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FORUM

The Viggers & Hearn conundrum: a kangaroo home range study with no implications for land management

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Summary

- 1. Viggers & Hearn (2005) examined the encroachment of native herbivores on to farmland. They presented kangaroo home range estimates and pasture biomass data for three sites in south-eastern Australia, then made broad management recommendations regarding the preservation of remnant habitat.
- 2. While Viggers & Hearn identified potentially important patterns, we believe that their data were neither sufficient nor appropriate to reveal the processes that underlie these patterns.
- 3. Specifically, their study was unreplicated at the land-use level, used inappropriate density estimates for their study populations, failed to measure resources adequately, used flawed methods of home range analysis, and demonstrated limited understanding of key concepts and of their study species and thus could not draw valid conclusions.
- **4.** Synthesis and applications. In view of these fundamental problems, we recommend that decisions on the management of kangaroos and remnant vegetation not be based on the work reported by Viggers & Hearn.

Key-words: dispersal, eastern grey kangaroo, *Macropus giganteus*, population density, ranging behaviour, remnant vegetation, resource availability, study design

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Introduction

In their paper 'The kangaroo conundrum: home range studies and implications for land management', Viggers & Hearn (2005) estimated the home range size of eastern grey kangaroos *Macropus giganteus* Shaw by radio-tracking 5–10 individuals at each of three sites (one farm, one water catchment, one wildlife reserve) in or near the Australian Capital Territory (ACT), southeastern Australia. They classed these sites as being of high or low kangaroo density based on previous density estimates in various land-use types within the ACT. They also estimated pasture biomass at each of

their study sites. From these data, they concluded that 'little incentive exists for farmers to preserve remnant vegetation, as it may be regarded as providing habitat for unwanted or "pest" kangaroos' without having further information on farmers' attitudes or decision making practices.

There is no question that Viggers & Hearn have identified a key management issue worthy of research attention: the movement of native herbivores between native vegetation and agricultural land. However, we have serious concerns about their research, in particular the study design, their poor understanding of the biology of the study species and the biological concepts relevant to this study, and the numerous shortcomings in their interpretation and extrapolation of their data. Viggers & Hearn concluded: 'The key processes influencing home range size of *M. giganteus* in our study were

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Response to Viggers & Hearn (2005) population density, presence of cover and reluctance to disperse across cleared landscapes. Resource availability was not important'. We argue that they failed to measure any of these factors accurately, and therefore made management recommendations based on flawed data. Although they identified some interesting and potentially important patterns, they did not collect sufficient data to reveal the underlying processes. Here, we highlight our concerns with specific reference to key terms and phrases (highlighted in bold type) within summary points 2 and 4–7 in their paper.

2. 'This study examined home range size and use in M. giganteus across different types of land use and in relation to population density and pasture availability'

Viggers & Hearn (2005) frequently referred to both farms and reserves in the plural, despite the fact that they studied only one farm site. They stated 'Although replication at the site- or land-use level was not possible because of logistical and resource limitations, we selected sites that not only covered a range of land uses but different vegetation types'. This justification is invalid. Investigation of the relationship between different types of land use and kangaroo ranging behaviour required replication at the appropriate scale (in this case land-use). Such replication is essential to delineate differences in the level of an effect (land-use) between sites and site-specific characteristics. All ecologists are sympathetic to the difficulties of replicating field-based studies, and accept that managementorientated studies may introduce greater constraints on what can be undertaken. However, it is crucial that researchers interpret the results of unreplicated studies cautiously and do not extrapolate beyond the limits of their design. The results of this study have no applicability beyond the three quite different sites studied.

To classify the population density of M. giganteus on their study sites (in 2001) as high or low, Viggers & Hearn drew on a broad-scale study (Kangaroo Advisory Committee 1996) which was conducted 5 years earlier; the reliance on these data for this purpose is unjustified. Without simultaneous and site-specific density estimates, Viggers & Hearn could not assume that the observed dichotomy in density of M. giganteus between farms and reserves was a universal pattern. Instead, we would expect variation in population density within and between sites. For example, an index of kangaroo density at Tidbinbilla Nature Reserve (one of the study sites) has shown strong cyclic variation over time (Bayliss & Choquenot 2002). In rural lands, the Kangaroo Advisory Committee's 1996) estimate of kangaroo density had a coefficient of variation of 20%, reflecting spatial variation across these non-reserve areas. Furthermore, the Googong Foreshores Reserve (the second reserve study site) is in New South Wales, about 10 km east of the boundary of the ACT, so was not included in the Kangaroo Advisory Committee's 1996) survey of reserve areas. In the absence of current estimates of local population density, it is neither valid to refer to particular sites as having low or high density populations, nor possible to assess the influence of population density on home range size.

As their measure of forage availability, Viggers & Hearn recorded pasture biomass, and used this term interchangeably with resource availability. Pasture biomass is a crude estimate of forage availability in the absence of detailed floristic and phenological information. Put simply, 100 g m² of one grass species is not equivalent to 100 g m² of another grass species or that same species at another growth stage. Macropus giganteus is predominantly a grazer, with up to 98% of the diet comprising native and introduced grasses (Taylor 1983, 1984; Jarman & Phillips 1989), but is known to be more sensitive to quality than quantity of forage (Hill 1982), and protein levels in grass have been shown to influence population density (Taylor 1984). The species composition and abundance of pasture plants almost certainly differed among the study sites because the sites were subject to different management regimes (e.g. Taylor 1985), but Viggers & Hearn provided no information on this point. Crude pasture biomass is therefore unlikely to be an appropriate measure of the quality of foraging resources available.

4. 'Home ranges of M. giganteus were significantly smaller in the reserves than in farm study sites where population densities were lower. At reserve sites, home range size was limited by higher population densities and limited opportunity for dispersal across surrounding open farmland because of a lack of cover. Home range size was not affected by resource availability'

Home range estimates

Of the many methods for home range analysis, kernel density estimators, as used by Viggers & Hearn, are among the best (Seaman & Powell 1996). However, strong inferences from home range studies depend on estimating range size accurately and may also require accurate estimations of distribution of use. The data presented by Viggers & Hearn overlook key factors that influence the accuracy of kernel estimators: sample size, the choice of smoothing parameter and the representativeness of the sample locations (Worton 1995; Seaman & Powell 1996; Seaman et al. 1999).

Viggers & Hearn did not report exact sample sizes, but specified that minima of 15 and 30 locations were used for seasonal and annual analysis, respectively. The sample sizes for the seasonal analysis are clearly inadequate even if, as the authors report, incremental area analysis was used to determine acceptable minima. For example, Rooney et al. (1998) showed that small sample sizes (17 and 20) underestimated the range size of Irish mountain hares Lepus timidus hibernicus, even when incremental area analysis showed that an asymptote had been reached. A widely cited simulation study by Seaman et al. (1999) found that kernel estimators produced acceptable results only when a

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representative sample of at least 30 and preferably 50 locations was used. The choice of smoothing factor is also vital for accurate range size estimation using the kernel method (Worton 1995; Seaman & Powell 1996), and available evidence shows that least squares cross validation (LSCV; Silverman 1986) produces the most appropriate value for sample sizes > 30 (Seaman *et al.* 1999). Viggers & Hearn instead chose their smoothing factor arbitrarily, and did not specify their chosen value.

The influence of location sample sizes and smoothing on kernel-based home range estimates depends on range shape and use patterns (Seaman et al. 1999). To demonstrate how these factors influence the range size of eastern grey kangaroos, we analysed radio-tracking data (collected between August 1994 and March 1995) from four female M. giganteus in the Yan Yean Reservoir catchment (Moore et al. 2002). Range size and shape and the internal distribution of locations were typical of kangaroos at Yan Yean, and appeared similar to those of Viggers & Hearn. Home ranges for each individual were well established (n = 95-122 locations), and we assumed that fixed kernel ranges calculated using LSCV provided a good estimate of true range areas (42.9-105.1 ha). For each kangaroo we used the Resample and Monte Carlo routines in POPTOOLS (Hood 2005) to create 500 simulated data sets for sample sizes between 10 and 80 drawn without replacement from the original set of locations. For each simulation we calculated the 95% fixed kernel range size (Ranges VI, Anatrack Ltd, www.anatrack.com) and used LSCV and the reference smoothing factor for comparison. Following Seaman et al. (1999) we expressed the difference between the true range (A) and its estimate (Â) by calculating percentage relative bias: $(\hat{A} - A)/A \times 100$.

Overall, LSCV substantially underestimated range size for small samples but produced more accurate estimates as sample size increased (Fig. 1). Estimates

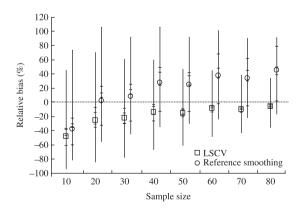


Fig. 1. The effect of sample size and smoothing factor on the accuracy and precision of range size estimates. *Y*-axis values represent the degree to which range size is over- or underestimated relative to the size of well-established (true) home ranges. Point estimates are medians of 2000 replicates (500 each from four kangaroos) and dashes are medians for each individual. Confidence limits are the 97·5 and 2·5 percentiles of the sample. Smoothing was selected using least squares cross validation (LSCV; squares) and the reference smoothing factor (circles).

using reference smoothing initially underestimated and then overestimated range size. An unbiased median estimate was produced at a sample size of 20, but the shape of the ranges in this set of simulations often approximated circles and did not model adequately the intricacies of true range outlines (data not shown). In general, when sample sizes were small, the range of plausible values was large and their distribution skewed. Results also varied substantially between LSCV and reference smoothing, demonstrating why the chosen smoothing factor should be reported. Our data suggest that LSCV provided less variable individual estimates, and while sample sizes as low as 20 occasionally gave adequate results, underestimates of around 20% were still observed when 50 locations were used.

Aside from these sources of inaccuracy, the data collected by Viggers & Hearn were unlikely to have been representative of the behaviour of individuals within a season. Viggers & Hearn collected seasonal data over only 6 days in a 2-week period; our experience is that M. giganteus rarely uses all of the range within such a short time. To demonstrate, we took 2 weeks of spring data (1 September–13 September 1994; n = 21) from one of the females used above, and compared that to her total spring data set (1 September–24 November; n = 41). Using the reference smoothing factor to standardize the comparison, range size changed from $3\cdot1$ ha (2 weeks) to $14\cdot4$ ha (all spring) for the 50% contour, and from $37\cdot6$ ha to $122\cdot3$ ha for the 95% contour.

Viggers & Hearn also failed to consider the influence of demographic classes on ranging behaviour. They did not report the age, sex or reproductive status of their study animals, other than that all females were reproductively active. However, male M. giganteus move more often and over longer distances than females (Jarman & Southwell 1986; Clarke et al. 1989, 1995; Jarman 1991, 1994), and thus tend to have much larger home ranges than females, sometimes with multiple activity centres separated by long distances (Jaremovic & Croft 1987, 1991). Females with newly emerged young-at-foot spend more time away from groups (Southwell 1984; Jarman & Southwell 1986; Jarman & Coulson 1989; Jarman 1991), and may reduce their ranges at this time (Jaremovic & Croft 1987). Thus, without knowing how many of each sex were radio-tagged at each site, or the reproductive status of females, it is impossible to gauge how representative the home range estimates may have

Furthermore, Viggers & Hearn did not consider the possible influence of the act of culling on the ranging behaviour of kangaroos. Apart from the likelihood that the disturbance would have displaced kangaroos from open habitat at their farm site, at least in the short term, the culling of every individual M. giganteus without a radio-collar (approximately 180 individuals) during the study is certain to have influenced the subsequent ranging behaviour of their study individuals (n = 5). Macropus giganteus relies on grouping as an antipredator strategy, forming larger groups when feeding in the open

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Response to Viggers & Hearn (2005) (Heathcote 1987), which allows individuals to allocate more time to foraging and less to vigilance (Jarman 1987; Colagross & Cockburn 1993; Coulson 1999). The observation by Viggers & Hearn that individuals rarely moved beyond the woodland margins of their farm site was hardly surprising, given how few were available to form groups for efficient exploitation of open habitat. Such an extensive population reduction is also likely to have disrupted the social structure within the farm population, with unpredictable consequences for ranging behaviour. *Macropus giganteus* is gregarious and forms open-membership groups of variable size (Jarman 1987; Clarke et al. 1995); the organization of these groups is loose and flux of individuals is common, but subtle matrilineal associations over long timescales are evident. Croft (2004) argued that shooting older, experienced females in the matrilines is likely to have direct consequences for the behaviour and fitness of younger orphans, as has been reported by Comer et al. (2005) for a heavily hunted population of whitetailed deer Odocoileus virginianus.

Resource availability

In addition to the issues concerning pasture biomass (point 2), Viggers & Hearn failed to take into account the influence of other resources for M. giganteus. This species has long been known to require dense vegetation for shelter from the elements during the day and for protection from predation (Caughley 1964). At a larger scale, M. giganteus avoids forest with little grass and shrub understorey, as well as heavily cleared land (Hill 1981), preferring partly cleared land with patches of dense lateral cover for shelter, together with open grassy areas for feeding (Hill 1981; McAlpine et al. 1999). The three study sites used by Viggers & Hearn apparently differed in the density and distribution of cover. Viggers & Hearn even identified the 'presence of cover' as influencing home range size of M. giganteus without measuring this variable, yet contrasted this with 'resource' (i.e. pasture) availability. In failing to recognize and measure one of the two essential resources for M. giganteus, Viggers & Hearn have reached a conclusion that is unsubstantiated.

5. 'Where suitable vegetation cover occurred on farmland (e.g. woodland remnants or scrub), M. giganteus occurred as **resident or roving small mobs**. This may be seen by farmers as a disincentive to preserve remnant vegetation as it can provide habitat for unwanted native wildlife'

Viggers & Hearn did not define the term 'roving small mob', and we cannot discern their meaning. Use of the term 'mob' also betrays confusion about relationships among the individuals they were sampling. They reported that home ranges overlapped between individuals at the high density sites, but that individuals were rarely sighted in the 'same social group', so could be considered to be independent. However, the open-

membership groups formed by *M. giganteus* (Jarman 1987) are flexible subsets of a larger, relatively stable social unit known as a mob (Kaufmann 1975). Home ranges of individuals in the same area may thus overlap extensively (Jaremovic & Croft 1987, 1991), and cannot be considered independent unless they are drawn from different mobs.

6. 'Home range attributes of M. giganteus suggest the species could be controlled by culling. However, **recolonization** occurs quickly and little is known of **dispersal**'

Viggers & Hearn presented no data to support the assertion that recolonization occurs quickly; it is unclear how they reached this conclusion. Furthermore, they confused the meaning of the term 'dispersal', using it to refer to daily movements of kangaroos within their home ranges and also to natal dispersal, which is the permanent movement made by an individual from its birth-site to a new area in which it will breed if it survives (Howard 1960; Greenwood 1980). By definition, an individual occupies a post-dispersal area that does not overlap with the area occupied before dispersal (Lidicker 1975). This confusion in the use of the term 'dispersal' results in multiple ambiguities within the text.

In *M. giganteus*, females are considered to be philopatric, while males usually undertake natal dispersal (Jarman 1991; Zenger *et al.* 2003). Contrary to the assumption made by Viggers & Hearn, dispersal events frequently involve individuals passing through suboptimal habitat (e.g. Ferreras *et al.* 2004; Selonen & Hanski 2004; Berry *et al.* 2005). Viggers & Hearn claimed that dispersal did not occur across open areas, but also stated that three individuals (of 20) moved away from the study sites. Unfortunately, they did not give any further information about these possible cases of genuine dispersal.

7. 'Synthesis and applications. Population density, presence of cover and reluctance to disperse across cleared landscapes are key factors influencing kangaroo home range size and use of adjacent farmland. Currently, little incentive exists for farmers to preserve remnant vegetation, as it may be regarded as providing habitat for unwanted or "pest" kangaroos ...'

Viggers & Hearn (2005) tackled an important and topical issue in wildlife management, and described some basic patterns of habitat use by *M. giganteus*. However, there are many serious shortcomings in this research: a lack of replication, the use of inappropriate density estimates, absence of suitable measures of resource availability, flawed home range analysis and limited understanding of the biology of the study species and of key concepts. Importantly, their data clearly do not permit them to extrapolate their conclusions beyond their three study sites, hence it is invalid for them to draw broad-scale management recommendations from their study.

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There is good evidence that management advice given in the *Journal of Applied Ecology* is indeed used by management agencies (Ormerod *et al.* 2002). Thus it is essential that management recommendations given in the journal are based on valid data and interpretation, rather than on invalid, inappropriate or unsubstantiated data and extrapolations.

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References

- Bayliss, P. & Choquenot, D. (2002) The numerical response: rates of increase and food limitation in herbivores and predators.

 Philosophical Transactions of the Royal Society, Series B, 357, 1233–1248.
- Berry, O., Tocher, M.D., Gleeson, D.M. & Sarre, S.D. (2005)
 Effect of vegetation matrix on animal dispersal: genetic evidence from a study of endangered skinks. *Conservation Biology*, 19, 855–864.
- Caughley, G. (1964) Density and dispersion of two species of kangaroo in relation to habitat. *Australian Journal of Zoology*, **12**, 238–249.
- Clarke, J.L., Jones, M.E. & Jarman, P.J. (1989) A day in the life of a kangaroo: activities and movements of eastern grey kangaroos *Macropus giganteus* at Wallaby Creek. *Kangaroos, Wallabies and Rat-Kangaroos II* (eds G. Grigg, P. Jarman & I. Hume), pp. 611–618. Surrey Beatty & Sons, New South Wales.
- Clarke, J.L., Jones, M.E. & Jarman, P.J. (1995) Diurnal and nocturnal grouping and foraging behaviours of freeranging eastern grey kangaroos. *Australian Journal of Zoology*, 43, 519–525.
- Colagross, A.M.L. & Cockburn, A. (1993) Vigilance and grouping in the eastern grey kangaroo, *Macropus giganteus*. *Australian Journal of Zoology*, **41**, 325–334.
- Comer, C.E., Kilgo, J.C., D'Angelo, G.J., Glenn, T.C. & Miller, K.V. (2005) Fine-scale genetic structure and social organization in female white-tailed deer. *Journal of Wildlife Management*, 69, 332–344.
- Coulson, G. (1999) Monospecific and heterospecific grouping and feeding behavior in grey kangaroos and red-necked wallabies. *Journal of Mammalogy*, **80**, 270–282.
- Croft, D.B. (2004) Kangaroo management: individuals and communities. Australian Mammalogy, 26, 101–108.
- Ferreras, P., Delibes, M., Palomares, F., Fedriani, J.M., Calzada, J. & Revilla, E. (2004) Proximate and ultimate causes of dispersal in the Iberian lynx *Lynx pardinus*. *Behavioral Ecology*, 15, 31–40.
- Greenwood, P.J. (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.
- Heathcote, C.F. (1987) Grouping of eastern grey kangaroos in open habitat. *Australian Wildlife Research*, **14**, 343–348.
- Hill, G.J.E. (1981) A study of habitat preferences in the grey kangaroo. *Australian Wildlife Research*, **8**, 245–254.
- Hill, G.J.E. (1982) Seasonal movement patterns of the eastern grey kangaroo in southern Queensland. *Australian Wildlife Research*, **9**, 373–387.
- Hood, G.M. (2005) *POPTOOLS*, version 2·6·7. Available at: http://www.cse.csiro.au/poptools (accessed 12 June 2006).

- Howard, W.E. (1960) Innate and environmental dispersal of individual vertebrates. *American Midland Naturalist*, **63**, 152–161.
- Jaremovic, R.V. & Croft, D.B. (1987) Comparison of techniques to determine eastern gray kangaroo home range. *Journal of Wildlife Management*, **51**, 921–930.
- Jaremovic, R.V. & Croft, D.B. (1991) Social organisation of the eastern grey kangaroo (Macropodidae, Marsupialia) in southeastern New South Wales. I. Groups and group home ranges. *Mammalia*, **55**, 169–185.
- Jarman, P.J. (1987) Group size and activity in eastern grey kangaroos. *Animal Behaviour*, 35, 1044–1050.
- Jarman, P.J. (1991) Social behaviour and organisation in the Macropodoidea. Advances in the Study of Behaviour, 20, 1– 50.
- Jarman, P.J. (1994) Individual behaviour and social organisation of kangaroos. Animal Societies: Individuals, Interactions and Organisations (eds P. Jarman & A. Rossiter), pp. 70–83. Kyoto University, Kyoto, Japan.
- Jarman, P.J. & Coulson, G.M. (1989) Dynamics and adaptiveness of grouping in macropods. *Kangaroos, Wallabies and Rat-Kangaroos II* (eds G. Grigg, P. Jarman & I. Hume), pp. 527–547. Surrey Beatty & Sons, New South Wales.
- Jarman, P.J. & Phillips, C.M. (1989) Diets in a community of macropod species. Kangaroos, Wallabies and Rat-Kangaroos (eds G. Grigg, P. Jarman & I. Hume), pp. 143– 149. Surrey Beatty & Sons, New South Wales.
- Jarman, P.J. & Southwell, C.J. (1986) Grouping associations and reproductive strategies in eastern grey kangaroos. *Ecological Aspects of Social Evolution* (eds D. Rubenstein & R. Wrangham), pp. 399–428. Princeton University Press, Princeton, USA.
- Kangaroo Advisory Committee (1996) Living with Kangaroos in the ACT: Rural Lands. First Report to the Minister for the Environment, Land and Planning, Canberra, Australia.
- Kaufmann, J.H. (1975) Field observations of the social behaviour of the eastern grey kangaroo, *Macropus giganteus*. Animal Behaviour, 23, 214–221.
- Lidicker, W.Z. (1975) The role of dispersal in the demography of small mammals. *Small Mammals: Their Productivity and Population Dynamics* (eds F.B. Golley, K. Petrusewicz, K. & L. Ryszkowski), pp. 103–128. Cambridge University Press, Cambridge, UK.
- McAlpine, C.A., Grigg, G.C., Mott, J.J. & Sharma, P. (1999) Influence of landscape structure on kangaroo abundance in a disturbed semi-arid woodland of Queensland. *Rangeland Journal*, **21**, 104–134.
- Moore, B.D., Coulson, G. & Way, S. (2002) Habitat selection by adult female eastern grey kangaroos. *Wildlife Research*, **29**, 439–445.
- Ormerod, S.J., Barlow, N.D., Marshall, E.J.P. & Kerby, G. (2002) The uptake of applied ecology. *Journal of Applied Ecology*, **39**, 1–7.
- Rooney, S.M., Wolfe, A. & Hayden, T.J. (1998) Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. *Mammal Review*, **28**, 89–98.
- Seaman, D.E., Millspaugh, J.J., Kernohan, B.J., Brundige, G.C., Raedeke, K.J. & Gitzen, R.A. (1999) Effects of sample size on kernel home range estimates. *Journal of Wildlife Management*, 63, 739–747.
- Seaman, D.E. & Powell, R.A. (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77, 2075–2085.
- Selonen, V. & Hanski, I.K. (2004) Young flying squirrels (*Pteromys volans*) dispersing in fragmented forests. *Behavioral Ecology*, 15, 564–571.
- Silverman, B.W. (1986) Density Estimation for Statistics and Data Analysis. Chapman & Hall, London.

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- Southwell, C.J. (1984) Variability in grouping in eastern grey kangaroo, *Macropus giganteus*. 2. Dynamics of group formation. *Australian Wildlife Research*, 11, 437–449.
- Taylor, R.J. (1983) The diet of the eastern grey kangaroo and wallaroo in areas of improved and native pasture in the New-England tablelands. *Australian Wildlife Research*, **10**, 203–211.
- Taylor, R.J. (1984) Foraging in the eastern grey kangaroo and the wallaroo. *Journal of Animal Ecology*, **53**, 65–74.
- Taylor, R.J. (1985) Effects of pasture improvement on the nutrition of eastern grey kangaroos and wallaroos. *Journal of Applied Ecology*, **22**, 717–725.
- Viggers, K.L. & Hearn, J.P. (2005) The kangaroo conundrum:

- home range studies and implications for land management. *Journal of Applied Ecology*, **42**, 99–107.
- Worton, B.J. (1995) Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management*, **59**, 794–800.
- Zenger, K.R., Eldridge, M.D.B. & Cooper, D.W. (2003)

 Intraspecific variation, sex-biased dispersal and phylogeny of the eastern grey kangaroo (*Macropus giganteus*). *Heredity*, **91**, 153–162.

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