Are Native Dung Beetle Species Following Mammals in the Critical Weight Range towards Extinction?

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Published on 28 August 2012 at http://escholarship.library.usyd.edu.au/journals/index.php/LIN

Coggan, N. (2012). Are native dung beetle species following mammals in the critical weight range towards extinction? *Proceedings of the Linnean Society of New South Wales* **134**, A5-A9.

Australian native mammal species within the 35 g - 5500 g critical weight range (CWR) have been declining rapidly over the last two centuries, with eighteen species becoming extinct. Inhabitants of arid and semi-arid zones are among those most at risk of extinction. Mammal declines threaten the efficiency of invertebrate-driven ecosystem processes such as nutrient recycling by artificially increasing the realised niche overlap for dung resources used by invertebrates involved with dung decomposition. Native dung beetles are one of the main taxa involved in dung decomposition, an ecosystem function necessary for nutrient recycling. Many native dung beetle species strongly prefer marsupial dung, due to their co-evolutionary history. Threatened populations of CWR species can be protected through species reintroductions. However, the long term absence of mainland CWR mammals may have compromised the effectiveness of dung decomposition as an ecosystem function by reducing dung availability. The compatibility of current coprophage assemblages with 'novel' inputs from reintroduced CWR species should therefore be questioned. Assessing the potential for persistence and/or relocation of coprophages in mainland habitats associated with CWR species will be an important part of restoring and monitoring habitats used for species recovery.

Manuscript received 18 October 2011, accepted for publication 29 February 2012.

KEYWORDS: critical weight range, conservation, decomposition, dung beetles, ecological co-extinction, ecological function, interaction, invertebrates, reintroduction.

A large proportion of Australia's mammal species have declined over the past two hundred years, a record which accounts for approximately fifty percent of mammal species extinctions worldwide (Short and Smith 1994). The largest number of mammal extinctions has occurred in semi-arid and arid habitats. The greatest risk of extinction is associated with species whose average mass falls within the 35 g - 5.5 kg critical weight range (CWR, Burbidge and McKenzie 1989). Species reintroductions into habitats within their historic range are a practical means of maintaining endangered species populations on the mainland. However, the original loss of native fauna from between 82 to more than 99 percent of their estimated ranges at European settlement (Lindenmayer 2007), is likely to have altered the effectiveness of ecosystem functions that are essential for robust species recovery (Bennett et al. 2009; Peh and Lewis in press). The scale and duration of CWR species' absences from Australian ecosystems may have significantly altered ecosystem functions such as dung decomposition by coprophages that specialised on CWR species' dung. Dung beetles are limited by their behaviour, morphology, and life history to the types of dung they utilize (Carpaneto et al. 2005; Chown et al. 1995; Tiberg and Floate 2011). Therefore, it is very likely that dung beetles will be one of the taxa that have responded negatively to the decline of species which were central to their food supplies.

Dung beetles are coprophages that play a substantial role in the decomposition and removal of dung. They often have highly specific habitat and food requirements, as well as distinct methods used by separate species to both store and feed on dung after removing it from the parent source (Doube 1990; Hanski and Cambefort 1991; Hill 1996; Slade et al. 2007). Dung beetle activity contributes significantly to nutrient recycling (Nichols et al. 2008). As an ecosystem process, nutrient recycling maintains plant access to limiting labile nutrients, including nitrogen, potassium and phosphorus (Loreau 1995). Australia's dung beetle fauna is comprised of 23 exotic dung beetle species (Edwards 2007; Ridsdill-Smith and Edwards 2011), as well as 437 known native species, of which 355 have been formally described (Cassis et al. 2002; Ridsdill-Smith and Edwards 2011). Of these, the majority of native dung beetles exhibit a strong preference for marsupial dung (Cassis et al. 2002; Matthews 1972; 1974; 1976), whereas the exotic dung beetles generally confine themselves to ruminant livestock dung (Doube et al. 1991).

Critical weight range marsupial declines may have impacted upon services dominated by native dung beetles by disrupting local dung supplies. Without dung inputs from CWR species, dung beetle recruitment to freshly deposited dung would decrease. In extreme cases, CWR species' dung decomposition as an ecosystem function would itself become 'ecologically extinct' by becoming so inefficient that it no longer contributes to the overall ecosystem process of nutrient recycling (e.g. Estes et al. 1989). Although this may not sound particularly damaging to ecosystems hosting reintroduced CWR species, it would mean that a proportion of the energy being removed from the system by the CWR species through foraging, for example, is not being effectively returned. Similar consequences of co-decline and extinction of both species and ecosystem functions have been recorded for frugivores and seed dispersal in Tongan and Philippine forests (Hamann and Curio 1999; McConkey and Drake 2006). Complementarity between species within coprophage assemblages influences the efficiency of dung decomposition (O'Hea et al. 2010; Ridsdill-Smith and Matthiessen 1988; Slade et al. 2007). Co-declines of CWR dungspecialised coprophages alongside their preferred CWR dung suppliers would affect how efficiently the remaining dung fauna can utilize dung supplies, by shifting the balance of species with different strategies for consuming dung (Slade et al. 2007). Incompatibility between dung producers and dung consumers has been recorded in Australia, where native dung beetle assemblages were not able to make efficient use of dung pads left by cattle (Bornemissza 1960). Only the introduction of exotic dung beetle species that had coevolved with ruminants and ungulates expedited dung decomposition in cattle pastures (Tyndale-Biscoe 1994). In itself, the lack of native dung beetles with the functional capacity to efficiently consume large dung deposits characteristic of ruminants is thought to be associated with the decline of large-bodied dung beetles associated with the mega fauna of the Pleistocene era (Cambefort 1991; Edwards 2007; Johnson 2009). If a substantial proportion of native dung fauna have been extirpated by CWR declines,

then the ability of current coprophage assemblages to effectively recognize and use dung from reintroduced CWR species may be compromised in habitats targeted for mammal reintroductions.

A high level of dung-specificity is a major assumption underpinning the suggestion that CWR species declines have negatively impacted upon dung beetle assemblages. Thus, their declines are expected to have impacted dung specialist over generalist dung beetle species. The level of specificity towards different types of marsupial dung exhibited by Australian native dung beetle species has been directly studied in tropical, but not arid and semiarid zone habitats. Evidence from two studies which directly tested preference using a variety of native mammal dung suggests that high specificity towards dung from particular mammal species by dung beetles does exist. For example, dung beetle species in the Queensland wet sclerophyll forest partitioned limiting dung resources through selective use of dung from locally occurring CWR mammals, which included northern bettongs (Bettongia tropica, Potoroidae), (Vernes et al. 2005). In addition, more dung beetle species were attracted to rufous bettong (Aepyprymnus rufescens, Potoroidae) dung over dung from Sharman's rock wallaby (Petrogale sharmani, Macropodidae), (Wright 1997).

In contrast to these two studies, the majority of species-specific knowledge about native dung beetle food preferences relate to those that were attracted to cow pads prior to the introduction of exotic beetles in Queensland, south western, and south eastern Australia (Hughes 1975; Ridsdill-Smith 1993; Tyndale-Biscoe 1994). At least 73 native species are known to be attracted to cow dung pads in Queensland (Edwards 2007), and 17 native species are attracted to human dung and/or carrion in southwestern Australia (Ridsdill-Smith et al. 1983). The most recent study conducted in NSW found 14 native species attracted to pig dung in riparian habitats during different stages of restoration (Gollan et al. 2011). In some cases therefore, native dung beetle species are able to recognize and utilise non-marsupial dung resources as alternative food supplies, although it is likely to be used as a marginal habitat (e.g. Morelli et al. 2002).

A targeted effort to assess the level of specificity demonstrated by arid and semi-arid zone dung beetles will be an important first-step towards assessing the status of invertebrate-driven ecosystem processes. Reintroducing CWR species into their former habitats is a practical method of preventing their extinction. Spatially isolated remnant populations of CWR marsupials on the mainland, such as the greater bilby (Macrotis lagotis, Thylacomidae) and bridled nail tail wallaby (Onychogalea fraenata, Macropodidae) could harbour populations of dung beetle species that are still closely affiliated with CWR marsupial dung. For example, some species within the genus Onthophagus (Scarabaeidae: Onthophagini) possess prehensile claws that allow them to cling to fur, and were detected in a recent Queensland survey which lured them with cow dung baits. However, it was unclear whether or not these beetles were using the baits as a food and/or breeding resource (Edwards, 2007). Of particular interest is a note in Matthews (1972) revision of the Onthophagini tribe. Matthews writes that all prehensile-clawed beetles were found exclusively on small and medium sized marsupials, and never on larger macropods or rat-kangaroos (Diprotodontia: Hypsiprymnodontidae). If these specialized dung beetles were able to move with their hosts during relocation, then it is possible that at least some beetles that had evolutionary associations with CWR species may have re-established themselves in their historic habitat. This would be of significant benefit to CWR reintroduction habitats that have potentially been without a diverse dung beetle fauna since the decline of CWR species. Additionally, this information can prove beneficial to conservation programs which eradicate co-dependent fauna such as gut parasites from founder colonies prior to their reintroduction into new habitats. It may in fact be more effective in some cases to reintroduce species with their co-dependent fauna intact, as their association may increase the target species chances of survival (Burbidge et al. 2012).

There is a clear need to assess the status of Australia's native dung beetle fauna in arid and semiarid habitats. First, we need to establish whether or not the decline of CWR species has led to a breakdown of dung beetle communities that were present in their former range. Baited pitfall trapping using fresh dung of CWR species can be used to determine whether or not dung beetle fauna caught in naturally persisting CWR species' habitats are similar to those in habitats where CWR species have been reintroduced. If the dung beetle assemblages are similar between both habitats, this indicates that none of the native beetle species were CWR species-specific. In contrast, if a subset of beetle species is found on CWR species dung in reintroduction habitats, then this may indicate some species were unable to adapt to the decline of CWR species and are likely to have become extinct, or do not occur naturally in the reintroduction habitat.

Second, we can assess the possibility of corelocation of dung beetle species that are known to be affiliated with CWR species, such as those with prehensile claws. Co-relocation of these beetle species should complement the dung fauna in the targeted reintroduction habitat, which may help to overcome ecological barriers to effective dung decomposition triggered by the original species decline. Captured CWR marsupials in source and relocation habitats can be examined for dung beetles clinging to the fur surrounding the cloaca. If prehensile-clawed dung beetles are found on the source population for reintroduction, then we can consider the feasibility of co-relocating the dung beetles with their hosts toward the long term success of conserving our CWR mammal species.

Finally, an experimental analysis of dung decomposition with and without dung beetle exclusion in 'reintroduction' versus 'persisting' habitats can be used to gain a comparative measure of dung decomposition and dispersal efficiency the current environment. Information gained in from targeted observation and analysis of dung beetle functional diversity, community assemblage and process efficiency will be an important part of restoring and monitoring managed habitats used in species recovery projects. It is vital that we determine how readily ecosystem processes in habitats targeted for CWR species reintroductions can readjust to the 'new' inputs from reintroduced species, and whether or not it will be necessary to reintroduce entire suites of organisms involved in ecological functioning to ensure the success of threatened species conservation (Burbidge et al. 2011).

ACKNOWLEDGEMENTS

This project is supported by The Australian Wildlife Conservancy, Arid Recovery Reserve, and volunteers. Funding is provided by the ANZ trustees' Holsworth Wildlife Research Endowment and the Australia and Pacific Science Foundation. Nicole is supported through an Australian Postgraduate Award. Dr. Bernard Doube and Dr. Penny Edwards provided valuable guidance and expertise regarding dung beetle distributions and field methods. Thanks to Dr. Heloise Gibb, Dr. Matt Hayward, Assoc. Prof. David Eldridge and an anonymous reviewer for their constructive criticism of this manuscript.

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