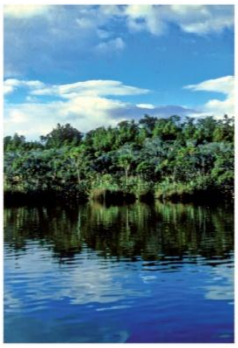

Dung beetle risk evaluation: no evidence that brushtail possums (*Trichosurus vulpecula*) forage on exotic pastoral dung beetles (Coleoptera: Scarabaeidae) in New Zealand

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Landcare Research
Manaaki Whenua

Dung beetle risk evaluation: no evidence that brushtail possums (*Trichosurus vulpecula*) forage on exotic pastoral dung beetles (Coleoptera: Scarabaeidae) in New Zealand

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Contents

Summary

Eleven exotic species of dung-burying beetle have recently been approved for unconditional release onto New Zealand pastures by New Zealand's Environmental Protection Authority. Here we test one perceived risk of such releases, that the utilisation of dung beetles on pasture as a food source by vertebrate wildlife reservoirs of *Mycobacterium bovis* (the causative agent of bovine tuberculosis, TB) may increase bush-to-pasture animal movements and, hence, potentially also increase rates of TB transmission between wildlife and cattle. As a model scenario we analysed the gut contents of 30 brushtail possums (*Trichosurus vulpecula*) trapped in Maunu, Whangarei, where the already established exotic Mexican dung beetle (*Copris incertus*) is present. Surveys of dung beetle activity and abundance were also carried out around the time of trapping. Although our dung beetle surveys clearly indicated a high prevalence and abundance of the Mexican dung beetle in pasture adjacent to where possums were trapped, and the grass content of the trapped possum guts demonstrates clearly they were foraging on pasture, no dung beetle parts were found in possum gut contents. We conclude the risk scenario of dung beetle presence affecting brushtail possum feeding behaviour is highly unlikely to be realised. Hence increased possum foraging on pasture due to dung beetle presence is unlikely to increase the potential for TB transmission both to and from cattle.

1 Introduction

Eleven exotic species of dung-burying beetle (Scarabaeinae) have recently been approved for unconditional release onto New Zealand agricultural pastures by New Zealand's Environmental Protection Authority (ERMA 2010). These will join four species previously introduced: the Mexican dung beetle *(Copris incertus)* that has persisted in Northland since its intentional introduction in 1956 (Thomas 1960), two Australian species (*Onthophagus granulatus* and *O. posticus*) that were accidently introduced over a century ago and are now patchily distributed over much of the country (Emberson & Matthews 1973), and one South African species (*Epirinus aeneus*) likewise accidently introduced and possibly established near Christchurch (Dymock 1993). Approval for the new releases was based on benefits of dung beetle activity on agricultural land (Fincher 1981; Dymock 1993; Nichols et al. 2008; ERMA 2010). These include increased soil health and fertility, reduced nutrient runoff and waterway pollution, reduced greenhouse gas emissions, and reduced parasitism of livestock, and are all principally due to the rapid mechanical transport of cattle dung underground for the creation of brood balls (Hanski & Cambefort 1991). The rationale for releasing a further 11 species was so each of the different pasture types and climate zones stocked with cattle in New Zealand would be able to support at least one of them (DBRSG 2010; Edwards 2010).

As is required by any risk assessment, the EPA review process considered potential adverse effects of releasing further dung beetle species onto New Zealand pastures, including the potential for (1) greater nutrient leaching leading to increased eutrophication, (2) the displacement of native beetle species, and (3) increases in some parasites (DBRSG 2010). These effects were considered either unlikely or negligible based on (1) the international literature, (2) there having been no observed or published adverse effects of the previous dung beetle introductions to New Zealand in over half a century, and (3) all species chosen for release having both narrow habitat preferences (open grassland) and specific host-preferences (ungulate dung; DBRSG 2010, and references therein). In addition, over 20 exotic dung beetle species have been introduced to both Australia and the United States with no adverse effects to native or beneficial species being reported (DBRSG 2010). As a result, the approval for release was made unconditionally (i.e. with no requirement for controls of any form).

In spite of the formal risk assessment approach taken by the EPA, the decision to grant approval for unconditional release has been questioned by several parties. Concerns raised include potential risks, both to native biodiversity and regarding spread of infectious diseases, for which those parties believe insufficient information is available on which to base sound judgement regarding unconditional release. A key concern is the enhanced livestock disease risks due to potential increases in the persistence and dissemination of *Mycobacterium bovis* (the causative agent of bovine tuberculosis, TB) and *M. avium* subsp. *pseudotuberculosis* (MAP, the causative agent of Johne's disease in livestock). Two risk scenarios implicate pastoral dung beetles as potential disseminators of *M. bovis* and MAP (Tompkins et al. 2012). First, the close association of dung beetles with faecal material means there is a potential risk of pathogen dissemination from infected dung via their internal or external contamination. Second, dung beetle presence may affect feeding behaviour of omnivorous brushtail possums (*Trichosurus vulpecula*), the primary wildlife reservoir of TB in New Zealand (Nugent 2011; Clout & Ericksen 2000). Possums living in forest and forest fragments within foraging range of pasture obtain at least 20% of their food from introduced grasses and clover (Coleman et al. 1985; Gilmore 1967; Harvie 1973, cited in Nugent et al. 2000), and their diet frequently includes invertebrates (Fitzgerald 1976; Clout 1977; Cowan & Moeed 1987; Owen & Norton 1995; Nugent et al. 2000; Glen et al. 2012). Increased possum foraging on pasture due to dung beetle presence has been suggested as a way the potential for disease transmission both to and from cattle might be increased.

Informing these two risks, previous trials have shown that (1) beetles are unlikely to become contaminated through utilising the dung of those infected cattle currently on farms in New Zealand, and (2) possums are not likely to forage for and eat dung beetles (Tompkins et al. 2012). However, with the feeding trial having taken place in captivity, it possibly did not reflect the situation in the wild. Hence, we further inform the risk of dung beetle presence affecting possum feeding behaviour by testing the hypothesis of possum predation on dung beetles through a diet survey of free-living individuals foraging in an area of high dung beetle availability.

2 Objectives

To inform the risk of dung beetle presence affecting possum feeding behaviour, by testing the hypothesis of possum predation on dung beetles through a diet survey of free-living individuals foraging in an area of high dung beetle availability.

3 Methods

3.1 Study site and dung beetle survey

The Mexican dung beetle (Fig. 1) was chosen as our test prey species because it is highly abundant in pastures around Whangarei, Northland, where it was introduced (Thomas 1960). We surveyed beetle activity and abundance at three sites in Maunu, SW Whangarei (35°45`S, 174°17`E). Each site (Site 1 – Maunu Heritage Park; Site 2 – opposite Maunu tennis club; Site 3 – Te Hape Rd) comprised livestock pasture interspersed with bush fragments, and were surveyed during April 2013 when beetles are still seasonally active (Blank et al 1983; Forgie, Dymock pers. obs.). The number of fresh cowpats per hectare (ha) ranged from 80/ha and 85/ha at sites 1 and 2, respectively, to 150/ha at site 3. Typically, chemical odours emitted from fresh cow pats attract dung beetles. Within a week suitable pats have undergone colonisation and the subsequent competitive dynamics associated with maturation feeding or nest building by Mexican dung beetles (Forgie, unpubl. data; Hanski & Cambefort 1991). Thus, a total of 156 cattle pats up to a week old were assessed for signs of beetle activity and abundance, by counting (1) the number of beetle-created soil extrusions around each pat, (2) the number of tunnels around and under each pat, and (3) the number of beetles present in either the tops of tunnels or within each pat. Additionally, each pat was checked for mechanical disturbance from possum foraging (or that of other vertebrates including birds).

Figure 1 Mexican dung beetle (Copris incertus), male. Scale bar = 5 mm. (Montage Image courtesy of Birgit Rhode, NZAC, Landcare Research, 2012.)

3.2 Brushtail possum trapping

A professional trapper was commissioned to trap possums across our sites. Humane kill-traps were elevated in native trees along the fringes of bush patches adjacent to the surveyed pastures (Fig. 2), and set for two consecutive nights in April 2013 when beetles were active.

Figure 2 Brushtail possums (Trichosurus vulpecula) killed in elevated humane kill-traps along bush-pasture fringe, Maunu, Whangarei. (Photo courtesy of Stephen Allen, 2013.)

3.3 Gut content analysis

The contents were extracted from the stomach, small intestine, caecum and colon of 30 trapped possums (Fig. 2). Extraction and analysis was based on a point-sampling technique (Sweetapple & Nugent 1998). Each stomach was emptied into an Endecott sieve (0.5 mm aperture size), rinsed with water to remove small pieces of leaf material, and assessed for the presence of clover, rye, and kikuyu fragments (pasture grass species, quantified as a proportion of stomach contents to the nearest 5%). Contents from the remaining digestive tract were combined with the stomach contents, rinsed, emptied into a shallow white plastic container, and immersed in water for examination of all floating or sunk invertebrate fragments. Fragments were identified where possible using a Leica MZ7 stereo microscope. A subsample of material from each gut, including any associated invertebrates, was preserved in 95% EtOH. Prevalence statistics (and 95% confidence intervals) were calculated in OpenEpi v3.01 (Dean et al. 2013).

4 Results

4.1 Dung beetle survey

The colonisation of dung pats by Mexican dung beetles ranged across our three sites (Table 1), from pats at site 1 being recently colonised (for less than 1 day) with little soil extrusion on their borders and relatively few tunnels underneath, to pats at site 2 being completely shredded by dung beetle activity and weathered by rain (being at least an estimated 5 days post-colonisation). Pats at site 3 were intermediate, being colonised for an intermediate time (an estimated 2–4 days) and with substantial soil extrusion on their borders and numerous tunnels beneath. Only one dung pat (at site 3) showed any sign of disturbance, with its crust divided into 4 chunks.

Thirty of 49 fresh to 1-week-old pats examined at site 1 contained a total of 141 dung beetles in the aboveground pat. Ninety-four dung beetle tunnels were observed beneath 32 of the pats (including the 30 pats above), while only four of the pats had soil extrusions on their borders. All but two of the 25 pats examined at site 2 pats were weathered by rain and shredded by dung beetle activity; nevertheless, eight of the pats contained a total of 46 dung beetles. Seventy-five of the 82 pats examined at site 3 had soil extrusions on their borders, of which 53 contained a total of 159 dung beetles in the aboveground pat. Only four of the pats examined at site 3 did not have any tunnels underneath, with 438 tunnels observed beneath the other 78.

4.2 Gut content analysis

No dung beetle remains (exotic or native) were found in the gut contents of any of the 30 possums examined (Table 2). This gives 95% Fisher Exact (Clopper-Pearson) confidence intervals for the proportion of possums foraging on dung beetles in the scenario examined of 0–12%. This result can be compared with the observation that other invertebrates occurred in the gut contents of 19 (63%) of the 30 individuals (giving 95% confidence intervals of 44–80%). The lack of dung beetles in the diet contrasts even more with the grass content: 18 of the individuals examined had recently been feeding on pasture, with pasture grass species accounting for 5–80% of their stomach contents (Table 2).

Table 1 Findings of the Mexican dung beetle (Copris incertus) survey at three sites in Maunu, Whangarei

Site 1			**Site 2**		**Site 3**			**Site 3**	**continued**	
soil extrusions/pad	tunnels/pad	dung beetles/pad	soil extrusions/pad	dung beetles/pad	soil extrusions/pad	tunnels/pad	dung beetles/pad	soil extrusions/pad	tunnels/pad	dung beetles/pad
0	0	0	shredded	14	4	5	5	2	2	0
0	6	1	shredded	10	4	4	0	1	1	0
0	5	1	shredded	7	3	3	0	4	5	0
0	3	0	shredded	1	2	2	1	1	1	1
0	10	1	shredded	1	1	4	3	4	4	0
0	0	0	shredded	2	4	6	0	0	0	1
0	0	0	shredded	9	2	6	0	1	1	1
0	0	8	shredded	0	5	5	0	0	2	1
0	8	0	1	0	2	3	0	0	0	1
0	0	0	shredded	0	1	2	0	4	9	3
0	2	1	shredded	0	2	2	0	4	4	3
0	0	0	shredded	0	4	4	0	3	3	1
0	3	3	1	0	4	4	0	7	9	2
0	2	2	shredded	0	4	5	0	7	8	1
1	3	3	shredded	0	7	10	0	3	4	2
0	3	3	shredded	2	4	7	0	5	5	4
0	5	4	shredded	0	4	2	1	6	15	6
0	2	2	shredded	0	1	1	1	5	12	3
0	10	20	shredded	0	3	8	1	shredded	4	1
0	0	0	shredded	0	5	5	2	3	7	2
0	0	0	shredded	0	4	4	0	2	3	3
0	4	3	shredded	0	0	4	2	4	5	3
1	1	2	shredded	0	0	0	2	6	8	0
1	3	5	shredded	0	5	6	0	5	6	1
0	0	0	shredded	0	4	8	0	0	0	3
0	1	1	***Total***	**46**	4	10	0	4	5	0
0	0	1			5	10	2	3	5	4
0	0	2			0	6	9	1	1	2
0	0	2			4	5	3	2	6	2
1	2	7			4	7	0	8	10	1
0	0	4			3	8	4	3	3	0
0	0	0			5	10	6	5	6	2
0	1	14			4	10	3	***Total***	**438**	**159**
0	0	1			3	3	1			
0	2	4			6	7	0			
0	0	0			7	8	0			
0	2	13			5	6	4			
0	0	0			4	5	4			
0	5	11			3	4	1			
0	6	15			4	4	2			
0	0	0			1	2	11			
0	0	3			2	3	7			
0	0	0			shredded	15	4			
0	0	0			shredded	20	14			
0	0	1			3	4	0			
0	0	0			3	4	7			
0	0	0			7	8	2			
0	0	0			2	2	1			
0	5	3			6	10	0			
Total	**94**	**141**			3	3	2			

Table 2 Gut contents of brushtail possums (Trichosurus vulpecula) trapped at Maunu, Whangarei, showing grass (%), Mexican and Native Dung Beetles, and other invertebrates

Sample #	Grass %	Mexican DB	Native DB	Other Invertebrates
1	20	0	0	2x stick insects (1x body: *Clitarchus hookeri*, 1x leg fragments: *Clitarchus* sp. or *Acanthoxyla* sp.), 1x ant (*Pachycondyla* sp. (native))
2	50	0	0	3x beetles (2x fungal feeding Scaphidiinae: *Brachynopus latus;* 1x weevil, *Mandalotus* sp.)
3	60	0	0	15x ants (*Prolasius advenus* (native))
4	0	0	0	1x ant (*Prolasius advenus*), 1x Stick insect body fragments (*Acanthoxyla* sp.)
5	20	0	0	0
6	0	0	0	2x beetle fragments (Steel blue ladybird: *Halmus chalybeus*)
7	10	0	0	13x ants (*Prolasius advenus*)
8	15	0	0	1x moth larva (Noctuidae: Indet.)
9	5	0	0	0
10	0	0	0	1x stick insect leg fragments (*Clitarchus* sp. or *Acanthoxyla* sp.)
11	0	0	0	0
12	0	0	0	0
13	0	0	0	1x aphid nymph (Aphididae: Indet.)
14	50	0	0	1x fly (*Hyberpygia varia*)
15	10	0	0	0
16	0	0	0	0
17	0	0	0	1x ant (*Pachycondyla* sp.)
18	20	0	0	7x ants (*Prolasius advenus*), 2x gnats (Diptera: Mycetophilidae: Indet.)
19	0	0	0	0
20	0	0	0	0
21	20	0	0	1x stick insect leg fragments (*Clitarchus* sp. or *Acanthoxyla* sp.)
22	10	0	0	1x fly leg (Syrphidae: *Eristalis* sp.)
23	0	0	0	0
24	40	0	0	1x stick insect leg fragments (*Clitarchus* sp. or *Acanthoxyla* sp.)
25	0	0	0	1x stick insect body fragments (*Acanthoxyla* sp.), 1x weevil (*Microcryptorhynchus* sp.)
26	60	0	0	1x stick insect body fragments (*Acanthoxyla* sp.)
27	70	0	0	1x beetle fragments (*Odontria* sp.)
28	40	0	0	1x mite (Oribatidae: Indet.)
29	80	0	0	0
30	20	0	0	0

5 Discussion

Several studies to date have documented invertebrates in brush-tail possum diets (through either gut content or scat analysis), at a range of prevalence. For example, Fitzgerald (1976) report invertebrates from 1 to 8% of individuals across 4 years of sampling, Glenn et al. (2012) report a 16% occurrence, Rickard (1996, cited in Nugent et al. 2000) reports a 17% occurrence, Cowan and Moeed (1987) report a 45% occurrence, and Clout (1977) reports fly larvae being recovered from 30 of 31 possum stomachs. This range of prevalence, and the wide taxonomic spread of species observed, strongly suggests that possum predation of invertebrates is highly opportunistic, with at least some being chance co-ingestion with plant material. With invertebrate remains identified from 19 (63%) of 30 possum gut contents, and in low amounts when present, the results from our current study show a similar pattern, if towards the high end of documented prevalence (Table 2).

Invertebrates recovered from possum gut contents here likewise covered a range of taxa, from physically smaller species (including aphids, mites and ants) to physically larger species (including weevils, (non-dung) beetles and stick insects). Although our dung beetle surveys clearly indicated a high prevalence and abundance of the Mexican dung beetles in pasture adjacent to where possums were trapped (Table 1), and the grass content of the trapped possum guts demonstrates clearly that they were foraging on pasture (Table 2), no dung beetle remains were recovered. This is surprising given that the Mexican dung beetle is a medium-sized beetle (12–15 mm; within the size range of the invertebrate species recovered from possum guts), is active at night, and is particularly abundant in spring and late summer/early autumn when new adults mass emerge and congregate in fresh dung pats to feed and nest build (Blank et al. 1983; unpublished data). The high prevalence of other invertebrates in our gut content analysis suggests that the association of dung beetles with cattle dung may make possums averse to foraging on them. This hypothesis is supported here both by the negligible observed disturbance of cow pats in their foraging range, and by the previous captive trial of Tompkins et al. (2012) in which dung beetles associated with cow pats were similarly not disturbed.

6 Conclusion

There are a few reports of dung beetle predation by mammals and birds (Obuch & Kristin 2004; Sleeman & Hutton 2005, cited in Piñero 2007), so we cannot be completely certain that possums will never eat dung beetles. However, there is now a mounting evidence base that any such occurrence is likely to be occasional at best. With the Mexican dung beetle being highly active and of a medium-large body size, it is a good model organism representative of the range of dung beetles approved by the EPA for unconditional release onto New Zealand pastures. Hence, our study confirms that the scenario the risk scenario of dung beetle presence affecting brushtail possum feeding behaviour is highly unlikely to be realised. There is thus little risk of such a mechanism increasing the potential for TB transmission both to and from cattle.

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8 References

Blank RH, Black H, Olson MH 1983. Preliminary investigations of dung removal and flight biology of the Mexican dung beetle *Copris incertus* in Northland (Coleoptera: Scarabaeidae). New Zealand Entomologist 7: 360–364.

Brown KP, Innes J, Shorten R 1993. Evidence that possums prey on and scavenge bird eggs, birds and mammals. Notornis 40: 169–177.

Brown KP, Moller H, Innes J 1996. Sign left by brushtail possums after feeding on bird eggs and chicks. New Zealand Journal of Ecology 20: 277–284.

Clout MN 1977. The ecology of the possum (*Trichosurus vulpecula* Kerr) in *Pinus radiata* plantations. Unpublished PhD Thesis, University of Auckland, Auckland, New Zealand.

Clout M, Ericksen K 2000. Anatomy of disastrous success; the brushtail possum as an invasive species. In: Montague TL. ed. The Brushtail Possum: biology, impact and management of an introduced marsupial. Lincoln, Canterbury, New Zealand. Manaaki Whenua Press. Pp. 1–9.

Coleman JD, Green WQ, Polson JG 1985. Diet of brushtail possums over a pasture-alpine gradient in Westland, New Zealand. New Zealand Journal of Ecology 8: 21–35.

Cowan PE 1990. Brushtail Possum. In: King CM. ed. The handbook of New Zealand mammals. Auckland, Oxford University Press. Pp. 68–98.

Cowan PE, Moeed A 1987. Invertebrates in the diet of brushtail possums, *Trichosurus vulpecula*, in lowland podocarp/mixed hardwood forest, Orongorongo Valley, New Zealand. New Zealand Journal of Zoology 14: 163–77.

Cruz J, Sutherland DR, Martin GR, Leung L K-P 2012. Are smaller subspecies of common brushtail possums more omnivorous than larger ones? Austral Ecology 37: 893–902.

Dean AG, Sullivan KM, Soe MM 2013. OpenEpi v.3.1: Open Source Epidemiologic Statistics for Public Health, Version. www.OpenEpi.com, updated 2013/04/06.

Dung Beetle Release Strategy Group (DBRSG) 2010. Importation and release of up to 10 beetles (Scarabaeinae) to bury livestock waste. ERMA Application for Approval. Wellington.

Dymock JJ 1993. A case for the introduction of additional dung burying beetles (Coleoptera: Scarabaeidae) into New Zealand. New Zealand Journal of Agricultural Research 36: 163–171.

Edwards P 2010. Biological control of pastoral dung in New Zealand. A report on the climatic suitability of exotic dung beetle species for introduction to New Zealand. Landcare Australia. 39 p.

ERMA 2010. Environmental Risk Management Authority Decision: Application ERMA200599. Wellington, New Zealand.

Emberson RM, Matthews EG 1973. Introduced Scarabaeinae (= Coprinae) (Coleoptera) in New Zealand. New Zealand Entomologist 5: 346–350.

Fincher GT 1981. The potential value of dung beetles in pasture ecosystems. Journal of the Georgia Entomological Society 16: 316–333.

Fischer O, Matlova L, Dvorska L, Svastova P, Bartl J, Melicharek I, Weston RT, Pavlik I 2001. Diptera as vectors of mycobacterial infections in cattle and pigs. Medical and Veterinary Entomology 15: 208–211.

Fischer O, Matlova L, Dvorska L, Svastova P, Bartos M, Weston RT, Kopecna M, Trcka I, Pavlik I 2005. Potential risk of *Mycobacterium avium* subspecies *paratuberculosis* spread by syrphid flies in infected cattle farms. Medical and Veterinary Entomology 4: 360–366.

Fischer O, Matlova L, Dvorska L, Svastova P, Peral DL, Weston RT, Bartos M, 2004. Beetles as possible vectors of infections caused by *Mycobacterium avium* species. Veterinary Microbiology 102: 247–255.

Fitzgerald AE 1976. Diet of the possum *Trichosurus vulpecula* (Kerr) in the Orongorongo valley, Wellingtron, New Zealand, in relation to food-plant availability. New Zealand Journal of Zoology 3: 399–419.

Glen AS, Byrom AE, Pech RP, Cruz J, Schwab A, Sweetapple PJ, Yockney I, Nugent G, Coleman M, Whitford J 2012. Ecology of bushtail possums in a New Zealand dryland ecosystem. New Zealand Journal of Ecology 36: 29–37.

Gilmore DP 1967. Foods of the Australian possum (*Trichosurus vulpecula* Kerr) on Banks Peninsula, Canterbury, and a comparison with other selected areas. New Zealand Journal of Science 10: 235–279.

Hanski I 1991. Epilogue. In: Hanski I, Cambefort Y eds Dung Beetle ecology. Princeton, NJ, Princeton University Press. Pp. 367–371.

Hanski I, Cambefort Y eds 1991. Dung Beetle ecology. Princeton, NJ, Princeton University Press. 481 p.

Harvie AE 1973. Diet of the possum (*Trichosurus vulpecula* Kerr) on farmland northeast of Waverley, New Zealand. Proceedings, New Zealand Ecological Society 20: 48–52.

Jones AG, Forgie SA, Scott DJ, Beggs JR 2012. Generalist dung attraction response in a New Zealand dung beetle that evolved with an absence of mammalian herbivores. Ecological Entomology 37: 124–133.

Morris RS, Pfeiffer DU 1995. Directions and issues in bovine tuberculosis epidemiology and control in New Zealand. New Zealand Veterinary Journal 43: 256–265.

Nichols E, Spector S, Louzada J, Larsen T, Amezquita S, Favila ME 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation 141: 1461–1474.

Nugent G 2011. Maintenance, spillover and spillback transmission of bovine tuberculosis in multi-host wildlife complexes: A New Zealand case study. Veterinary Microbiology 151: 34–42.

Nugent G, Sweetapple PJ, Coleman J, Suisted P 2000. Possum feeding patterns: dietary tactics of a reluctant folivore. In: Montague TL ed. The Brushtail Possum: biology, impact and management of an introduced marsupial. Lincoln, Canterbury, New Zealand, Manaaki Whenua Press. Pp. 10–33.

Nugent G, Whitford EJ, Hunnam JC, Wilson PR, Cross ML, de Lisle GW 2011. *Mycobacterium avium* subsp. *paratuberculosis* infection in wildlife on three deer farms with a history of Johne's disease. New Zealand Veterinary Journal 59: 293–298.

Obuch J, Kristin A 2004. Prey composition of the little owl *Athene noctua* in an arid zone (Egypt, Syria, Iran). Folia Zoologica 53: 65–79.

O’Reilly LM, Daborn CJ 1995. The epidemiology of *Mycobacterium bovis* infections in animals and man – a review. Tubercle and Lung Disease 76: 1–46.

Owen HJ, Norton DA 1995. The diet of introduced brushtail possums *Trichosurus vulpecula* in a low-diversity New Zealand *Nothofagus* forest and possible implications for conservation management. Biological Conservation 71: 339–345.

Pavlik I, Horvathova A, Bartosova L, Babak V, Moravkova M 2010. IS900 RFLP types of *Mycobacterium avium* subsp. *paratuberculosis* in faeces and environmental samples on four dairy cattle farms. Veterinární Medicína 55: 1–9.

Payton IL 2000. Damage to native forests. . In: Montague TL ed. The Brushtail Possum: biology, impact and management of an introduced marsupial. Lincoln, Canterbury, New Zealand, Manaaki Whenua Press. Pp. 111–125.

Piñero FS 2007. Predation of *Scarabaeus cristatus* F. (Coleoptera, Scarabaeidae) by jerboas (*Jaculus* sp.: Rodentia, Dipodidae) in a Saharan sand dune ecosystem. Zoologica Baetica 18: 69–72.

Ramsey D, Spencer N, Caley P, Efford M, Hansen K, Lam M, Cooper D 2002. The effects of reducing population density on contact rates between brushtail possums: implications for transmission of bovine tuberculosis. Journal of Applied Ecology 39: 806–818.

Rickard CG 1996. Introduced small mammals and invertebrate conservation in a lowland podocarp forest, South Westland, New Zealand. Unpublished MForSc Thesis, University of Canterbury, Christchurch, New Zealand.

Seldon DS 2002. A comparison of ground insect distributions from several New Zealand fragmented forest habitats. BSc(Hons) Dissertation, University of Auckland. 60 p.

Sleeman DP, Hutton SA 2005. Dung beetles *Geotrupes stercorarius* (L.) (Coleoptera: Geotrupidae) detected in diet of mink on Gola Island, Co. Donegal. Irish Naturalists’ Journal 28: 136.

Sweetapple PJ, Nugent G 1998. Comparison of two techniques for assessing possum (*Trichosurus vulpecula*) diet from stomach contents. New Zealand Journal of Ecology 22: 181–188.

Thomas WP 1960. Notes on a preliminary investigation into the habits of the life cycle of *Copris incertus* Say (Coprini: Coleoptera) in New Zealand. New Zealand Journal of Science 3: 8–14.

Tompkins D, Forgie S, Aislabie J, Nugent G, Gourlay H, McGill A, McLeod M, Yockney I, Paynter Q, Fowler S, Hayes L 2012. Informing the infectious disease risks of dung beetle releases into New Zealand. Landcare Research Internal Report LC908. 17 p. (http://dungbeetle.org.nz/wp-content/uploads/2012/08/Tompkins_Dung_Beetle_Disease_Report.pdf)

Whittington RJ, Marsh IB, Reddacliff LA2005. Survival of *Mycobacterium avium* subsp. *paratuberculosis* in dam water and sediment. Applied and Environmental Microbiology 71: 5304–5308.