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# Interacting biocontrol programmes: invasive cane toads reduce rates of breakdown of cowpats by dung beetles

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**Abstract** Ecological interactions among invasive species can affect not only the success of the invaders, but also their impact on ecosystems in the invaded range. In Australia, both dung beetles (subfamily Scarabaeinae) and cane toads (*Rhinella marina*) were introduced for biocontrol: the beetles to break down bovine faeces piles (cowpats) that otherwise accumulate and reduce pasture productivity, and the cane toad to consume scarab beetles that eat sugarcane and thus reduce sugar production. The dung beetles have been a success, whereas the toads have been a failure. Our experimental studies show that as well as impacting native fauna directly, cane toads reduce the rate of cowpat breakdown by consuming dung beetles. In the laboratory, dehydrated toads actively sought out cowpats based on scent cues, and in field enclosures, the presence of a cane toad significantly reduced rates of cowpat decomposition. Although toads have benefited from agricultural activities, their spread across Australia likely has reduced the effectiveness of one of the most successful biocontrol programmes ever conducted in that continent.

**Key words:** alien species, dung beetle, invasional meltdown, livestock production, *Rhinella marina*.

## INTRODUCTION

Many areas worldwide have been the recipients of multiple invasive species, often belonging to a wide range of phylogenetic lineages, and operating at a wide range of trophic levels (Vitousek *et al.* 1996, 1997; Mack *et al.* 2000; Pimentel *et al.* 2001; Frenot *et al.* 2005). For example, southern Florida has been subjected to invasion by more than 111 exotic vertebrate species (Ferriter *et al.* 2008). That diversity of invasive taxa within a newly colonized area inevitably results in ecological interactions not only between invaders and native species, but also among the invasive species (Carleton & Owre 1975; Nadel *et al.* 1992; Didham *et al.* 2007; Liu & Pemberton 2009). Such interactions are likely to be as complex as those between invaders and natives, and include processes such as competition, predation and infection. The outcomes of such interactions may have significant effects on native fauna – for example, suppression or facilitation of an invader by another, newly arriving invader, may change the impact of the former invader (Grosholz 2005; Griffen *et al.* 2008; Green *et al.* 2011). Alternatively, an earlier invasion may preadapt the native fauna or flora in ways that facilitate their ability to deal with subsequent invasions by other taxa (Price-Rees *et al.* 2012). Such outcomes may differ geographically, when the same species encounter each other in different environments (King *et al.* 2011).

Research attention on interacting impacts of invaders has focused primarily upon the potential for a subsequent invasion to facilitate success of an earlier invasion ('invasional meltdown': Simberloff & Von Holle 1999; Adams *et al.* 2003; Simberloff 2006; Montgomery *et al.* 2012). However, the reverse is true also: an invasive species may hinder the spread or success of another invader (Moulton & Pimm 1983; Simberloff & Stiling 1996; Simberloff 2006). Indeed, many classical examples of biocontrol are based on the idea that we can control an existing invader by bringing in a new invasive species (often, a parasite or pathogen from the native range of the earlier invader). That approach has succeeded in a number of well-documented cases: for example, the abundance of devastating invasive plants (prickly pear, *Opuntia monacantha*) and animals (rabbits, *Oryctolagus cuniculus*) in Australia has been reduced by the introduction of moths (*Cactoblastis cactorum*) and viruses (myxomatosis, calicivirus) respectively (Imms 1941; Kovaliski 1998; Fenner & Fantini 1999). As these examples illustrate, the negative (or positive) effect of one invader on another may have significant impacts on the native biota. Given that many areas worldwide are subject to invasion by many species, managers need to understand the ecological interactions between multiple invaders.

In the present study, we examine a case involving two taxa that were introduced to Australia, one in 1935 (cane toads) and the other (dung beetles) 30 years later, both for biological control. Unlike native mammalian herbivores, cattle produce cowpats (faeces

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piles) too large for native dung beetles to break down, and thus, livestock producers were faced with an increasing loss of pasture due to the accumulation of cowpats (Waterhouse 1974). Dung beetles (subfamily Scarabaeinae) from Africa, capable of breaking down such cowpats, were introduced several times from 1965 to 1985 (Nichols *et al.* 2008; Ridsdill-Smith & Edwards 2011). The new arrivals thrived, and successfully reduced cowpat coverage of pastureland (Waterhouse 1974). The second invasive species (the cane toad, *Rhinella marina* Bufonidae) proved to be far less successful. Brought to Australia in 1935 to eat beetles (*Lepidoderma albobirtum*, *Lepidiota frenchi*) that were threatening the commercial sugarcane crop (*Saccharum officinarum*), the toads apparently failed to affect beetle numbers, but spread widely and inflicted severe ecological damage (Lever 2001; Shine 2010). The major stimulus for the toads' introduction – their fondness for consuming beetles – raised concern that these large anurans also would eat 'helpful' dung beetles, and thus reduce the effectiveness of beetle-based cowpat control (Waterhouse 1974; Hughes 1975; Low 1999). Recent studies have shown that cane toads in tropical Australia are significantly more likely to be on or beside cowpats than expected by chance, and that they often consume dung beetles (González-Bernal *et al.* 2012). Our observations from toad dissections show that a toad on a cowpat can consume up to 23 beetles in a single night's foraging (see fig. 1 in González-Bernal *et al.* 2012) but other authors have found as many as 80 dung beetles in a single toad preying next to cowpats (Waterhouse 1974).

This scenario suggests that, especially if cane toads can locate cowpats at a distance and are actively attracted to them, a foraging toad might reduce dung beetle abundance enough to slow down the decomposition rate of a cowpat. In the present study we conducted experimental trials to ask: (1) are cane toads actively attracted to cowpats, based on scent cues; and (2) what effect does a toad's presence have on the rate of cowpat breakdown?

## METHODS

### Are cane toads attracted to the scent of cowpats?

We used T-maze experiments to measure the responses of dehydrated cane toads to cow dung. The toads were collected in and near Beatrice Hill Farm on the Adelaide River floodplain, 60 km east of Darwin (12°38'S, 131°19'E), on the night before the experiment. The day of the experiment, each toad was given access to free water in which to hydrate for 60 min, and then dehydrated (by at least 10% of their original hydrated body mass) by exposing it to wind flow (see Tingley *et al.* 2012 for detailed methods). After this, the toad

was placed at the base of a T-maze. The T-maze was constructed with 3 × 1.2-m lengths of black plastic guttering and enclosed above with clear perspex. Air was drawn through the two terminal ends of the T by a quiet 12-volt computer fan. We placed 100 g of freshly deposited cow dung (collected from cattle-handling yards at the nearby farm a few hours before) in a perforated opaque container at one end of the T, with an identical opaque container (containing dry paper towel of similar volume to the cow dung, to adjust the amount of air flowing through the container) as a control at the other end. Between trials, the maze was cleaned with 1% bleach to remove scent clues, and the position of the cow dung was alternated between successive trials. The experiment was run at night (when adult toads are active), in a dark room with a red light for illumination. Trials were run for a maximum of 15 min, starting from the moment that the individual was placed inside the T-maze (toads took on average 6.5 min to make a decision). The choice made by each toad (whether it reached the control *versus* treatment end of the T-maze, among those that voluntarily left the starting area) was recorded.

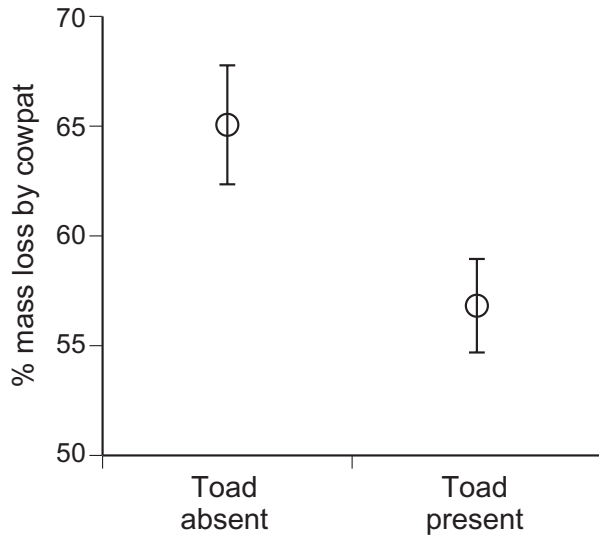
### Does the presence of a cane toad affect the rate of cowpat breakdown?

We constructed 12 outdoor enclosures, each measuring 2.4 × 1.2 m, with metal walls 1 m high. Each enclosure contained a substrate of natural soil and vegetation, plus a pool of water (replenished daily to maintain a constant level). Fresh bovine dung (collected in the morning) was kept in closed buckets until use, and mixed to ensure that any beetles in it were evenly distributed. At dusk, a 3-kg cowpat was formed and placed at a randomly selected site within each enclosure. Toads were collected at the field site (see above) the previous night, and were weighed, measured and then allowed access to water for rehydration. Six enclosures were each allocated three toads, whereas the other six enclosures served as controls, containing cowpats but without toads. After 10 days, the artificial cowpat was removed and weighed. We used loss in mass (as a proportion of initial mass) as our measure of cowpat decomposition rate. We replicated these trials four times over the period September to November 2010 and July 2011, yielding data for a total of 24 enclosures with toads present (the other six trials used an alternative food source, and are not included in this analysis), and 30 with toads absent. Our analysis included treatment (toad present or absent) and time period as factors.

## RESULTS

### Are cane toads attracted to the scent of cowpats?

Of the 75 toads tested, 27 chose the control arm of the T-maze (containing paper towel) while 48 went to the T-arm containing the cowpat. Thus, dehydrated toads showed a significant tendency to move towards the cowpat ( $\chi^2 = 5.34$ , d.f. = 1,  $P = 0.02$ ).



**Fig. 1.** Effect of the presence of cane toads (*Rhinella marina*) on the rate of breakdown of cowpats in outdoor experimental enclosures, showing that cowpats exposed to cane toads decomposed less rapidly than did cowpats not exposed to toads. Graph shows mean values and associated standard errors, based on 24 replicate enclosures with toads present, and 30 enclosures with toads absent.

### Does the presence of a cane toad affect the rate of cowpat breakdown?

After 10 days, all cowpats had lost considerable mass (from 783 to 2866 g; mean = 1777 g). Rates of mass loss were higher in some trial periods than others ( $F_{4,44} = 3.77$ ,  $P = 0.01$ ) but with no significant interaction between time period and treatment ( $F_{4,44} = 0.16$ ,  $P = 0.96$ ). Overall, cowpats that had been exposed to toads lost 9% less mass, on average, than had cowpats in adjacent enclosures without toads (Fig. 1;  $F_{1,44} = 6.67$ ,  $P = 0.01$ ).

## DISCUSSION

In previous work on this system, we have shown that cane toads frequently use cowpats in the field, and thereby enhance their hydric balance and feeding rate (González-Bernal *et al.* 2012). The present study builds upon those results by showing that dehydrated cane toads can detect the scent of a cowpat, and are actively attracted to that scent. Our field enclosure experiments show that the toads' consumption of dung beetles can significantly reduce the rate at which a cowpat decomposes.

Our T-maze experiment was designed to mimic the situation encountered by cane toads during the prolonged dry season in the Australian wet-dry tropics. In many livestock-producing areas, water sources are

scarce and the closest moist microhabitat may be a freshly deposited cowpat. Because cattle travel long distances daily between watering points and foraging areas (Low *et al.* 1981; Pickup & Chewings 1988), cowpats deposited along cattle trails may provide toads with a vital connectivity between otherwise-distant rehydration opportunities. Clearly, toads are able to locate cowpats using scent cues alone (because our T-maze design eliminated visual cues, etc.). Thus, cowpats may enhance the toad's ability to disperse across dry areas, at least in country that is devoted to livestock production (approximately 70% of the arid areas in Australia: James *et al.* 1999). Provision of artificial watering points for stock also has facilitated cane toad invasion through semi-arid regions (Florance *et al.* 2011). However, artificial waterbodies are on average about 10 km apart (James *et al.* 1999), whereas adult cane toads disperse less than 2 km per night (Phillips *et al.* 2007). Thus, cowpats might act as hydric islands between permanent artificial water sources. Furthermore, where artificial livestock watering points are in the form of raised troughs (and thus, inaccessible to toads), cowpats may serve as a mechanism for transferring moisture from troughs to the ground, and thus provide hydration sites for toads.

Our results fit well with our earlier work on the benefits of cowpats to cane toads (González-Bernal *et al.* 2012). The current study suggests that predation on dung beetles by cane toads around cowpats directly reduces the rate of cowpat decomposition. Other studies show that the rate of cowpat decomposition is proportional to the number of active beetles; field observations in Hawaii (where dung beetles have been introduced also) estimate dung beetle densities at around 15 to 40 pairs of beetles per 1000 cc of cow dung (Bornemissza 1970). In a previous study (González-Bernal *et al.* 2012), we recorded individual toads on 1000 cc cowpats consuming between two and 23 dung beetles in a single night (average = 6.3). Thus, rates of toad predation on dung beetles may be high enough to substantially influence cowpat breakdown. The only alternative reason that cowpats might have been heavier due to toad presence was reduced water loss, but we can see no plausible mechanism for this effect (toads were usually beside not on top of cowpats, and water would be as likely to move from a cowpat to a toad, as from a toad to a cowpat).

A toad-induced decrease in rates of cowpat decomposition likely has several effects. First, the negative effects of dung accumulation on local grasses (Waterhouse 1974) will be magnified. Second, greater longevity of cowpats may enhance survival and, thus, the rate of emergence of pest insects that develop within the dung. Such insects include the bush fly *Musca vetustissima* and the buffalo fly *Haematobia exigua*. The former species is a nuisance to humans in Australia, and the latter is a blood sucking introduced

fly that can reduce body condition of cattle and promote the transmission of stephanofilaria (Hughes & Morton 1985; Williams *et al.* 1985). Although there are no quantitative studies on the abundance of these fly species before *versus* after the introduction of dung beetles, anecdotal reports suggest that fly numbers depend upon dung availability (Hughes *et al.* 1978; Doube & Dalton 2003). Direct comparisons show that dung beetles have reduced the rate of emergence of these flies in Australia. By mechanical damage to fly eggs and through competition for dung, dung beetles reduce both the emergence and body size of flies (Bornemissza 1970; Hughes 1975; Nichols *et al.* 2008). In addition, dung beetles offer other ecosystem services such as nutrient replacement in the soil by dung burial, plant growth enhancement through nutrient redistribution, seed dispersal and parasite suppression (Bryan 1976; Nichols *et al.* 2008; Ridsdill-Smith & Edwards 2011). Thus, predation by cane toads on dung beetles (the only effective bovine dung decomposers in Australia) may reduce nutrient recycling and plant growth, and thus induce a wide-ranging cascade of effects on ecosystem functioning (Wu *et al.* 2011).

Tropical Australia contains a wide range of introduced dung beetle species, and the impact of cane toads may well be worse for some taxa than for others. Because adult cane toads forage at night (Pizzatto & Shine 2008) nocturnally active dung beetles are likely to be most vulnerable (e.g. *Onitis alexis*, *Onitis viridulus*, *Onthophagus gazella* and *Onthophagus sagittarius* in the Northern Territory). During our own study, we identified three species from cane toad stomachs (the introduced taxa *Onthophagus gazella* and *Onitis alexis* and one native taxon, probably *Onthophagus chepara*).

In summary, our study provides an example of one invader (the cane toad) modifying the success of another invader (dung beetles), with possible collateral impacts on the ecological effects of a third suite of invaders (cattle, bush flies, blood-sucking flies). Interestingly, all of the taxa involved in this interaction were brought to Australia by an earlier invader (Europeans). Changes in cowpat abundance and size wrought by these interactions likely have many impacts, economically (in terms of livestock production) as well as ecologically, on a diverse array of native taxa that live in the areas affected.

Although our study reveals that toad impacts on cowpat breakdown are strong enough to be detectable, the magnitude of such effects on a broader spatial scale remains unclear. Based on the abundance of dung beetles even in areas of eastern Australia that have been colonized by cane toads, the negative impact of cane toads on dung beetle populations may be trivial (Hughes 1975). Cane toads are not specialized predators on dung beetles, but can consume high numbers of them when this prey type is available. To evaluate the broader-scale impact of cane toads on cowpat

degradation and its associated consequences, we would need ambitious field experiments. In the absence of such work, any evaluation of overall impacts remains speculative. The vast extent of livestock-grazing activities in Australia, and the large and expanding distribution of cane toads, means that the possibility of significant ecological interactions between these introduced taxa warrants further study.

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## REFERENCES

- Adams M. J., Pearl C. A. & Bury R. B. (2003) Indirect facilitation of an anuran invasion by non-native fishes. *Ecol. Lett.* **6**, 343–51.
- Bornemissza G. F. (1970) Insectary studies on the control of dung breeding flies by the activity of the dung beetle *Onthophagus gazella* F. (Coleoptera: Scarabaeinae). *J. Aust. Entomol. Soc.* **9**, 31–41.
- Bryan R. P. (1976) The effect of the dung beetle, *Onthophagus gazella*, on the ecology of the infective larvae of gastrointestinal nematodes of cattle. *Aust. J. Agric. Res.* **27**, 567–74.
- Carleton A. R. & Owre O. T. (1975) Red-whiskered bulbul in Florida: 1960–71. *Auk* **92**, 40–57.
- Didham R. K., Tylianakis J. M., Gemmill N. J., Rand T. A. & Ewers R. M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* **22**, 489–96.
- Doube B. & Dalton G. (2003) *Dung Beetles: Transform a Pollutant into an Environmental and Agricultural Benefit*. Fleurieu Beef Group Inc., Strathalbyn.
- Fenner F. & Fantini B. (1999) *Biological Control of Vertebrate Pests: The History of Myxomatosis – An Experiment in Evolution*. CABI Publishing, Wallingford.
- Ferriter A., Doran B., Winston R. *et al.* (2008) *South Florida Environmental Report. Chapter 9: The Status of Nonindigenous Species in the South Florida Environment*. South Florida Water Management District, West Palm Beach, FL, USA.
- Florance D., Webb J. K., Dempster T., Kearney M. R., Worthing A. & Letnic M. (2011) Excluding access to invasion hubs can contain the spread of an invasive vertebrate. *Proc. R. Soc. B* **278**, 2900–8.
- Frenot Y., Chown S. L., Whinam J. *et al.* (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biol. Rev.* **80**, 45–72.

- González-Bernal E., Greenlees M., Brown G. P. & Shine R. (2012) Cane toads on cowpats: commercial livestock production facilitates toad invasion in tropical Australia. *PLoS ONE* **7**, e49351.
- Green P. T., O'Dowd D. J., Abbott K. L., Jeffery M., Retallick K. & Mac Nally R. (2011) Invasional meltdown: invader-invader mutualism facilitates a secondary invasion. *Ecology* **92**, 1758–68.
- Griffen B. D., Guy T. & Buck J. C. (2008) Inhibition between invasives: a newly introduced predator moderates the impacts of a previously established invasive predator. *J. Anim. Ecol.* **77**, 32–40.
- Grosholz E. D. (2005) Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 1088–91.
- Hughes R. D. (1975) Introduced dung beetles and Australian pasture ecosystems: papers presented at a symposium during a meeting of the Australia and New-Zealand Association for Advancement of Science at Canberra in January 1975. *J. Appl. Ecol.* **12**, 819–37.
- Hughes R. D. & Morton R. (1985) Bush fly abundance in an overwintering zone during 1979–82 compared with some data collected before the introduction of exotic dung beetles. *J. Aust. Entomol. Soc.* **24**, 65–8.
- Hughes R. D., Tyndale-Biscoe M. & Walker J. (1978) Effects of introduced dung beetles (Coleoptera: Scarabaeidae) on the breeding and abundance of the Australian bushfly, *Musca vetustissima* Walker (Diptera: Muscidae). *Bull. Entomol. Res.* **68**, 361–72.
- Imms A. D. (1941) The prickly-pear problem in Australia. *Nature* **148**, 303–5.
- James C. D., Landsberg J. & Morton S. R. (1999) Provision of watering points in the Australian arid zone: a review of effects on biota. *J. Arid Environ.* **41**, 87–121.
- King C. M., Foster S. & Miller S. (2011) Invasive European rats in Britain and New Zealand: same species, different outcomes. *J. Zool.* **285**, 172–9.
- Kovaliski J. (1998) Monitoring the spread of rabbit hemorrhagic disease virus as a new biological agent for control of wild European rabbits in Australia. *J. Wildl. Dis.* **34**, 421–8.
- Lever C. (2001) *The Cane Toad. The History and Ecology of a Successful Colonist*. Westbury Academic Press, Otley.
- Liu H. & Pemberton R. W. (2009) Solitary invasive orchid bee outperforms co-occurring native bees to promote fruit set of an invasive *Solanum*. *Oecologia* **159**, 515–25.
- Low T. (1999) *Feral Future: The Untold Story of Australia's Exotic Invaders*. Viking Press, Ringwood.
- Low W. A., Dudzinski M. L. & Muller W. J. (1981) The influence of forage and climatic conditions on range community preference of shorthorn cattle in central Australia. *J. Appl. Ecol.* **18**, 11–26.
- Mack R. N., Simberloff D., Lonsdale W. M., Evans H., Clout M. & Bazzaz F. A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* **10**, 689–710.
- Montgomery W., Lundy M. & Reid N. (2012) 'Invasional meltdown': evidence for unexpected consequences and cumulative impacts of multispecies invasions. *Biol. Invasions* **14**, 1111–25.
- Moulton M. P. & Pimm S. L. (1983) The introduced Hawaiian avifauna – biogeographic evidence for competition. *Am. Nat.* **121**, 669–90.
- Nadel H., Frank J. H. & Knight R. J. (1992) Escapees and accomplices – the naturalization of exotic *Ficus* and their associated faunas in Florida. *Fla. Entomol.* **75**, 29–38.
- Nichols E., Spector S., Louzada J., Larsen T., Amequita S., Favila M. E. & The Scarabaeinae Research Network (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol. Conserv.* **141**, 1461–74.
- Phillips B. L., Brown G. P., Greenlees M., Webb J. K. & Shine R. (2007) Rapid expansion of the cane toad (*Bufo marinus*) invasion front in tropical Australia. *Austral Ecol.* **32**, 169–76.
- Pickup G. & Chewings V. H. (1988) Estimating the distribution of grazing and patterns of cattle movement in a large arid zone paddock. An approach using animal distribution models and Landsat imagery. *Int. J. Remote Sens.* **9**, 1469–90.
- Pimentel D., McNair S., Janecka J. et al. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agr. Ecosyst. Environ.* **84**, 1–20.
- Pizzatto L. & Shine R. (2008) The behavioral ecology of cannibalism in cane toads (*Bufo marinus*). *Behav. Ecol. Sociobiol.* **63**, 123–33.
- Price-Rees S. J., Brown G. P. & Shine R. (2012) Interacting impacts of invasive plants and invasive toads on native lizards. *Am. Nat.* **179**, 413–22.
- Ridsdill-Smith T. J. & Edwards P. B. (2011) Biological control: ecosystem functions provided by dung beetles. In: *Ecology and Evolution of Dung Beetles* (eds L. W. Simmons & T. J. Ridsdill-Smith) pp. 245–64. Wiley-Blackwell Publishing Ltd., Oxford.
- Shine R. (2010) The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *Q. Rev. Biol.* **85**, 253–91.
- Simberloff D. (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecol. Lett.* **9**, 912–19.
- Simberloff D. & Stiling P. (1996) How risky is biological control? *Ecology* **77**, 1965–74.
- Simberloff D. & Von Holle B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions* **1**, 21–32.
- Tingley R., Greenlees M. J. & Shine R. (2012) Hydric balance and locomotor performance of an anuran (*Rhinella marina*) invading the Australian arid zone. *Oikos* **121**, 1959–65.
- Vitousek P. M., Dantonio C. M., Loope L. L., Rejmanek M. & Westbrooks R. (1997) Introduced species: a significant component of human-caused global change. *N. Z. J. Ecol.* **21**, 1–16.
- Vitousek P. M., Dantonio C. M., Loope L. L. & Westbrooks R. (1996) Biological invasions as global environmental change. *Am. Sci.* **84**, 468–78.
- Waterhouse D. F. (1974) The biological control of dung. *Sci. Am.* **230**, 100–9.
- Williams J. D., Sutherst R. W., Maywald G. F. & Petherbridge C. T. (1985) The southward spread of buffalo fly *Haematobia irritans exigua* in eastern Australia and its survival through a severe winter. *Aust. Vet. J.* **62**, 367–9.
- Wu X. W., Duffy J. E., Reich P. B. & Sun S. C. (2011) A brown-world cascade in the dung decomposer food web of an alpine meadow: effects of predator interactions and warming. *Ecol. Monogr.* **81**, 313–28.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Appendix S1.** Toad sitting on a cowpat, and with ingested dung beetles.