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Short communication

Foraging activity by the southern brown bandicoot (*Isoodon obesulus*) as a mechanism for soil turnover

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Abstract. Mammals that forage for food by biopedturbation can alter the biotic and abiotic characteristics of their habitat, influencing ecosystem structure and function. Bandicoots, bilbies, bettongs and potoroos are the primary digging marsupials in Australia, although most of these species have declined throughout their range. This study used a snapshot approach to estimate the soil turnover capacity of the southern brown bandicoot (*Isoodon obesulus*, Shaw 1797), a persisting digging Australian marsupial, at Yalgorup National Park, Western Australia. The number of southern brown bandicoots was estimated using mark–recapture techniques. To provide an index of digging activity per animal, we quantified the number of new foraging pits and bandicoot nose pokes across 18 plots within the same area. The amount of soil displaced and physical structure of foraging pits were examined from moulds of 47 fresh foraging pits. We estimated that an individual southern brown bandicoot could create ~45 foraging pits per day, displacing ~10.74 kg of soil, which extrapolates to ~3.9 tonnes of soil each year. The digging activities of the southern brown bandicoots are likely to be a critical component of soil ecosystem processes.

Additional keywords: biopedturbation, ecosystem engineering, soil movement.

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Introduction

Mammals that move or manipulate soil for food or to create shelter (biopedturbation) can act as ecosystem engineers (Whitford 1999), creating disturbances that may be essential for maintaining ecosystem health (Eldridge and James 2009; Eldridge *et al*. 2009). Mammalian biopedturbation creates small-scale disturbances via soil turnover (Whitford 1999; Eldridge *et al*. 2012) and can subsequently alter the physical properties of soil, including soil compaction and water infiltration (Garkaklis *et al*. 1998, 2000, 2003). Several Australian marsupials dig, though the bettongs (*Bettongia* spp., *Aepyrymnus rufescens*), potoroos (*Potorous* spp.), bilbies (*Macrotis* spp.) and bandicoots (*Perameles* spp., *Isoodon* spp. and *Echymipera rufescens*) are the main marsupials in Australia responsible for creating foraging pits (Martin 2003). These marsupials are adapted to digging in soil, and use their strong forefeet and claws to create foraging pits while searching for food, such as invertebrates, tubers, seeds and fungi. The soil-turnover capacity of these digging marsupials is impressive, with individual woylies (*Bettongia penicillata*) estimated to displace ~4.8 tonnes of soil each year (Garkaklis *et al*. 2004).

Australian digging marsupials (here defined as bettongs, potoroos, bilbies and bandicoots) are all within the critical weight range and considered most at risk from introduced predators (Johnson and Isaac 2009), and most of these species have suffered drastic declines in mainland populations and substantial range contractions (Van Dyck and Strahan 2008). Of the 16 extant digging marsupial species, 11 are considered to be of conservation concern, while a third (5 species) are considered critically endangered or endangered (*Environment Protection and Biodiversity Conservation Act 1999*). Despite the grim conservation status of most Australian digging marsupials, several species (e.g. *Isoodon macrourus*, *I. obesulus* and *Perameles nasuta*) persist within parts of their former range on mainland Australia, sometimes in highly modified environments (e.g. Hughes and Banks 2010). However, the potential ecosystem role of these species has not been investigated.

The southern brown bandicoot (*I. obesulus*, Shaw 1797) is a medium-sized omnivorous marsupial that occurs in scattered areas across parts of eastern, southern and south-western Australia (Van Dyck and Strahan 2008). Home-range estimates for the southern brown bandicoot vary from 0.5 to 6.0 ha (Lobert 1990), with males typically having larger home ranges than females (Heinsohn 1966), and in areas of high density (and correspondingly high food supply) home ranges are likely to overlap (Broughton and Dickman 1991). Although the eastern subspecies (*I. obesulus obesulus*) is listed as endangered (*Environment Protection and Biodiversity Conservation Act 1999*), in south-western Australia the southern brown bandicoot (*I. obesulus fusciventer*) is the only persisting commonly occurring digging marsupial, especially within the urban–wildland interface. Foraging pits are created by bandicoots when digging with their strong forefeet for fungal fruiting bodies, invertebrates and subterranean plant material (Van Dyck and Strahan 2008). Previous observations have indicated that southern brown bandicoots may be prolific 'diggers'(Heinsohn 1966; Quin 1985).

The southern brown bandicoot occur in two distinct habitats in south-western Australia – open forest, and dense vegetation around swamps and watercourses (Cooper 2000*a*, 2000*b*) – and this mammal has consequently been identified as susceptible to declining groundwater and rainfall (Wilson *et al*. 2012). In the urban–wildland interface surrounding Perth, populations of the southern brown bandicoot persist in the bush fragments and conservation reserves, often without predator control. In this study, we quantified the physical structure of southern brown bandicoot foraging pits and estimated soil turnover in a small area, to compare with other digging marsupial species and to assist in determining the potential role of the southern brown bandicoot in maintaining ecosystem processes.

Materials and methods

Study site

This study was conducted at Martin's Tank at the edge of Martin's Lake, Yalgorup National Park on the Swan Coastal Plain IBRA region (Thackway and Cresswell 1995) in south-western Australia (32°50′54.52″S, 115°40′8.72″E). Yalgorup National Park (~12 888 ha) has high regional biodiversity values based around the chain of 10 coastal lakes, swamps and tuart (*Eucalyptus gomphocephala*) forests (Portlock *et al*. 1993). Although sections of the national park are baited with 1080 (sodium fluoroacetate) to assist in the control of the introduced red fox (*Vulpes vulpes*), the area surrounding Martin's Lake is not currently baited. The region has a Mediterranean-type climate with hot dry summers and mild wet winters and an average annual rainfall of 864 mm (Bureau of Meteorology, Lake Preston Lodge 2 Comp., #009679). Yalgorup National Park contains three major dune systems: the Quindalup, Spearwood and Bassendean Dunes (Portlock *et al*. 1993). Our research focussed on foraging activity and soil turnover of bandicoots within a small section of the National Park, consisting of a 2-ha area (200 m × 100 m) in the vegetation running parallel to Martins Lake. Our study site was located on Spearwood Dunes, where soils were predominantly yellow-phase Karrakatta sands. Vegetation in the study area included lake-fringing vegetation dominated by *Melaleuca preissiana* and *M. rhaphiophylla* and interspersed with tuarts, with a dense understorey of sedges (mostly *Gahnia trifida*) transitioning to a combination of tuart trees, peppermint (*Agonis flexuosa*) and paperbark (*M. rhaphiophylla*), and a tuart, jarrah (*E. marginata*) and marri (*Corymbia calophylla*) overstorey with a mid-storey layer of scattered *Banksia grandis*, *B. attenuata* and grasstrees (*Xanthorrhoea* spp.), and an open understorey of zamia palms (*Zamia* spp.) and various herbaceous species (e.g. *Jacksonia sternbergiana*, *Hibbertia hypericoides*) (Portlock et al. 1993).

Estimating soil turnover by the southern brown bandicoot

Bandicoot foraging activity was assessed for 18 plots (each 10 m × 10 m), with plots haphazardly stratified along the vegetation gradient described above, with each plot separated from each other by a minimum of 30 m. We counted the number of new foraging pits and nose pokes created within each plot during a 24-h period in June and in August 2011. A bandicoot 'foraging pit' was defined as having a clear point at the bottom of the pit and a spoil heap adjacent to the pit (where displaced soil was accumulated via the digging activities of the bandicoots). A 'nose poke' was defined as an obvious movement of the ground debris and soil but without a defined point or adjacent spoil heap. Due to rain occurring in the days before examining foraging activity (but not during the sample period), new foraging pits and nose pokes were easily identified during both sampling sessions (as rain in the previous day had left impressions in the spoil of existing foraging pits).

After counting foraging pits (described above), we used mark–recapture trapping (three nights in June and August 2011) to estimate the number of southern brown bandicoots potentially responsible for creating the foraging pits in the 2-ha study area. A transect of 10 cage traps (Sheffields: 20 cm × 20 cm × 56 cm) were spread evenly across the study area. All traps were baited with universal bait (a combination of peanut butter, rolled oats, sardines and truffle oil). Hessian bags and pieces of tarpaulin were placed over all cage traps to provide shelter and to prevent rain entering the cage. The traps were open in the afternoon each day and checked within 3 h of sunrise the following morning. All animals captured were weighed, measured (head length and long pes), sexed and individually marked using ISO FDX-B microchips (OzMicrochips, NSW) inserted subcutaneously on the nape of the neck. Retrapped animals were detected using the RT100 ISO Scanner (Real Trace, NSW). In this study we have not assessed home-range sizes for the southern brown bandicoot, although previous work in south-western Australia indicates that home ranges are ~2.3 ha for males and ~1.8 ha for females, but they may overlap (Broughton and Dickman 1991). As we did not estimate the spatial range of the animals at Martins Tank, we used the total number of animals captured (both trapping sessions combined) as our estimate of the number of bandicoots creating foraging pits within the 2-ha area.

The number of foraging pits was quantified by averaging the number of new foraging pits per plot counted in June and August 2011 and extrapolating this value to a per-hectare estimate. Plaster of Paris (Diggers Plaster of Paris, South Australia) was poured into 47 fresh bandicoot diggings that were representative of the range of foraging pit sizes observed in plots. We measured the width (at soil surface) and depth of the plaster moulds, and the volume of each mould (in millilitres) was estimated by water displacement (1200 mL graduated cylinder). Measurements reported are the average ± standard error. Soil density (1.25 g cm^{-3}) was estimated as the average density obtained from four soil core samples of known volume (~1021 cm^3) that were oven-dried for 72 h (K. Ruthrof, unpubl. data). The amount of soil displaced by one bandicoot in a night was calculated as:

$$\begin{aligned}&\text{Soil displaced (g individual}^{-1}\text{ (24-h period)}^{-1})\\&\quad=(\text{no. of new foraging pits bandicoot}^{-1}\text{ (24-h period)}^{-1})\\&\qquad\times(\text{foraging pit volume})\times(\text{soil density})\end{aligned}$$

This figure was also then expressed as tonnes individual^{-1} year^{-1}.

Limitations to this study

Our study provides a snapshot approach at estimating the soil-turnover capacity of the southern brown bandicoot, and has several limitations that should be considered. First, we used a single location, Martins Tank, to obtain our estimates of foraging activity and foraging pit dimensions for the southern brown bandicoot. These values may vary depending on location, habitat, soil type and bandicoot density. Second, to estimate the number of bandicoots creating the foraging pits, we have used the total number of bandicoots captured within the 2-ha area. Given our uncertainty of the spatial range of foraging bandicoots, the foraging pits within our study area may have been created by one or several bandicoots. Using the total number of captured bandicoots may overestimate the number of bandicoots creating the foraging pits and thus could represent a conservative estimate of the soil-turnover capacity of this species. Third, our estimates of foraging activity are based on two nights' data collection and the extrapolation to an annual estimate of soil turnover does not reflect seasonal differences in foraging behaviour and intensity.

Results

In total, eight bandicoot individuals were captured in the 2-ha area over 60 trap-nights (June and August sessions combined). Six bandicoots (two female, four male) were captured in June and recaptured in August, along with an additional two individuals (one male, one escaped before it was sexed). Males were typically larger and heavier ($n=5$, mean ± s.e.: body mass = 1724 ± 107 g; head length = 93.2 ± 2.1 mm, pes length = 65.0 ± 1.3 mm) than females (n = 2, mean ± s.e.: body mass = 1165 ± 15 g; head length = 85.1 ± 6.0 mm; pes length = 60.6 ± 2.0 mm). The eight individuals were all in visibly good condition, with no fur loss, scratches or other signs of fighting.

Across the 18 survey plots there were 36 new foraging pits and 88 new nose pokes in June and 32 new foraging pits and 122 new nose pokes in August, with a range of 0–6 foraging pits and 0–21 nose pokes observed per plot in both sampling periods. The mean number of new foraging pits day^{-1} averaged 1.8 plot^{-1} (10 × 10 m), which extrapolated to 180 new foraging pits ha^{-1} in a 24-h period. For the purposes of this study, we have assumed that all eight individual southern brown bandicoots created the foraging pits (i.e. 4 individual bandicoots ha^{-1}), which equates to 45 foraging pits day^{-1} (individual bandicoot)$^{-1}$.

Moulds of 47 fresh foraging pits indicated that foraging pits were fairly consistent in their physical size. Foraging pits were conical in shape, measuring 100.9 ± 3.9 mm across at the soil surface with a mean depth of 69.6 ± 3.2 mm (depth range 35–135 mm). The mean volume of these foraging pits was 191 ± 15 mL. In a single night of our study, the soil displaced by one bandicoot at Martins Tank was therefore estimated as 8595 cm^3 or 10.74 kg (calculated as follows: 10 743.75 g soil displaced individual^{-1} (24-h period)$^{-1}$ = 45 foraging pits bandicoot^{-1} (24-h period)$^{-1}$ × 191 mL soil displaced × 1.25 g cm^{-3} soil density). Assuming no seasonal differences in foraging activity, this value can then be extrapolated to an annual turnover of 3.14 m^3 or 3.92 tonnes for each individual.

Discussion

Southern brown bandicoots are opportunistic omnivores that forage for a variety of food, consuming invertebrates, fungi, plant material and occasionally small vertebrates, with diets reflecting seasonally and locally abundant food items (Heinsohn 1966; Quin 1988; Van Dyck and Strahan 2008). Foraging of bandicoots via nose pokes may assist bandicoots in detecting subterranean prey items (Quin 1992) and/or target invertebrates (e.g. cockroaches, crickets, spiders) that commonly occur in the leaf litter layer (Hattenschwiler *et al*. 2005). In Tasmania, a single wild bandicoot was observed digging 21 foraging pits within 36 min (Heinsohn 1966), while bandicoots in captivity have been observed digging up to 32 foraging pits in an evening (Quin 1985). In our study, we estimated that a single bandicoot dug ~45 foraging pits each day, representing a considerable impact in terms of soil turnover.

Bettongs and potoroos forage principally on fruiting bodies of underground fungi (Van Dyck and Strahan 2008) and may create higher numbers of foraging pits while searching for food (e.g. woylie: 38–114 foraging pits individual^{-1} (Garkaklis *et al*. 2004); southern brown bandicoot: ~45 foraging pits individual^{-1}). Although we did not examine the density of foraging pits throughout seasons, previous research has indicated that the densities of foraging pits of digging marsupials may vary throughout the year, potentially in relation to the availability of hypogeal fungal fruiting bodies (Claridge *et al*. 1993). As the diet of the southern brown bandicoot varies seasonally (Quin 1988), the number of foraging pits created by this species is also likely to vary seasonally. Foraging pits created by the greater bilby and burrowing bettong are ~80 mm deep (James and Eldridge 2007), similar in size to those of the southern brown bandicoot (~70 mm). The long-nosed potoroo (*P. tridactylus*) creates foraging pits that vary in depth from 56 to 120 mm (Claridge *et al*. 1993), while the woylie creates deeper foraging pits (100–115 mm: Garkaklis *et al*. 2004).

Although our study is restricted to a small area and represents a 'snapshot' of foraging activities of the southern brown bandicoot, it is the first to estimate soil turnover rates of the southern brown bandicoot, with an individual bandicoot (average body mass 1.6 kg) turning over ~10.74 kg day^{-1}. This equates to ~3.9 tonnes of soil bandicoot^{-1} year^{-1} and falls within the range of soil displaced (2.7–9.7 tonnes year^{-1}) by the similar-sized woylie (body mass: 1.0–1.5 kg) (Garkaklis *et al*. 2004). Marsupials that burrow for food and live underground produce even greater soil turnover. For example, in predator-free enclosures in arid zones, where bilbies and burrowing bettongs are held together (therefore values are for both species combined), these animals excavate ~30 tonnes of soil individual^{-1} year^{-1} (Newell 2008).

The loss of once widespread digging mammals in Australia is likely to have major ramifications for ecosystem processes. Further research on the foraging activities of the southern brown bandicoot, preferably over a longer time frame and across several sites, is necessary to elucidate the soil-turnover capacity of this digging marsupial. Although the range and population of the southern brown bandicoot has declined since European settlement (Abbott 2008), these animals persist in urban, periurban and rural regions of south-western Australia, where they are likely to be playing an important role in ecosystem processes, contributing to the health and function of the woodlands and forests. Understanding the role of these animals may therefore contribute towards conservation management decisions. Since the southern brown bandicoot appears to be more resilient to human-mediated disturbances compared with other digging marsupials (e.g. woylie), they provide us with an ideal opportunity to reintroduce them into landscapes where soil turnover is required for ecosystem health and function.

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References

Abbott, I. (2008). Historical perspectives of the ecology of some conspicuous vertebrate species in south-west Western Australia. *Conservation Science Western Australia* **6**, 1–214.

Broughton, S. K., and Dickman, C. R. (1991). The effect of supplementary food on home range of the southern brown bandicoot, *Isoodon obesulus* (Marsupialia: Peramelidae). *Australian Journal of Ecology* **16**, 71–78. doi:10.1111/j.1442-9993.1991.tb01482.x

Claridge, A. W., Cunningham, R. B., and Tanton, M. T. (1993). Foraging patterns of the long-nosed potoroo (*Potorous tridactylus*) for hypogeal fungi in mixed-species and regrowth eucalypt forest stands in southeastern Australia. *Forest Ecology and Management* **61**, 75–90. doi:10.1016/0378-1127(93)90191-O

Cooper, M. L. (2000*a*). Random amplified polymorphic DNA analysis of southern brown bandicoot (*Isoodon obesulus*) populations in Western Australia reveals genetic differentiation related to environmental variables. *Molecular Ecology* **9**, 469–479. doi:10.1046/j.1365-294x.2000.00883.x

Cooper, M. L. (2000*b*). Temporal variation in skull size and shape in the southern brown bandicoot, *Isoodon obesulus* (Peramelidae: Marsupialia) in Western Australia. *Australian Journal of Zoology* **48**, 47–57. doi:10.1071/ZO99047

Eldridge, D. J., and James, A. I. (2009). Soil-disturbance by native animals plays a critical role in maintaining healthy Australian landscapes. *Ecological Management & Restoration* **10**, S27–S34. doi:10.1111/j.1442-8903.2009.00452.x

Eldridge, D. J., Whitford, W. G., and Duval, B. D. (2009). Animal disturbances promote shrub maintenance in a desertified grassland. *Journal of Ecology* **97**, 1302–1310. doi:10.1111/j.1365-2745.2009.01558.x

Eldridge, D. J., Koen, T. B., Killgore, A., Huang, N., and Whitford, W. G. (2012). Animal foraging as a mechanism for sediment movement and soil nutrient development: evidence from the semi-arid Australian woodlands and the Chihuahuan Desert. *Geomorphology* **157–158**, 131–141. doi:10.1016/j.geomorph.2011.04.041

Garkaklis, M. J., Bradley, J. S., and Wooller, R. D. (1998). The effects of woylie (*Bettongia penicillata*) foraging on soil water repellency and water infiltration in heavy textured soils in southwestern Australia. *Australian Journal of Ecology* **23**, 492–496. doi:10.1111/j.1442-9993.1998.tb00757.x

Garkaklis, M., Bradley, J., and Wooller, R. D. (2000). Digging by vertebrates as an activity promoting the development of water-repellent patches in sub-surface soil. *Journal of Arid Environments* **45**, 35–42. doi:10.1006/jare.1999.0603

Garkaklis, M. J., Bradley, J. S., and Wooller, R. D. (2003). The relationship between animal foraging and nutrient patchiness in south-west Australian woodland soils. *Australian Journal of Soil Research* **41**, 665–673. doi:10.1071/SR02109

Garkaklis, M. J., Bradley, J. S., and Wooller, R. D. (2004). Digging and soil turnover by a mycophagous marsupial. *Journal of Arid Environments* **56**, 569–578. doi:10.1016/S0140-1963(03)00061-2

Hattenschwiler, S., Tiunov, A. V., and Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics* **36**, 191–218. doi:10.1146/annurev.ecolsys.36.112904.151932

Heinsohn, G. E. (1966). Ecology and reproduction of the Tasmanian bandicoots (*Perameles gunni* and *Isoodon obesulus*). *University of California Publications in Zoology* **80**, 1–96.

Hughes, N. K., and Banks, P. B. (2010). Heading for greener pastures? Defining the foraging preferences of urban long-nosed bandicoots. *Australian Journal of Zoology* **58**, 341–349. doi:10.1071/ZO10051

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. doi:10.1016/j.biocon.2007.04.029

Johnson, C. N., and Isaac, J. L. (2009). Body size and extinction risk in Australian mammals: back to the Critical Weight Range. *Austral Ecology* **34**, 35–40. doi:10.1111/j.1442-9993.2008.01878.x

Lobert, B. (1990). Home range and activity period of the southen brown bandicoot (*Isoodon obesulus*) in a Victorian heathland. In 'Bandicoots and Bilbies'. (Eds J. H. Seebeck, P. R. Brown, R. L. Wallis and C. M. Kemper.) pp. 319–325. (Surrey Beatty: Sydney.)

Martin, G. (2003). The role of small ground-foraging mammals in topsoil health and biodiversity: implications to management and restoration. *Ecological Management & Restoration* **4**, 114–119. doi:10.1046/j.1442-8903.2003.00145.x

Newell, J. (2008). The role of the reintroduction of greater bilbies (*Macrotis lagotis*) and burrowing bettongs (*Bettongia lesueur*) in the ecological restoration of an arid ecosystem: foraging diggings, diet and soil seed banks. Ph.D. Thesis, School of Earth and Environmental Sciences, University of Adelaide.

Portlock, C., Koch, A., Wood, S., Hanly, P., and Dutton, S. (1993). Yalgorup National Park Management Plan. Department of Conservation and Land Management, Perth, Western Australia.

Quin, D. G. (1985). Aspects of the feeding ecology of the bandicoots *Perameles gunnii* (Gray 1838) and *Isoodon obesulus* (Shaw and Nodder 1797) (Marsupialia: Peramelidae) in southern Tasmania. B.Sc.(Honours) Thesis. University of Tasmania, Hobart.

Quin, D. G. (1988). Observations on the diet of the southern brown bandicoot, *Isoodon obesulus* (Marsupialia: Peramelidae), in southern Tasmania. *Australian Mammalogy* **11**, 15–25.

Quin, D. G. (1992). Observations of prey detection by the bandicoots, *Isoodon obesulus* and *Perameles gunnii* (Marsupialia: Peramelidae). *Australian Mammalogy* **15**, 131–133.

Thackway, R., and Cresswell, I. D. (1995). ‘An Interim Biogeographic Regionalisation of Australia: a Framework for Establishing the National System of Reserves.’ (Australian Nature Conservation Agency: Canberra.)

Van Dyck, S., and Strahan, R. (2008). ‘The Mammals of Australia.’ 3rd edn. (Reed New Holland: Sydney.)

Whitford, W. G. (1999). Biopedturbation by mammals in deserts: a review. *Journal of Arid Environments* **41**, 203–230. doi:10.1006/jare.1998.0482

Wilson, B. A., Valentine, L. E., Reaveley, A., Isaac, J., and Wolfe, K. M. (2012). Terrestrial mammals of the Gnangara Groundwater System, Western Australia: history, status and the possible impacts of a drying climate. *Australian Mammalogy* **34**, 202–216. doi:10.1071/AM11040

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