

## Mammalian Insectivores Exert Top-Down Effects on *Azteca* Ants

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### ABSTRACT

Insectivorous mammals are hypothesized to reduce the abundance of their insect prey. Using a 14-yr mammal exclusion experiment, we demonstrate for the first time that a widespread and abundant Neotropical mammalian insectivore (Tamandua: *Tamandua mexicana*) reduced *Azteca* ant abundance. *Azteca* ant nests inside mammal enclosures were significantly larger than nests in control plots, where tamanduas were more abundant. These top-down effects were caused not only by direct consumption, but also through non-trophic direct effects, specifically nest damage. In contrast, tamanduas appeared to exert no significant top-down effect on termite prey, which have strong chemical defenses. Our results are consistent with theory that strong defenses against predation can mitigate the top-down effects of predators on some prey species. We argue that predicting the degree of top-down effects caused by predators requires both a quantitative knowledge of prey choice and an understanding of the anti-predator defenses of prey.

Abstract in Spanish is available in the online version of this article.

*Key words:* anti-predatory defenses; *Azteca*; BCI; indirect predation effects; tamandua; top-down effects; trophic interactions.

THERE IS COMPELLING EVIDENCE THAT BIRDS, BATS, AND INSECTIVOROUS REPTILES CAN REDUCE THE ABUNDANCE OF THEIR INVERTEBRATE PREY (Dial & Roughgarden 1995, Borkhataria *et al.* 2006, Feeley & Terborgh 2008, Kalka *et al.* 2008, Koh 2008, Mooney *et al.* 2010, Bohm *et al.* 2011). In contrast, few studies have demonstrated that terrestrial insectivorous mammals can reduce the abundance of their invertebrate prey (but see: Rao 2000, Terborgh *et al.* 2001 discussed below). As an illustration, a recent meta-analysis of 113 studies of insectivore effects on arthropod communities included birds, bats, and lizards, but not a single terrestrial mammal (Mooney *et al.* 2010). This taxon gap is surprising because terrestrial insectivorous mammals have evolved in the majority of temperate and tropical habitats and can be the largest insectivore in these food webs (39 kg giant anteaters [Myrmecophagidae] and 70 kg armadillos [Orycteropodidae] McNab 1986). Currently, the best evidence of top-down effects by terrestrial mammalian insectivores are studies by Terborgh *et al.* (2001) and Rao (2000) that concluded that armadillos inhabiting predator-free islands reduced leaf-cutter ant colony survivorship. Here, we examine top-down effects involving a different mammalian insectivore (northern tamanduas), and its ant and termite prey (Fig. 1).

Ants and termites are some of the most abundant potential sources of animal prey in the tropics (Redford & Dorea 1984, Montgomery 1985b). Studies have estimated that ants and ter-

mites compose over 30 percent of total animal biomass and up to 75 percent of total insect biomass in Amazonian rain forests, with ants comprising the bulk of individuals and biomass both in the canopy and on the ground (Fittkau & Klinge 1973, Erwin 1983, Adis *et al.* 1984). Termites in tropical savannah and cerrado (dry woodlands) can outweigh the per hectare biomass of many groups of vertebrates in Amazonian forests (Redford 1986, Vasconcellos & Moura 2010). Colonies of ants and termites are relatively long-lived and overall population numbers do not fluctuate widely during the year making them particularly reliable sources of food across space and time (Lubin *et al.* 1977, Baroni-Urbani *et al.* 1978, Thorne 1985, Thorne & Haverly 2000). In spite of the ubiquity and availability of ants and termites as prey items, it remains unknown whether their abundance can be reduced by one of their primary mammalian predators within a tropical forest. Here, we take advantage of a 14-yr mammal exclusion study to evaluate the degree to which northern tamanduas reduce the abundance of their insect prey, and test the hypothesis that tamanduas will have a strong top-down impact on their primary prey.

### METHODS

**STUDY SITE AND SPECIES.**—We conducted this study within the Barro Colorado Nature Monument (BCNM), Panama in a seasonally moist semi-deciduous tropical forest where rainfall typically exceeds more than 2.2 m annually. These semi-deciduous forests have a distinct dry season that lasts from December until

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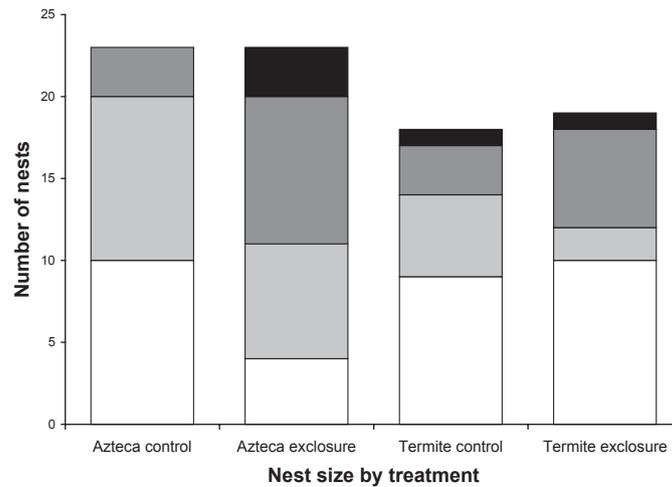


FIGURE 1. Effect of tamanduas on nest size in *Azteca* and termites. Nest size categories: □ small, ■ medium, ■ large, ■ very large. There were no very large *Azteca* nests outside the enclosures, and the number of large nests was significantly lower. For nest dimensions see Methods.

April. Additional details regarding the flora, fauna, and climate of this area are contained in Leigh *et al.* (1996).

The northern tamandua (4–6 kg, hereafter ‘tamandua’) is a member of the Neotropical order Xenarthra and the anteater family Myrmecophagidae. The species’ distribution extends from southern Mexico to northwestern Peru below 1000 m in a variety of forest and woodland habitats (Navarrete & Ortega 2011, Nuñez-Perez *et al.* 2011). Tamanduas are a common mammal in the BCNM, and occur at densities similar to other Neotropical forests (Glanz 1982, Wright *et al.* 2000, Guariguata *et al.* 2002, Van Hulle & Vaughan 2009). Tamanduas are specialist predators of ants and termites, with prehensile tails that allow them to enter arboreal insect nests (Montgomery & Lubin 1977). They feed on a wide variety of species including Formicine, Myrmecine, and Dolichoderine ants as well as *Nasutitermes* spp. and *Microcerotermes* spp. termites (Lubin *et al.* 1977, Lubin & Montgomery 1981).

Most tamandua predator species have greatly reduced densities on Barro Colorado Island (BCI), or are absent almost entirely (Harpy eagles: *Harpia harpyja*, pumas: *Puma concolor*, and jaguars: *Panthera onca*, Rettig 1978, Touchton *et al.* 2002, Moreno *et al.* 2006, Ford & Boinski 2007). In contrast, the density of ocelots (*Leopardus pardalis*) on BCI (1.6 individuals per km<sup>2</sup>) is higher than any Central or South American site where ocelot population density has been measured (Emmons 1988, Moreno *et al.* 2006, Di Bitetti *et al.* 2008). We conclude that ocelots are the primary predation threat to tamanduas on BCI. However, puma and ocelot scats found on BCI contained few tamandua remnants (2.3% of puma scats,  $N = 88$ ; 2.1% of ocelot scats,  $N = 190$ ; Moreno *et al.* 2006). Tamandua densities on BCI (0.053/ha Glanz 1982, 0.014/ha Wright *et al.* 1994, 0.042/ha Wright *et al.* 2000, 0.041–0.068/ha Brown 2011) are similar to other tropical forest sites (*Tamandua mexicana*: Costa Rica: 0.06/ha Guariguata *et al.* 2002, 0.057/ha Van Hulle & Vaughan 2009, *Tamandua tetradactyla*: Brazil: 0.004/ha Desbiez *et al.* 2010, Venezuela: 0.06/ha Eisenberg *et al.* 1979).

The Dolichoderine genus *Azteca* is a strictly Neotropical group of arboreal ants that can be the dominant ant genus

across pristine forest and human-dominated ecosystem canopies (Longino 2007, Ribeiro *et al.* 2013). *Azteca* species occur as both generalist insectivores and as specialized inhabitants of myrmecophytic plants, forming mutualistic relationships with their host trees and providing a biotic defense against herbivorous insects (Schupp 1985, Sanders *et al.* 2007). Some species build pendulous papery carton nests (Fig. S1) that can reach up to 2 m long and persist for several years (Longino 2007). *Azteca* defend their nests by rapidly swarming over intruders in large numbers, biting them, and using repellent secretions. There is some evidence that this defense limits the duration of predatory attacks by tamandua anteaters (Montgomery & Lubin 1977).

*Nasutitermes* spp. (*N. corniger*, *N. nigriceps* and *N. costalis*) are all arboreally nesting termites that are found commonly on BCI (Lubin & Montgomery 1981). Like other termites, *Nasutitermes* spp. remove massive quantities of plant material and play a critical role in cycling nutrients through their ecosystems (Wood & Sands 1978, Vasconcellos & Moura 2010). Although colonies can persist inside of wood, *Nasutitermes* workers construct rounded, irregularly shaped epigeal nests of a mud-like carton formed from saliva and digested wood pulp. Compared to ants, many termites are relatively easy prey because the numerically dominant workers move slowly along predictable foraging trails and have no defensive abilities (Scholtz *et al.* 2008). However, the soldier caste of *Nasutitermes* species produces a sticky defensive secretion through a long, pointed rostrum and mammalian *Nasutitermes* predators, including the tamandua, tend to show strong preferences for reproductive and worker castes over soldiers (Lubin & Montgomery 1981, Redford 1985, Oyarzun *et al.* 1996). *Nasutitermes* soldiers recruit rapidly and in large numbers to breaks in their carton nests, and mammalian predation on *Nasutitermes* is typically accompanied by intense grooming behavior (Lubin & Montgomery 1981, Redford 1985). As in *Azteca*, *Nasutitermes* defenses appear to limit, but not prevent, tamandua predation (Redford 1986).

**EXCLOSURE DESIGN.**—In 1994, we constructed eight  $30 \times 45$  m enclosure plots on Barro Colorado Island ( $N = 4$ ) and the adjacent Gigante Peninsula ( $N = 4$ ; Royo & Carson 2005). We randomly selected enclosure plots and surrounded them with 2.2 m tall steel fencing, using a  $1.3 \times 1.3$  cm mesh around the base that extended to 0.25 m belowground. We paired each enclosure plot with an adjacent control plot of equal size located adjacent to the enclosures. The enclosures effectively reduced the abundance of most terrestrial mammalian vertebrates on BCI, such as agoutis (*Dasyprocta punctata*), pacas (*Agouti paca*), armadillos (*Dasyfus novemcinctus*), brocket deer (*Mazama americana*), white tail deer (*Odocoileus virginianus*), spiny rats (*Proechimys semispinosus*), peccaries (*Ayassu tajacu*), and tapirs (*Tapirus bairdii*; Royo & Carson 2005).

While tamanduas can travel both terrestrially and arboreally (Brown 2011), travel costs related to climbing and descending the fences and the novel non-biotic fence substrate should cause a reduction in tamandua activity inside the enclosures. We used infrared motion sensitive wildlife cameras (Reconyx RC55, Holmen, WI, U.S.A.) to quantify differences in tamandua abundance in enclosures vs. control plots (Rowcliffe *et al.* 2008, 2011). We placed cameras in each treatment area for 41 d from August–October 2008, resulting in a total of 656 trap days (for further details, see: Kurten 2010). Tamanduas are the only mammal on BCI that commonly feed on arboreal termite and *Azteca* nests. All nests we found were at least 1 m above the ground, thus it is highly unlikely that they could have been affected by armadillos or other terrestrial mammals. Although silky anteaters (*Cyclopes didactylus*) also consume *Azteca* ants, only a very small percentage of insect remains in silky anteater fecal samples were *Azteca* (1.6%; Montgomery 1985a, 0.3%; Best & Harada 1985). In contrast, *Azteca* ants make up 7 percent of the diet of tamanduas (Montgomery 1985b). Based on observations of tamandua feeding behavior and observed damage to *Azteca* nests, both Lubin *et al.* (1977) and Montgomery (1985b) concluded that tamanduas are the major predator of *Azteca* on BCI. Indeed, Lubin *et al.* (1977) found that all observed damage to *Azteca* nests was caused by tamanduas (for tamandua nest damage description see: Fig. S1), whereas termite nests were also damaged by nesting birds, bats, and to a lesser degree, euglossine bees (see also: Dechmann *et al.* 2004). Any differences in *Azteca* nest size or abundance between the enclosure and control plots should have been the result of changes in tamandua abundance, while termite nests were also damaged by several species that were not affected by the mammal enclosures. In addition, the enclosure design should not have affected the resource base for these insects.

**PREY CENSUS.**—We visually censused *Azteca* spp. and termite (*Nasutitermes* spp. and *Microcerotermes exiguus*) nests in the enclosure and control plots during August–September, 2010. Due to the height of the nests (1–20 m), it was not possible to directly measure the nests, and we used visual estimates of nest size. We categorized conical *Azteca* nests by their length: small (0–25 cm), medium (25–65 cm), large (65–110 cm), and very large

(110–250 cm); and categorized circular termite nests by their diameter: small (0–20 cm), medium (20–40 cm), large (40–65 cm), and very large (>65 cm). Nest size has repeatedly been verified to be strongly correlated with ant and termite density (Collins 1981, Franks *et al.* 1992, Tschinkel 1993, 1999, Rasse & Deneubourg 2001). We performed analyses in JMP 5.1 (SAS Institute Inc., Cary, NC, U.S.A.).

**TAMANDUA SITE REVISITATION RATES.**—Tamanduas may repeatedly revisit and damage individual *Azteca* nests (Lubin *et al.* 1977, Montgomery & Lubin 1977). Because ants are able to repair their nests and conceal prior damage, it is difficult to calculate how frequently tamanduas may revisit a given nest. We used direct observations and GPS tracking data from BCI tamanduas to determine the average time between repeated visits to known feeding areas and estimate the potential for nest revisitation. We captured a total of 17 tamanduas (eight male, nine female) and fitted them with GPS receivers (e-obs GmbH, Grünwald, Germany) between November 2008 and March 2010 (full details for capture and anesthetization methods can be found in: Brown 2011). GPS receivers remained on the tamanduas for an average of 13 d (range 6–20) and had an average 19.3 m error ( $\pm 8.2$  m,  $N = 1121$ ; Brown 2011). We entered all GPS locations into ArcGIS 9.3 (Esri, Redlands, CA, U.S.A.), and consecutive fixes were connected to construct animal movement paths. We were able to observe 16 of the 17 tamanduas feeding on insects (the genera of which were not always possible to identify from the ground) and we recorded these locations with a handheld GPS unit (Garmin 60CSX). We calculated the revisitation times to these insect-feeding locations based on the animal paths constructed in ArcGIS 9.3. If a tamandua passed within 9.6 m ( $1/2$  average GPS error) of this point, it was classified as a revisitation, and the time between the observed feeding event and the GPS derived revisit was recorded.

## RESULTS

We observed tamanduas six times more frequently in control plots than inside the enclosures (average daily trap rate control = 0.018, enclosure = 0.003, one-tailed paired  $t$ -test,  $t = 2.376$ ,  $df = 7$ ,  $P = 0.025$ ). The tamandua enclosure plots contained a significantly greater proportion of large and very large *Azteca* nests (Pearson  $\chi^2_{3,37} = 9.10$ ,  $P = 0.028$ ). Large *Azteca* nests were three times more abundant in the enclosures and very large nests were completely absent outside the enclosures (Fig. 1). The size of *Nasutitermes* and *Microcerotermes* termite nests were not significantly different between the enclosure and control plots (Pearson  $\chi^2_{3,36} = 2.31$ ,  $P = 0.510$ ). Tamanduas did not cause a significant reduction in *Azteca* nest density (enclosure mean and SD =  $3.13 \pm 2.53$ , control mean =  $3.00 \pm 3.02$ , paired  $t$ -test  $P_{2,8} = 0.928$ ) or termites (enclosure mean =  $2.50 \pm 2.20$ , control mean =  $3.00 \pm 1.96$ , paired  $t$ -test  $P_{2,8} = 0.685$ ). GPS tracked tamanduas revisited the feeding locations on average every 5.04 d ( $\pm 5.02$  SD, range = 0.99–25 d,  $N = 29$  feeding sites).

## DISCUSSION

Our findings strongly support the hypothesis that an insectivorous mammal (tamanduas), exert top-down effects on at least one of its prey (*Azteca* ant nests). Because nest size is strongly correlated with ant density (Franks *et al.* 1992, Tschinkel 1993, 1999, Rasse & Deneubourg 2001), the substantial reduction in ant nest size we observed means fewer ants, thus we found strong evidence of top-down effects due to tamandua predation. Although we have no measure of insect canopy herbivory, we hypothesize that if *Azteca* ants exert top-down effects on herbivorous insects, herbivory levels should be lower in the exclusion plots compared to the control plots. Terborgh *et al.* (2001) found similar results on predator-free islands in Venezuela, but these authors concluded that armadillos were able to exert top-down effects on leaf-cutter ants *because* their apex predators were absent. In this study, we found that tamanduas exert top-down effects *despite* the presence of their predators.

While we were not able to control or manipulate predator density (*sensu*: Terborgh *et al.* 2001), we posit that the presence or absence of felid predators may play little role in controlling tamandua populations because tamandua remains were uncommon in felid scats on BCI (Moreno *et al.* 2006). Similarly low levels of tamandua predation have been found in numerous studies of ocelots, pumas, and jaguars in other Central American forests (range = 0–9.3%, Chinchilla 1997, Novack *et al.* 2005, Weckel *et al.* 2006, Foster *et al.* 2010), suggesting that tamanduas are not a preferred prey species. Tamanduas have effective morphological anti-predator defenses (long sharp claws which can kill hunting dogs; Koster 2008), and reportedly taste bad to human hunters (Alvard 1993, Altrichter 2005, Maldonado 2010). We posit that strong anti-predatory defenses of tamanduas may partially mitigate the top-down effects of their felid predators.

While the top-down effects documented here are consistent with predictions arising from basic ecological models, the most thorough previous studies of BCI anteaters suggested that tamanduas would *not* reduce ant and termite abundance. Indeed, Montgomery (1985b) concluded that tamanduas would not reduce prey abundance because strong insect defenses kept feeding bouts quite short (<1 min) which would ‘prevent destruction of arboreal ant colonies, and probably limit population densities of [anteaters] below levels which the apparently rich food source represented by arboreal ants might allow’ (see also Montgomery & Lubin 1977). However, tamanduas have been documented attacking the same nest multiple times, and our data suggest that tamanduas repeatedly visit nests, on the order of once every 5 d. Consequently, tamanduas rarely destroy *Azteca* nests (Lubin *et al.* 1977), but repeatedly harvest a proportion of the ants each visit while also causing severe nest damage. Montgomery (1985a) concluded that the time and energy needed to repair nest damage following a tamandua attack was more deleterious than direct consumption alone, thus tamanduas likely exert top-down effects on *Azteca* nests via the repeated nest damage they cause in addition to direct consumption. We posit that tamanduas reduce prey

abundance more by non-trophic indirect effects of nest damage than through direct trophic (direct consumption) effects. This suggests that in general, insectivores that simultaneously cause physical damage and consume prey will likely result in stronger trophic cascades.

While tamanduas exerted top-down effects on *Azteca* ants, we did not detect a reduction in termite nest size or abundance outside the mammal exclosures. Lubin *et al.* (1977) argued that the chemical defenses of termites were particularly effective against tamandua predation because tamanduas were observed to be highly selective when feeding in termite nests, and reject or ignore the majority of termite nests they encountered (Montgomery & Lubin 1977). Montgomery and Lubin (1977) posited that tamanduas target termite nests during periods when their nest defenses are somehow reduced, or when the presence of highly preferred food items in the nest (termite alates) shifts the cost-benefit ratio such that tamanduas tolerate the strong chemical defenses. This strong aversion to termite chemical defenses at nest sites may explain why no top-down impacts on termites were found. Alternately, termites suffer from nest damage by nesting birds and other animal species much more frequently than *Azteca* (Lubin *et al.* 1977, Dechmann *et al.* 2004), and this increased damage may have masked any top-down effects by tamanduas.

Our results support the hypothesis that a single medium-sized terrestrial insectivore species is able to exert strong top-down effects on their insect prey in a complex ecosystem. Our findings may apply much more broadly to other ecologically similar mammals such as armadillos, pangolins, and other similar species found in many habitats worldwide. We predict that these top-down effects will be greater when coupled with strong indirect effects, such as damage caused by frequent attacks on a nest (Lima 1998, Zanette *et al.* 2011). However, the patterns documented here varied depending on the particular insectivore-insect dyad. Our results are consistent with the hypothesis that strong chemical defenses prevent tamanduas from exerting significant top-down pressure on termites. Our results suggest that predicting top-down effects of predators will require greater knowledge of prey choice and the anti-predatory defenses of prey. Furthermore, we posit that prey choice, as dictated by predator defenses and palatability, may be particularly important in mitigating the top-down effects of predators (Strong 1992, Polis & Strong 1996).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Photograph of tamandua damage to *Azteca* nest.

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