas currently being present in coastal areas such as southeast Queensland and eastern New South Wales. Conversely, the predicted entire range (1 - 100th percentiles) included regions where there are currently no koalas such as Tasmania, Western and Central Australia.

Predicted LGM range of *P. cinereus*

With temperature reduced by 6 ° C and rainfall reduced by 20 % (Fig. 3-b), a highly restricted core range (10th- 90th percentiles) for koalas to southeast Queensland and coastal northern New South Wales

Table 1. Abbreviated Bioclimatic profile (percentiles) of *Ph. cinereus* for Queensland, New South Wales and Victoria showing the seven key parameters used for the Biomap LGM predictions. ('C of V') = Coefficient of variation.

Parameter	Mean	S.D	5	10	25	50	75	90	95	Max	Min
1. Annual Mean Temperature	16.4	3.39	11.3	12	13.5	16.5	19.2	21.2	22.1	24.2	6
2. Max.Temp. Warmest Period	29	3.67	23.2	24.1	26	28.8	31.8	34.4	35.3	37.7	18.9
3. Min. Temp. Coldest Period	3.7	2.65	-0.6	0.4	2.1	3.5	5.3	7.3	8.8	15.7	-4
4. Annual Precipitation	863	327.58	447	493	601	796	1061	1333	1528	2480	234
5. Precipitation Seasonality (C of V)	36	18.43	10	14	23	35	47	59	70	122	6
6. Precipitation Warmest Quarter	290	153.28	88	115	178	255	376	510	599	1011	61
7. Precipitation Coldest Quarter	172	83.02	49	78	107	159	227	293	329	611	17

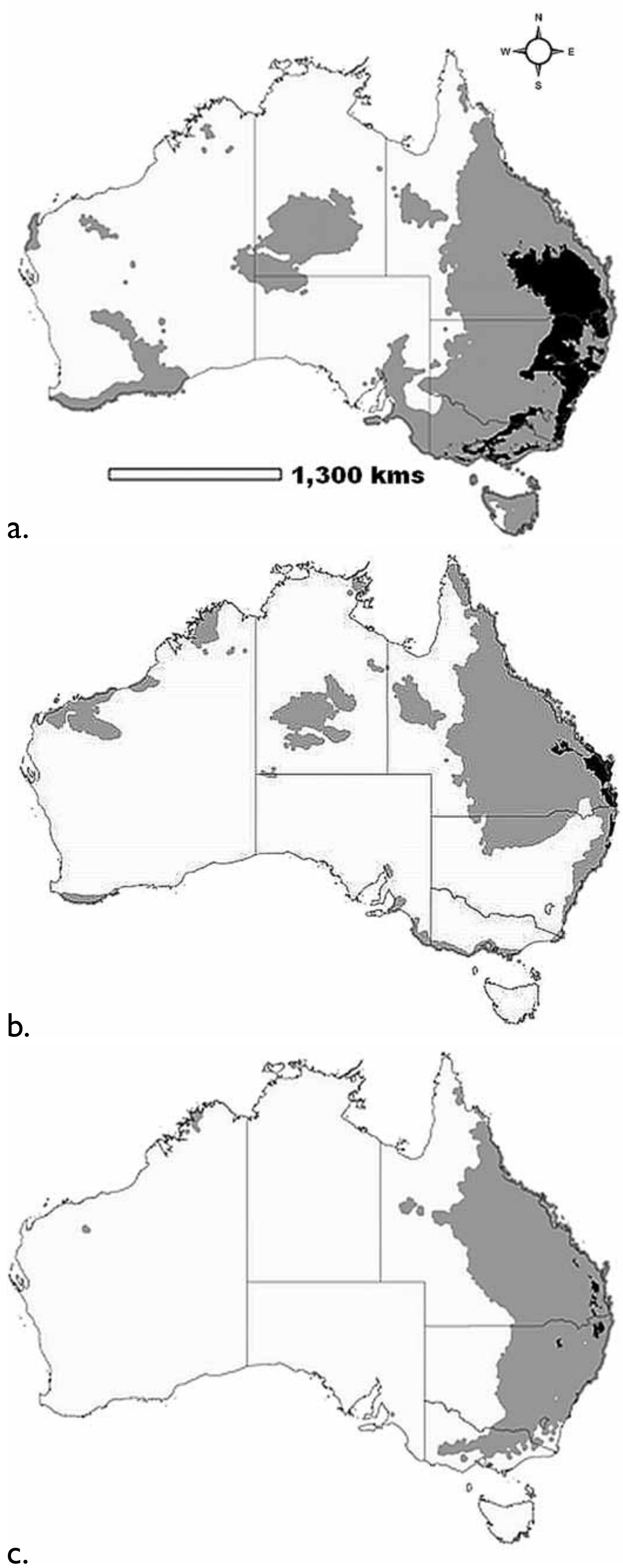

Figure 3. Bioclim models of (a) modern predicted entire range and core range, (b) LGM predicted entire range and core range with temperature reduced by 6 °C and rainfall reduced by 20%, (c) LGM predicted entire range and core range with temperature reduced by 6 °C and rainfall reduced by 40%.

was indicated. The entire predicted range (1-100th percentiles) incorporated most of Queensland, some of coastal and northern New South Wales, small areas of coastal Victoria, South Australia and Western Australia and an area in the central Northern Territory. When the rainfall was further reduced by 40% (Fig. 3-c), the predicted core range contracted away from the coast to highland areas in southeast Queensland and northern New South Wales. The entire predicted range contracted to eastern Queensland and New South Wales and highland areas of Victoria.

Discussion

Change in range boundaries

We were able to model the potential distribution of *P. cinereus* at the LGM to demonstrate range contractions to areas that may have provided climatic refugia suitable for koalas during the severe conditions of past glacial periods. Our predictions concord with Korsten *et al*. (2009) whose mitochondrial DNA sequences for the brown bear *Ursus arctos* suggest that a small number of bears were restricted to a single refuge area during the last glacial maximum. The refugial hypothesis that populations retracted during glacial maxima is further discussed for wolves *Canis lupus* (Weckworth *et al*. 2010) and European deer *Cervus elaphus* and *Capreolus capreolus* (Sommer and Zachos 2009). *Phascolarctos cinereus* fossils dated prior to the LGM are recorded in Western Australia's Mammoth Cave (Glauret 1910) and Devil's Lair (~31-43 thousand years ago) (Balme *et al*. 1978) as well as Madura Cave (>24-<101 thousand years ago) (Lundelius and Turnbull 1982). We predicted a potential climatically-induced range contraction and eventual disappearance when we reduced rainfall by 40% in southwest Western Australia (Fig. 3c) that may indicate that as climatic conditions became more severe, there were no climatic refugia for koala populations to be sustained during the LGM. However any assumptions should be treated with caution due to uncertainty in fossil dating and the possibility of future palaeoecological information that may come to light. The question of whether Aboriginal hunting played a role in the disappearance of koalas from this region remains unresolved.

Future distribution of koalas: climatic refugia

The Pleistocene (2.6 million to 10,000 years ago), which incorporates the LGM, is considered an important period for assessing the impact of climate change on biodiversity due to its multiple oscillations between cold, dry glacial and warm, wet interglacial conditions. During this period, climatic fluctuations had profound effects on the distribution of vegetation (Johnson 2006), particularly impacting tree species and their distribution. Drought-induced deaths of eucalypts in Central Queensland are suggested to be more severe in species with roots confined to upper soil layers (Fensham and Fairfax 2007) and forest dieback is predicted to increase worldwide with climate change (Cunningham *et* *al*. 2010). It can therefore be expected that future koala distributions will be affected not only by the direct effects of a warming climate in terms of their thermoregulatory limitations but also by the indirect effects of food tree availability (Hughes *et al*. 1996; Allen and Breshears 1998) and foliar chemistry (Moore *et al*. 2005; DeGabriel *et al*. 2010), particularly in regions that become hotter and drier.

To counter the impacts on koalas of rapid climate change, it may become necessary to consider conserving adequate and climatically suitable contemporary habitat, plus undertake novel conservation strategies such as assisted colonisation/migration (McLachlan *et al*. 2007; Hoegh-Guldberg *et al*. 2008). The latter option could involve moving koalas outside their current distribution, to climatically and ecologically suitable future climatic refugia. For example, the current range modelled here suggests koalas could survive in Tasmania and the alpine regions of Victoria, areas which are presently too cold and/or wet for their climate envelope. It is of interest that our predictions included Kangaroo Island (Fig. 3 a, b), which currently supports a large introduced koala population (Fig. 1). Similarly, a small number of koalas translocated from Kangaroo Island currently inhabit Yanchep National Park in Western Australia. They are reportedly healthy and consuming *Eucalyptus rudis,* a species endemic to Western Australia (H. Beswick *pers. comm.)*. However the problems that have developed with the introduction of koalas to Kangaroo Island (Duka and Masters 2005) demonstrate that assisted colonisation would firstly require precautionary prior field-based scientific experiments to test for the ecological and physiological viability and impacts of such measures.

Our koala case study provides an historical context for the future conservation planning of this species in the wild and demonstrates the sensitivity of koalas to changes in climate, highlighting the importance of climatic refugia during the LGM. We suggest that historically, koalas have utilised such refugia during the harsher conditions of glacial maxima. This historical context and predictions of potential past range contractions to climatic refugia during harsh climatic conditions demonstrates that in planning for the future conservation of species threatened by rapid climate change, the identification of future climate change refugia will be a vital component.

Acknowledgements

We are grateful to Michael Hutchinson for advising on Bioclim and supplying the Digital Elevation Model used for this study. We thank Tim Barrows for assistance with gathering the LGM climate data and Gilbert Price, whose interest and knowledge enhanced this manuscript. We are also grateful to the Queensland Department of Environment and Resource Management, the New South Wales Department of Environment and Climate Change, the Victorian Department of Environment and Conservation and the South Australian Department of Environment and Natural Resources for providing the modern koala records used in this study. Christine Adams-Hosking was supported by a University of Queensland Special Graduate School Scholarship and part-funding from the Australian Koala Foundation and the National Climate Change Adaptation Research Facility.

References

Allen, C. D. and Breshears, D. D. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences of the United States of America* **95**: 14839-14842.

Archer, M. 1972. Phascolarctos (Marsupialia, Vombatoidea) and associated fossil fauna from Koala Cave near Yanchep, Western Australia. *Helictite* 49-59.

Archer, M., Hand, S.J., and Godthelp, H. 2000. *Australia's Lost World: Riversleigh, World Heritage Site.* Reed New Holland, Australia.

Ashcroft, M.B. 2010. Identifying refugia from climate change. *Journal of Biogeography* **37:** 1407-1413.

Balme, L.M., Merrilees, D. and Porter, J.K. 1978. Late Quaternary mammal remains spanning 30,000 years from excavations in Devil's Lair, Western Australia. *Journal of the Royal Society of Western Australia* **61**: 33-65.

Barrows, T. T., Juggins, S., De Deckker, P., Calvo, E. and Pelejero, C. 2007. Long-term sea surface temperature and climate change in the Australian-New Zealand region. *Paleoceanography* **22**, 2: Article number PA2215.

Bartholomai, A. 1977. The fossil vertebrate fauna from Pleistocene deposits at Cement Mills, Gore, southeastern Queensland. *Memoirs of the Queensland Museum* **18**: 41-51.

Beaumont, L. J., Hughes, L. and Poulsen, M. 2005. Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological Modelling* **186**: 250-269.

Black, K. 1999. Diversity and relationships of living and extinct koalas (Phascolarctidae, Marsupialia). *Australian Mammalogy* **21**: 16-17.

Box, E. O. 1981. Predicting physiognomic vegetation types with climate variables. *Plant Ecology* **45**: 127-39.

Cunningham, S.C., Thomson, J.R., Read, J., Baker, P.J. and Nally, R.M. 2010. Does stand structure influence susceptibility of eucalypt floodplain forests to dieback? *Austral Ecology* **35:** 348-356.

DeGabriel, J., Moore, B., Marsh, K. and Foley, W. 2010. The effect of plant secondary metabolites on the interplay between the internal and external environments of marsupial folivores. *Chemoecology* **20**:97-108.

Dique, D.S., Thompson, J., Preece, H.J., Penfold, G.C., de Villiers, D.L. and Leslie, R.S. 2003. Koala mortality on roads in south-east Queensland: the koala speed-zone trial *Wildlife Research* **30**: 419 – 426.

Duka, T. and Masters, P. 2005. Confronting a tough issue: fertility control and translocation for over-abundant koalas on Kangaroo Island, South Australia. *Ecological Management & Restoration* **6**: 172-81.

Ellis, W.A.H., Melzer, A., Carrick, F.N. and Hasegawa, M. 2002. Tree use, diet and home range of the koala (Phascolarctos cinereus) at Blair Athol, central Queensland. *Wildlife Research* **29**: 303-311.

Fensham, R. J. and Fairfax, R. J. 2007. Drought-related tree death of savanna eucalypts: species susceptibility, soil conditions and root architecture. *Journal of Vegetation Science* **18**: 71-80.

Fowler, G. 1993. 'Black August' Queensland's Open Season on Koalas in 1927. Honours Thesis, Australian National University.

Gallagher, S. J., Greenwood, D. R., Taylor, D., Smith, A. J., Wallace, M. W. and Holdgate, G. R. 2003. The Pliocene climatic and environmental evolution of southeastern Australia: evidence from the marine and terrestrial realm. *Palaeogeography, Palaeoclimatology, Palaeoecology* **193:** 349-382.

Glauret, L. 1910. The Mammoth Cave. *Records of the Western Australian Museum and Art Gallery* **1**: 11-36.

Gordon, G., Brown, A.S. and Pulsford, T. 1988. A koala (Phascolarctos cinereus Goldfuss) population crash during drought and heatwave conditions in south-western Queensland. *Austral Ecology* **13**: 451-461.

Green, K., Stein, J. A. and Driessen, M. M. 2008. The projected distributions of *Mastacomys fuscus* and *Rattus lutreolus* in south-eastern Australia under a scenario of climate change: potential for increased competition? *Wildlife Research* **35**: 113-9.

Heikkinen, R. K., Luoto, M., Leikola, N., Poyry, J., Settele, J., Kudrna, O., Marmion, M., Fronzek, S. and Thuiller, W. 2009. Assessing the vulnerability of European butterflies to climate change using multiple criteria. *Biodiversity and Conservation* **19**: 695-723.

Hernandez, P. A., Graham, C. H., Master, L. L. and Albert, D. L. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* **29**: 773-85.

Hewitt, G. 2000. The genetic legacy of the Quaternary ice ages. *Nature* **405**: 907-913.

Hijmans, R. J. and Graham, C. H. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* **12:** 2272-2281.

Hocknull, S. A., Zhao, J.-x., Feng, Y.-x. and Webb, G. E. 2007. Responses of Quaternary rainforest vertebrates to climate change in Australia. *Earth and Planetary Science Letters,* **264**: 317-31.

Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D. B., Parmesan, C., Possingham, H. P. and Thomas, C. D. 2008. Assisted colonization and rapid climate change. *Science* **321**: 345-346.

Houlder, D., Hutchinson, M., Nix, H. and McMahon, J. 1999. *ANUCLIM Version 5.0 User Guide*. The Australian National University, Centre for Resource and Environmental Studies, Canberra.

Hrdina, F., and Gordon, G. 2004. The koala and possum trade in Queensland, 1906-1936. *Australian Zoologist* **32**: 543-584.

Hughes, L., Cawsey, E. M. and Westoby, M. 1996. Climatic range sizes of Eucalyptus species in relation to future climate change. *Global Ecology and Biogeography Letters* **5**: 23-29.

Jackson, S. 2007. *Koala Origins of an Icon*. Jacana Books, an imprint of Allen & Unwin, Crow's Nest, N.S.W. Australia.

Jackson, M., White, N., Giffard, P. and Timms, P. 1999. Epizootiology of Chlamydia infections in two free-range koala populations. *Veterinary Microbiology* **65**: 225-234.

Johnson, C. 2006. *Australia's Mammal Extinctions A 50 000 year history*. Cambridge University Press, New York.

Klicka, J. and Zink, R. M. 1997. The importance of recent ice ages in speciation: a failed paradigm. *Science* **277**: 1666-1669.

Knapp, S. and Mallet, J. 2003. Refuting refugia? *Science* **300**: 71-72.

Korsten, M., Ho, S.Y.W., Davison, J., Pahn, B., Vulla, E., Roht, M., Tumanov, I.L., Kojola, I., Andersone-Lilley, Z., Ozolins, J., Pilot, M., Mertzanis, Y., Giannakopoulos, A., Vorobiev, A.A., Markov, N.I., Saveljev, A.P., Lyapunova, E.A., Abramov, A.V., Mannil, P., Valdmann, H., Pazetnov, S.V., Pazetnov, V.S., Rokov, A.M. and Saarma, U. 2009. Sudden expansion of a single brown bear maternal lineage across northern continental Eurasia after the last ice age: A general demographic model for mammals? *Molecular Ecology* **18**: 1963-1979.

Krockenberger, A. 2003. Meeting the energy demands of reproduction in female koalas, Phascolarctos cinereus: evidence for energetic compensation. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology* **173**: 531-40.

Long, J., Archer, M., Flannery, T. and Hand, S. 2002. *Prehistoric Mammals of Australia and New Guinea One Hundred Million Years of Evolution*. University of New South Wales Press Limited, NSW.

Louys, J., Aplin, K., Beck, R.M.D., and Archer, M. 2009. Cranial anatomy of Oligo-Miocene koalas (diprotodontia: phascolarctidae): stages in the evolution of an extreme leaf-eating specialization.

Lundelius Jr., E.L. and Turnbull, W.D. 1982. The mammalian fauna of Madura Cave, Western Australia. Part V: Diprotodonta (Part). *Fieldiana: Geology* **11**: 1-31.

Lunney, D., Crowther, M.S., Shannon, I., and Bryant, J. V. 2009. Combining a map-based public survey with an estimation of site occupancy to determine the recent and changing distribution of the koala in New South Wales. *Wildlife Research* **36**: 262–273.

Manning, A.D., Lindenmayer, D.B., Nix, H.A. and Barry, S.C. 2005. A bioclimatic analysis for the highly mobile Superb Parrot of south-eastern Australia. *Emu* **105**: 193-201.

Marshall, L.G. 1973. Fossil vertebrate faunas from the Lake Victoria region, S.W. New South Wales, Australia. *Memoirs of the National Museum of Victoria* **34**: 151-172.

McAlpine, C.A., Rhodes, J.R., Callaghan, J.G., Bowen, M.E., Lunney, D., Mitchell, D.L., Pullar, D.V. and 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.

McKenney, D. W., Pedlar, J. H., Lawrence, K., Campbell, K. and Hutchinson, M. F. 2007. Beyond traditional hardiness zones: using climate envelopes to map plant range limits. *BioScience* **57**: 929-37.

McLachlan, J. S., Hellmann, J. J. and Schwartz, M. W. 2007. A framework for debate of assisted migration in an era of climate change. *Conservation Biology* **21**: 297-302.

Merrilees, D, 1967. Man the destroyer: late Quaternary changes in the Australian marsupial fauna. *Journal of the Royal Society of Western Australia* **51**: 1-24.

Mesquita, S. and Sousa, A. J. 2009. Bioclimatic mapping using geostatistical approaches: application to mainland Portugal. *International Journal of Climatology* **29**: 2156-2170.

Moore, B. D. and Foley, W. J. 2000. A review of feeding and diet selection in koalas (*Phascolarctos cinereus*). *Australian Journal of Zoology* **48**: 317-33.

Moore, B.D., Foley, W.J., Wallis, I.R., Cowling, A. and Handasyde, K.A. 2005. Eucalyptus foliar chemistry explains selective feeding by koalas. *Biology Letters* **1**: 64-67.

Moss, P. T. and Kershaw, P. A. 2000. The last glacial cycle from the humid tropics of northeastern Australia: comparison of a terrestrial and a marine record *Palaeogeography, Palaeoclimatology, Palaeoecology* **155**: 155-176.

Nevill, P. G., Bossinger, G. and Ades, P. K. 2009. Phylogeography of the world's tallest angiosperm, *Eucalyptus regnans*: evidence for multiple isolated Quaternary refugia. *Journal of Biogeography* **37**: 179-192.

Petherick, L., McGowan, H. and Moss, P. 2008. Climate variability during the Last Glacial Maximum in eastern Australia: evidence of two stadials? *Journal of Quaternary Science* Published Online. DOI: 10.1002/ JQS.1186.

Piper, K.J. 2007. Early Pleistocene mammals from the Nelson Bay local fauna, Portland, Victoria, Australia. *Journal of Vertebrate Paleontology* **27**: 492-503.

Pledge, N.S. 1992. The Curramulka local fauna: a new late tertiary fossil assemblage from Yorke Peninsula, South Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* **9**: 115-142.

Price, G.J. 2008. Is the modern koala (*Phascolarctos cinereus)* a derived dwarf of a Pleistocene giant? Implications for testing megafauna extinction hypothesis. *Quaternary Science Reviews* **27**: 2516-2521.

Price, G. J., Zhao, J.-x., Feng, Y.-x. and Hocknull, S. A. 2009. New records of Plio-Pleistocene koalas from Australia: palaeoecological and taxonomic implications. *Records of the Australian Museum* **61**: 39-48.

Prideaux, G.J., Roberts, R.G., Megirian, D., Westaway, K.E., Hekkstrom, J.C. and Olley, J.M. 2007. Mammalian responses to Pleistocene climate change in southeastern Australia. *Geology* **35:** 33-36.

Rhodes, J. R., Callaghan, J. G., McAlpine, C. A., De Jong, C., Bowen, M. E., Mitchell, D. L., Lunney, D. and Possingham, H. P. 2008. Regional variation in habitat-occupancy thresholds: a warning for conservation planning. *Journal of Applied Ecology* **45**: 549-557.

Sommer, R. S. and Zachos, F. E. 2009. Fossil evidence and phylogeography of temperate species: 'glacial refugia' and post-glacial recolonization. *Journal of Biogeography* **36**: 2013-2020.

State of Queensland 2009. *Decline of the Koala Coast Koala Population: Population Status in 2008*. Department of Environment and Resource Management, Queensland, Australia. http://www.derm.qld.gov.au/register/p02966aa.pdf. Accessed December 2009.

Stirton, R.A. 1957. A new koala from the Pliocene Palankarinna Fauna of South Australia. *Records of the South Australian Museum* **13**: 71-81.

Svenning, J., Normand, S. and Kageyama, M. 2008. Glacial refugia of temperate trees in Europe: insights from species distribution modelling. *Journal of Ecology* **96**: 1117-27.

Turney, C.S.M., Haberle, S., Fink, D., Kershaw, A.P., Barbetti, M., Barrows, T.T., Black, M., Cohen, T.J., Correge, T., Hesse, P.P., Hua, Q., Johnston, R., Morgan, V., Moss, P., Nanson, G., Van Ommen, T., Rule, S., Williams, N.J., Zhao, J.-X., D'Costa, D., Feng, Y.-X., Gagan, M., Mooney, S. and Xia, Q. 2006. Integration of ice-core, marine and terrestrial records for the Australian Last Glacial Maximum and Termination: a contribution from the OZ INTIMATE group. *Journal of Quaternary Science* **21**: 751-761.

Van der Kaars, S., De Deckker, P. and Gingele, F. X. 2006. A 100 000-year record of annual and seasonal rainfall and temperature for northwestern Australia based on a pollen record obtained offshore. *Journal of Quaternary Science* **21**: 879-89.

Weckworth, B.V., Talbot, S.L. and Cook, J.A. 2010. Phylogeography of wolves (Canis lupus) in the Pacific Northwest. *Journal of Mammalogy* **91**: 363-375.

Williams, M., Cook, E., Van der Kaars, S., Barrows, T., Shulmeister, J. and Kershaw, P. 2009. Glacial and deglacial climatic patterns in Australia and surrounding regions from 35 000 to 10 000 years ago reconstructed from terrestrial and near-shore proxy data. *Quaternary Science Reviews* **28**: 2398-2419.

Willis, K. J. and Whittaker, R. J. 2000. Palaeoecology: The refugial debate. *Science* **287**: 1406-1407.

Yokoyama, Y., Lambeck, K., De Deckker, P., Johnston, P. and Fifield, L. K. 2000. Timing of the Last Glacial Maximum from observed sea-level minima. *Nature* **406**: 713-716.