

How Might Terrestrial Arthropod Assemblages Have Changed After the Dramatic Decline of Critical Weight Range (CWR) Mammals in Australia? Using Reintroductions at Scotia Sanctuary as a Model for Pre-European Ecosystems

HELOISE GIBB

Department of Zoology, La Trobe University, Melbourne, Victoria 3086, Australia
h.gibb@latrobe.edu.au

Published on 28 August at <http://escholarship.library.usyd.edu.au/journals/index.php/LIN>

Gibb, H. (2012). How might terrestrial arthropod assemblages have changed after the dramatic decline of Critical Weight Range (CWR) mammals in Australia? Using reintroductions at Scotia Sanctuary as a model for pre-European ecosystems. *Proceedings of the Linnean Society of New South Wales* **134**, A19-A26.

In Australia, populations of mammals within the critical weight range (CWR) of 35 to 5500 g have been severely affected by European settlement, with twenty-two species having become extinct over the past 200 years. Many highly threatened CWR mammals, such as bilbies, bandicoots and numbats, are insectivorous or omnivorous, and invertebrates comprise a significant portion of their diet. Additionally, such mammals cause significant disturbance to arthropod habitats through burrowing and engage in a range of other interactions with arthropods, including mutualisms, parasitism and competition. The loss of this trophic level is thus likely to have had considerable impacts on arthropods. Here, I consider the potential effects of the dramatic decline of native omnivores on the abundance, diversity, composition, morphology and functional roles performed by arthropods. I also discuss reintroductions such as that at Scotia Sanctuary in western NSW and other conservation sites as a model for understanding the pre-European state of arthropod-CWR mammal interactions.

Manuscript received 19 October 2011, accepted for publication 9 January 2012.

KEYWORDS: ants, arthropod assemblage, critical weight range mammal, insectivore, interactions, omnivore, predation, pre-European Australia, reintroduction, termites

INTRODUCTION

Biological invasions have been associated with extinctions world-wide, particularly on islands (Diamond 1989, Steadman 1995, Blackburn et al. 2004). On the island continent of Australia, the invasion of European humans and their associated fauna is thought to be responsible for the extinction of twenty-two mammal species within the critical weight range (CWR) of 35 to 5500 g (Burbidge and McKenzie 1989, Dickman 1996, Johnson et al. 2007, McKenzie et al. 2007). In addition, numerous previously common and widespread native mammals are now critically endangered and can be considered 'ecologically extinct' in much of Australia, i.e., they are too rare to continue to play important ecological roles (Estes et al. 1989).

CWR mammals had direct and indirect relationships with a range of other organisms. Insects and other arthropods are the key contributors to animal biodiversity worldwide (Hickman et al. 2008) and engage in a range of interactions with mammals. Although they are poorly studied, interactions between arthropods and mammals are diverse, including mutualisms, parasitism, predation, competition, necrophagy, commensalism and amensalism (Fig. 1). Some of these interactions may be species specific, whilst others are more generalised or diffuse. The ecological extinction of CWR mammals may have had significant consequences for Australian terrestrial arthropods.

Efforts to conserve CWR mammals have focused on reintroduction into large-scale predator-proof enclosures. Such sites present an opportunity

EFFECTS OF CWR MAMMAL DECLINE ON ARTHROPODS

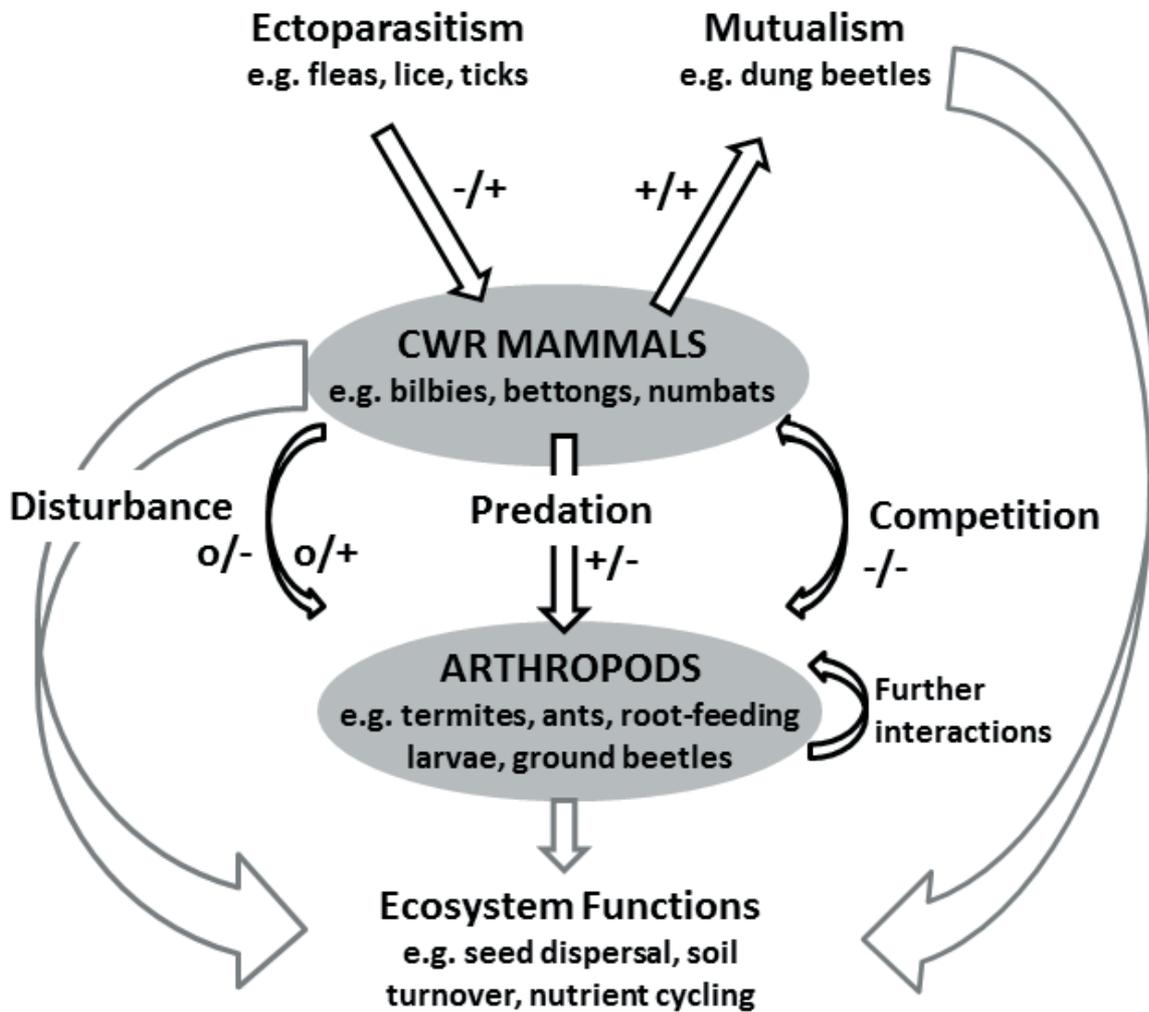


Figure 1: Interactions between critical weight range mammals and arthropods. The effects of interactions for each partner is shown the arrows (e.g. +/-). The first symbol reflects the effect of the interaction on CWR mammals, the second its effect on the arthropods involved. Arrows for biotic interactions are shown with black outlines; those for functions are shown with grey outlines. Effects on ecosystem functions are also shown. These functions may in turn benefit CWR mammals and arthropods (not shown).

to investigate the structure of Australian ecosystems in a pre-European state, where CWR mammals were common and introduced predators and herbivores rare. Scotia Sanctuary, situated in the semi-arid mallee biome in western NSW and owned by the Australian Wildlife Conservancy, presents such an opportunity. The site supports significant reintroduced populations of the bridled nail-tail wallaby (*Onychogalea fraenata*), the greater bilby (*Macrotis lagotis*), the burrowing bettong (*Bettongia lesueur*), the brush-tailed bettong (*Bettongia penicillata*), the numbat (*Myrmecobius fasciatus*) and the greater stick-nest

rat (*Leporillus conditor*) in two 4 000 ha predator-proof enclosures. Here, I consider how arthropods may have been affected by the ecological extinctions of CWR mammals and discuss Scotia Sanctuary as a model for understanding pre-European Australia. This question is not only of academic interest, but also has implications for target states for reintroduction sites.

PREDATION

Predatory impacts of some CWR mammals on arthropods may have been significant where

population densities were high. Of the six species reintroduced at Scotia Sanctuary, numbats feed only on social insects, while arthropods make up a significant proportion of the diet of the bilby (Calaby 1960, Gibson 2001, Southgate and Carthew 2006, Bice and Moseby 2008, Navnith et al. 2009). Just 5-10% of the diet of the brush-tailed and burrowing bettong is arthropods (Robley et al. 2001, Bice and Moseby 2008, Zosky et al. 2010), while the greater stick-nest rat and bridled nail-tail wallaby can be considered herbivores (Dawson et al. 1992, Ryan et al. 2003). The numbat specialises on termites (Isoptera), but may also consume ants (Hymenoptera: Formicidae), probably accidentally (Calaby 1960). The frequency of occurrence of arthropods in greater bilby scats across a range of locations is consistently >90%, with arthropods making up 30-56% of non-soil scat volume (Gibson 2001, Southgate and Carthew 2006, Bice and Moseby 2008, Navnith et al. 2009). Given the greater digestibility of arthropods relative to plant material, it is likely that their representation as a component of scat volume is an underestimate. Termites make up the greatest proportion of scat volume, followed by ants, beetles (Coleoptera), grasshoppers and crickets (Orthoptera). The remains of larvae from a range of holometabolous insects are common in scats, even though it is commonly only mouthparts that survive digestion. Cockroaches (Blattodea), flies (Diptera), moths (Lepidoptera), lace wings and ant lions (Neuroptera), spiders (Araneae), mites (Acarina), scorpions (Scorpionida) and centipedes (Chilopoda) constitute a smaller proportion of the diet (Gibson 2001, Southgate and Carthew 2006, Bice and Moseby 2008, Navnith et al. 2009, Silvey 2011). The abundance of these groups in the diet of the bilby roughly appears to reflect their relative abundances in typical arid or semi-arid zone arthropod assemblages (e.g., Kwok et al. 2010), suggesting a lack of specificity. This is also reflected by seasonal changes in arthropod composition that allow bilbies to respond to outbreaks of taxa such as locusts (Gibson 2001, Bice and Moseby 2008, Navnith et al. 2009). Arthropods in the diet of the two bettong species similarly suggest low specificity. In addition to direct predation on arthropods, bilbies have been reported to consume the seed caches of seed harvester ants (Gibson et al. 2002), which could be considered as cleptoparasitism of ants, although it is probably also associated with predation.

In the absence of ecologically equivalent species, arthropod biomass, particularly that of termites, may have increased in areas in which CWR mammals with insectivorous or omnivorous diets have become extinct or ecologically extinct. There may also have

been significant turnover in species composition and trophic structure due to differing vulnerability to predation or disturbance. Previous studies suggest that invertebrates are smaller and less abundant in the presence of predatory vertebrates, even in complex systems with intra-guild predation (Spiller and Schoener 1990, Dial and Roughgarden 1995). In addition, the exclusion of vertebrate insectivores has been shown to affect above- and below-ground insect-driven ecosystem processes, such as herbivory and nutrient cycling (Spiller and Schoener 1990, Dial and Roughgarden 1995, Dunham 2008). However, the impact on arthropod diversity and abundance in Australian ecosystems depends on a number of poorly known factors. These include the pre-European population densities of CWR mammals, which are reported to have been high across much of Australia (discussed in Jones 1924, Finlayson 1958, Seebeck and Rose 1989), the metabolic rates of CWR mammals, examined in a few studies (e.g. Gibson et al. 2002, Cooper et al. 2003), and the response of arthropod populations to predation and other interactions with CWR mammals, which remains unknown.

It is likely that there is some redundancy in the generalised predatory role: predation pressure from CWR mammals may have been replaced by that from invaders such as cats and foxes. The diets of these invaders generally include at least 5% arthropod prey and sometimes up to 83% in bogong moth-rich alpine areas (Paltridge 2002, Green 2003, Claridge et al. 2010, Glen et al. 2011). Many non-threatened native species, such as lizards, consume arthropods, but the behaviour involved is often different from that of CWR mammals. Most lizards are small and diurnal and not capable of the significant foraging excavations (up to 40 cm deep, pers. obs.) created by species such as the bilby and burrowing bettong. There are exceptions to this, such as insectivorous skinks of the genus *Lerista*, and goannas (Varanidae), which burrow extensively for prey (Cogger 2000). Despite some functional redundancy, it is likely that the contemporary insectivorous assemblage targets a different component of the arthropod fauna from that consumed by pre-European insectivore assemblages. Arthropod assemblages may therefore have changed significantly since the loss of predators such as the bilby and numbat.

Effects of the loss of predation by CWR mammals on arthropod assemblages are likely to be complex and not limited to the loss of individuals through consumption. Predators have previously been shown to alter the behaviour of their arthropod prey (Venzon et al. 2000, Logan et al. 2007) and therefore the potential of prey to reproduce. In addition, predation

EFFECTS OF CWR MAMMAL DECLINE ON ARTHROPODS

by CWR mammals on predatory arthropods such as scorpions may have cascading effects on arthropod assemblages (Silvey 2011).

DISTURBANCE

The burrowing activity of mammals such as the greater bilby, burrowing bettong and numbat is extensive (Eldridge and James 2009, James and Eldridge 2010) and likely to affect a range of non-prey arthropods. These interactions are either commensal or amensal, depending on whether the response of arthropods to the increased abundance of foraging pits and burrows in the presence of CWR mammals is positive or negative, respectively. Some arthropod taxa, such as opportunistic ants of the genus *Rhytidoponera* (Andersen 1990, Hoffmann and Andersen 2003), are likely to benefit directly from the increased disturbance of their habitats. Other taxa will benefit indirectly, for example improved nutrient cycling in the presence of burrowing mammals leads increased germination success of some plants (James and Eldridge 2007, 2010), which may benefit herbivorous arthropods. In addition, bilby and bettong warrens provide retreats for some arthropods that are not favoured by the warrens of introduced rabbits (Read et al. 2008).

However, the effects of changes in habitat structure due to frequent burrowing may be negative for some arthropod species. For example, gallery structures may be destroyed by foraging pits. Small-scale structural changes to habitats have previously been shown to alter the foraging success of ground-dwelling arthropod species (e.g. Sarty et al. 2006, Parr et al. 2007, Gibb and Parr 2010) and high densities of foraging pits may have a similar effect. Changes to the soil surface may alter the mobility of species (Loiterton and Magrath 1996) and foraging pits and burrows in loose soil have the additional potential to act as natural pitfall traps, ensnaring flightless foraging insects such as ants.

PARASITISM

A range of ectoparasitic arthropods, including fleas (Siphonaptera), lice (Phthiraptera), ticks and mites (Acarina) and louse and bot flies (Diptera) are associated with native Australian mammals. These taxa are commonly associated with disease transmission so may have important consequences for the health of native mammals (Ladds 2009). Several ectoparasites have been reported from the CWR

mammal species present at Scotia Sanctuary. Four different native flea species are reported from the burrowing bettong and two of these, *Echnidophaga aranka* and *E. macronychia* are known only from a few examples from this host (Dunnet and Mardon 1974), so could be at risk of co-extinction. Use of marsupial hosts by the Acarina, Phthiraptera and Diptera appears less specialised, so co-extinction risk may be low (Ladds 2009).

COMPETITION

Competitive interactions between CWR mammals and arthropods may also be important, although they would likely have been diffuse, with the effect of reducing populations. Herbivorous mammals alter the success of herbivorous arthropods (e.g. Rambo and Faeth 1999, Suominen et al. 2003, Den Herder et al. 2004, Barton et al. 2011). However, herbivorous CWR mammals have commonly been replaced with introduced herbivores, such as the rabbit, *Oryctolagus cuniculus*, and a range of ungulates, so it is unclear whether effects on arthropod herbivores would differ. Competition for other plant resources, such as seeds, may have been important, evidenced by bilby usurpation of harvester ant seed caches (Gibson et al. 2002). However, the ability of more successful groups, such as the native rodents, to expand to absorb additional seed availability (Letnic et al. 2005) suggest that effects of CWR mammals on seed predation by arthropods may be limited. Many arthropods feed on invertebrate prey, presenting another avenue for competitive interactions, but little is known of the effects of this interaction on predatory arthropods.

MUTUALISMS AND NUTRIENT RECYCLING

Arthropods perform a number of functions that benefit CWR mammals, including necrophagy and coprophagy. Necrophagous arthropods such as blowflies (Muscidae), fleshflies (Sarcophagidae), hide beetles (Trogidae) and hister beetles (Histeridae) have limited specificity, consuming a range of vertebrate carcasses (Gennard 2007). Carcass availability has likely increased since European colonisation of Australia, due to large numbers of road kills (Taylor and Goldingay 2004, Kloecker et al. 2006) and culling of native and introduced species, thus boosting populations of these taxa. However, no evidence exists to indicate that changes in the availability of carcasses of CWR mammals affect necrophagous arthropods.

Mutualisms between dung beetles and mammals can be critical in reducing parasite loads, recycling nutrients, and allowing the persistence of dung beetles (Loreau 1995, Slade et al. 2007, Nichols 2008). Australian dung beetles are commonly specific to marsupial dung, but it is unclear how species-specific they might be and therefore how much they may have been affected by the ecological extinction of CWR mammals throughout much of Australia (see Coggan, next article).

BROADER IMPACTS

Interactions between CWR mammals and arthropods have the potential to influence more than just the diversity and abundance of arthropods. Arthropods play a range of important functional roles, for example, acting as seed dispersers, enhancing soil structure and recycling nutrients (Folgarait 1998, Mayer 2008, Nichols 2008). How the loss of CWR mammals affects these functions is unclear, but preliminary data suggests it may have had significant consequences for arthropod-driven functions. For example, rates of removal of seeds, mealworms and bird droppings by ants all appear slower in sites without CWR mammals (Gibb unpublished). At larger scales, CWR mammals may alter litter loads (James et al. 2009, 2010), potentially leading to impacts on nutrient cycling that would further alter biotic assemblages. The lack of baseline data for the pre-European state of Australia inhibits our ability to evaluate these changes.

SCOTIA SANCTUARY AS A MODEL FOR PRE-EUROPEAN ARTHROPOD ASSEMBLAGES

Although we lack knowledge of the pre-European state of epigeic arthropod assemblages, reintroductions such as those behind two 4 000 ha predator-proof fences at Scotia Sanctuary, western NSW, present an opportunity to test the impact of CWR mammals on other species. Unfortunately, baseline data on arthropod assemblages does not exist for Scotia Sanctuary or any of the other Australian semi-natural reintroduction sites. While it is possible to compare inside and outside the exclusion fences, such studies are always limited by the similarity of sites. Spatial autocorrelations in the environment and biotic assemblages mean that measured differences inside and outside a single fence must be considered very cautiously, with an understanding of the limitations of pseudoreplication (Hulbert 1984). A

thorough research program should work at multiple scales and experimentally eliminate the multitude of potentially confounding factors. One way in which to do this is to use replicated experimental enclosures within a reintroduction site to allow comparison of replicated sites with and without CWR mammals. Although this frees the observer from confounding factors, the scale at which such enclosures are usually constructed may limit our ability to observe changes in more mobile species. Fortunately, multiple large-scale reintroduction sites are in operation around Australia and can complement a smaller-scale approach. While few arthropod species are shared between these sites, functional approaches yield comparable results. For example, the morphologies of arthropods or the rates at which arthropod-driven functions are performed can be compared. Behavioural studies exploring the mechanisms behind observed effects are also critical in understanding how impacts are achieved.

The removal of introduced predators and the European rabbit is likely to affect populations of other vertebrates and CWR mammal-free enclosures may also be free of other arthropod predators, such as the echidna, *Tachyglossus aculeatus*. This necessitates careful interpretation of results. In addition, it is unclear whether densities of CWR mammals at Scotia Sanctuary, where mammals are protected by predator-proof fences, are similar to those in pre-European arid Australia. However, some of the limitations in terms of densities at this site can be addressed by comparing the two stages, which differ in mammal densities. Difference in depletion rates of arthropods from sites with differing CWR mammal densities could inform management by allowing us to determine sustainable carrying capacities for reintroduction sites. Key groups to investigate are the termites and ants, which constitute a large proportion of numbat and bilby prey and are functionally important (Calaby 1960, Folgarait 1998, Gibson 2001, Evans et al. 2011). Much of the burrowing activity is likely to be directed at extracting larvae, particularly the root feeding cockchafers (Coleoptera: Scarabaeidae: Melolonthinae), so this group should also be central to research efforts. In addition, an understanding of interactions with mutualists, such as dung beetles, may be critical to maximising reintroduction success (Coggan, next article).

Given the dramatic changes in CWR mammal assemblages since European colonisation of Australia, it is appalling that we know so little of the broader consequences for the Australian biota. Work on CWR mammal interactions with arthropod assemblages will fill a critical gap in our knowledge and improve our capacity to restore Australian ecosystems.

EFFECTS OF CWR MAMMAL DECLINE ON ARTHROPODS

REFERENCES

- Andersen, A.N. (1990) The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia*, **16**, 347-357.
- Barton, P.S., Manning, A.D., Gibb, H., Wood, J.T., Lindenmayer, D.B. and Cunningham, S.A. (2011) Experimental reduction of native vertebrate grazing and addition of logs benefit beetle diversity at multiple scales. *Journal of Animal Ecology* **48**, 943-951.
- Bice, J. and Moseby, K.E. (2008) Diet of the re-introduced greater bilby (*Macrotis lagotis*: Peramelidae) and burrowing bettong (*Bettongia lesueur*: Potoroidae) in the Arid Recovery Reserve, northern South Australia. *Australian Mammalogy*, **30**, 1-12.
- Burbidge, A.A., McKenzie, N.L. (1989) Patterns in the modern decline of western Australia's vertebrate fauna: Causes and conservation implications. *Proceedings of the Royal Society B: Biological Sciences* **270**: 1801-1808
- Calaby JH (1960) Observations on the banded ant-eater *Myrmecobius f. fasciatus* Waterhouse (Marsupialia), with particular reference to its food habits. *Proceedings of the Zoological Society of London* **135**:183-207.
- Claridge, A.W., Mills, D.J. and Barry, S.C. (2010) Prevalence of threatened native species in canid scats from coastal and near-coastal landscapes in south-eastern Australia. *Australian Mammalogy*, **32**, 117-126.
- Cogger, H. (2000) *Reptiles and Amphibians of Australia*. Reed New Holland, Terry Hills, NSW, Australia.
- Cooper, C.E., Withers, P.C. and Bradshaw, S.D. (2003) Field metabolic rate and water turnover of the numbat (*Myrmecobius fasciatus*). *Journal of Comparative Physiology B*, **173**, 687-693.
- Dawson, T.J., Tierney, P.J. and Ellis, B.A. (1992) The diet of the Bridled nailtail wallaby (*Onychogalea fraenata*). I Site and seasonal influences and dietary overlap with the black striped wallaby (*Macropus dorsalis*) and domestic cattle. *Wildlife Research*, **19**, 65-77.
- Den Herder, M., Virtanen, R. and Roininen, H. (2004) Effects of reindeer browsing on tundra willow and its associated insect herbivores. *Journal of Applied Ecology*, **41**, 870-879.
- Dial, R. and Roughgarden, J. (1995) Experimental removal of insectivores from rain forest canopy: direct and indirect effects. *Ecology* **76**: 1821-1834
- Diamond, J.M. (1989) The present, past and future of human-caused extinctions. *Philosophical Transactions - Royal Society of London, B* **325**, 469-477.
- Dickman, C.R. (1996) Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology* **2**: 185-195
- Dunham, A.E. (2008) Above and below ground impacts of terrestrial mammals and birds in a tropical forest. *Oikos* **117**: 571-579
- Dunnet, G.M. and Mardon, D.K. (1974) A monograph of Australian fleas. *Australian Journal of Zoology*, **30**, 1-274.
- Eldridge, D.J. and James, A.I. (2009) Soil disturbance by native animals plays a critical role in maintaining healthy Australian landscapes. *Ecological Management and Restoration*, **10**, S27-S34.
- Estes, J.A., Duggans, D.O. and Rathbun, G.B. (1989) The ecology of extinctions in kelp forest communities. *Conservation Biology*, **3**, 252-264.
- Evans, T.A., Dawes, T.Z., Ward, P.R. and Lo, N. (2011) Ants and termites increase crop yield in a dry climate. *Nature Communications*, **2**, art. no. 262.
- Finlayson, H.H. (1958). On Central Australian mammals (with notice of related species from adjacent tracts) Part III, the Potoroinae. *Records of the South Australian Museum* **3**: 235-302
- Folgarait, P.J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, **7**, 1221-1244.
- Gennard, D.E. (2007) *Forensic Entomology: An Introduction*. John Wiley and Sons, Chichester, United Kingdom.
- Gibb, H. and Parr, C.L. (2010) How does habitat complexity affect ant foraging success? A test of functional responses on three continents. *Oecologia*, **164**, 1061-1073.
- Gibson, L.A. (2001) Seasonal changes in the diet, food availability and food preference of the greater bilby (*Macrotis lagotis*) in south-western Queensland. *Wildlife Research* **28**: 121-134
- Gibson, L.A., Hume, I.D. and McRae, P.D. (2002) Ecophysiology and nutritional niche of the bilby (*Macrotis lagotis*), an omnivorous marsupial from inland Australia: a review. *Comparative Biochemistry and Physiology*, **133**, 843-847.
- Glen, A.S., Pennay, M., Dickman, C.R., Wintle, B.A. and Firestone, K.B. (2011) Diets of sympatric native and introduced carnivores in the Barrington Tops, eastern Australia. *Austral Ecology*, **36**, 290-296.
- Green, K. (2003) Altitudinal and temporal differences in the food of foxes (*Vulpes vulpes*) at alpine and subalpine altitudes in the Snowy Mountains. *Wildlife Research*, **30**, 245-253.
- Hickman, C.P., Roberts, L.S., Keen, S.L., Larson, A. and Eisenhour, D.J. (2008) *Animal Diversity*. McGraw Hill, USA.
- Hoffmann, B.D. and Andersen, A.N. (2003) Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* **28**, 444-464.
- Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187-211.
- James, A.I. and Eldridge, D.J. (2007) Reintroduction of fossorial native mammals and potential impacts

- on ecosystem processes in an Australian desert landscape. *Biological Conservation*, **138**, 351-359.
- James, A.I., Eldridge, D.J. and Hill, B.M. (2009) Foraging animals create fertile patches in an Australian desert shrubland. *Ecography*, **32**, 723-732.
- James, A.I., Eldridge, D.J. and Moseby, K.E. (2010) Foraging pits, litter and plant germination in an arid shrubland. *Journal of Arid Environments*, **74**, 516-520.
- Johnson, C.N., Isaac, J.L., Fisher, D.O. (2007) Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of the Royal Society B*, **274**, 341-346.
- Jones, F. Wood (1924). *The Mammals of South Australia*. Part II Government Printer, Adelaide pp. 133-270
- Kloecker, U., Croft, D.B. and Ramp, D. (2006) Frequency and causes of kangaroo-vehicle collisions on an Australian outback highway. *Wildlife Research*, **33**, 5-15.
- Kwok, A.B.C., Eldridge, D.J. and Oliver, I. (2010) Do landscape health indices reflect arthropod biodiversity status. *Austral Ecology*, **36**, 800-813.
- Ladds, P.W. (2009) *Pathology of Australian Native Wildlife*. CSIRO Publishing, Collingwood, Victoria, Australia.
- Letnic, M., Tamayo, B. and Dickman, C.R. (2005) The responses of mammals to La Niña (El Niño Southern Oscillation)-associated rainfall, predation, and wildfire in central Australia. *Journal of Mammalogy*, **86**, 689-703.
- Logan, J.D., Wolesensky, W. and Joern, A. (2007) Insect development under predation risk, variable temperature, and variable food quality. *Mathematical Biosciences and Engineering*, **4**, 47-65.
- Loiterton, S.J. and Magrath, R.D. (1996) Substrate type affects partial prey consumption by larvae of the antlion *Myrmeleon acer* (Neuroptera: Myrmeleontidae). *Australian Journal of Zoology*, **44**, 589-597.
- Loreau, M. (1995) Consumers as maximizers of matter and energy flow in ecosystems. *American Naturalist*, **145**, 22-42.
- Mayer, P.M. (2008) Ecosystem and decomposer effects on litter dynamics along an old field to old-growth forest successional gradient. *Acta Oecologia*, **33**, 222-230.
- McKenzie, N.L., Burbidge, A.A., Baynes, A., Brereton, R.N., Dickman, C.R., Gordon, G., Gibson, L.A., Menkhorst, P.W., Robinson, A.C., Williams, M.R., Woinarski, J.C.Z. (2007) Analysis of factors implicated in the recent decline of Australia's mammal fauna. *Journal of Biogeography* **34**: 597-611
- Navnith, M., Finlayson, G.R., Crowther, M.S. and Dickman, C.R. (2009) The diet of the re-introduced greater bilby (*Macrotis lagotis*) in the mallee woodlands of western New South Wales. *Australian Zoologist*, **53**, 90-95.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcuita, S. and Favila, M.E. (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, **141**, 1461-1474.
- Paltridge, R. (2002) The diet of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research*, **29**, 389-403.
- Parr, C.L., Andersen, A.N., Chastagnol, C. and Duffaud, C. (2007) Savanna fires increase rates and distances of seed dispersal by ants. *Oecologia*, **151**, 33-41.
- Rambo, J.L. and Faeth, S.H. (1999) Effect of vertebrate grazing on plant and insect community structure. *Conservation Biology*, **13**, 1047-1054.
- Read, J.L., Carter, J., Moseby, K.M. and Greenville, A. (2008) Ecological roles of rabbit, bettong and bilby warrens in arid Australia. *Journal of Arid Environments*, **72**, 2124-2130.
- Robley, A.J., Short, J. and Bradley, S. (2001) Dietary overlap between the burrowing bettong (*Bettongia lesueur*) and the European rabbit (*Oryctolagus cuniculus*) in semi-arid coastal Western Australia. *Wildlife Research*, **28**, 341-349.
- Ryan, S.A., Moseby, K.E. and Paton, D.C. (2003) Comparative foraging preferences of the greater stick-nest rat (*Leporillus conditor*) and the European rabbit (*Oryctolagus cuniculus*): Implications for regeneration of arid lands. *Australian Mammalogy*, **25**, 135-146.
- Sarty, M., Abbott, K.L. and Lester, P.J. (2006) Habitat complexity facilitates coexistence in a tropical ant community. *Oecologia*, **149**, 465-473.
- Seebeck, J.H. AND Rose, R.W., (1989) Potoroidae. Pp.716-739 in *Fauna of Australia. Volume 1B. Mammalia* ed by D.W. Walton and B.J. Richardson. Australian Government Publishing Service: Canberra, Australia.
- Silvey, C.J. (2011) *Threatened native omnivores affect ground dwelling arachnid assemblages: Mesopredator release and implications for intraguild predation*. Honours thesis, La Trobe University, Melbourne, Australia.
- Slade, E.M., Mann, D.J., Villanueva, J.F. and Lewis, O.T. (2007) Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology*, **76**, 1094-1104.
- Southgate, R. and Carthew, S.M. (2006) Diet of the bilby (*Macrotis lagotis*) in relation to substrate, fire and rainfall characteristics in the Tanami Desert. *Wildlife Research*, **33**, 507-519.
- Spiller, D.A. and Schoener, T.W. (1990) A terrestrial field experiment showing the impact of eliminating top predators on foliage damage. *Nature* **347**: 469-472.
- Steadman, D.W. (1995) Prehistoric extinction of pacific island birds – biodiversity meets zooarchaeology. *Science* **267**, 1123.
- Suominen, O., Niemela, J., Martikainen, P., Niemela, P. and Kojola, I. (2003) Impact of reindeer grazing on ground-dwelling Carabidae and Curculionidae assemblages in Lapland. *Ecography*, **26**, 503-513.

EFFECTS OF CWR MAMMAL DECLINE ON ARTHROPODS

- Taylor, B.D. and Goldingay, R.L. (2004) Wildlife road-kills on three major roads in north-eastern New South Wales. *Wildlife Research*, **31**, 83-91.
- Venzon, M., Janssen, A., Pallini, A. and Sabelis, M.W. (2000) Diet of a polyphagous arthropod predator affects refuge seeking of its thrips prey. *Animal Behaviour*, **60**, 369-375.
- Zosky, K., Bryant, K., Calver, M. and Wayne, A. (2010) Do preservation methods affect the identification of dietary components from faecal samples? A case study using a mycophagous marsupial. *Australian Mammalogy*, **32**, 173.