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Article *in* The Science of Nature · February 2006

DOI: 10.1007/s00114-005-0064-z · Source: PubMed

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DOI 10.1007/s00114-005-0064-z

SHORT COMMUNICATION

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Prey-rolling behavior of coatis (*Nasua* spp.) is elicited by benzoquinones from millipedes

Received: 23 August 2005 / Accepted: 27 October 2005 / Published online: 4 January 2006

Abstract Coatis (*Nasua* spp.), gregarious, omnivorous carnivores that range in forests from the southwestern USA to South America, dispatch millipedes by rolling them on the ground using rapid, alternating movements of their forepaws. Prey rolling of millipedes is thought to stimulate the depletion of their defensive secretions and to wipe off secretions before millipedes are consumed. We report that prey-rolling behavior in *Nasua* spp. is elicited by 1, 4-benzoquinone; 2-methyl-1,4-benzoquinone; and 2-methoxy-3-methyl-1,4-benzoquinone, the chief components of the defensive secretions of julidan, spirobolidan, and spirostreptidan millipedes. Chemicals elaborated for defense sometimes evolutionarily "backfire," providing cues to predators on the presence or identity of prey. The elicitation of prey-rolling behavior in *Nasua* spp. by benzoquinones illustrates this effect for millipedes (and possibly other arthropods) that defensively discharge these compounds.

Introduction

Arthropods exhibit a myriad of morphological, behavioral, and chemical defenses, but some predators adopt special methods to circumvent them. Coatis (*Nasua* spp.), gregarious, omnivorous carnivores that range in forests from the southwestern USA to South America, dispatch millipedes, spiders, and other noxious arthropods by rolling them on the ground using rapid, alternating movements of their forepaws [1, 7, 8]. Similar prey-handling behavior is reported for other carnivores, including the North American striped skunk (*Mephitis mephitis*) [9, 13] and, from Africa, the meerkat (*Suricata suricatta*) [5] and the banded mongoose (*Mungos mungo*) [10]. Prey rolling, in general, is thought to disable arthropods, remove their urticating hairs, and deplete their reserves of defensive chemicals by stimulating glandular discharge ([1, 5, 8] and others).

Millipedes, when disturbed, typically discharge defensive secretions from their numerous segmental glands. Millipedes of the orders Julida, Spirobolida, and Spirostreptida, which collectively occur throughout the tropical and temperate regions, characteristically secrete benzoquinones, chiefly 1,4-benzoquinone; 2-methyl-1,4-benzoquinone (toluquinone); and 2-methoxy-3-methyl-1,4-benzoquinone (MMB) [6]. We report that these compounds elicit prey-rolling behavior in *Nasua* spp.

Methods and results

Captive-reared, 4- to 7-year-old, white-nosed coatis (*Nasua narica*) (approximately 5 kg) were observed in staged encounters with live millipedes, and first tested for responses to toluquinone, in outdoor fenced enclosures (7.5×2.1×1.8 m). Each enclosure housed two to five animals; dominant individuals were tested and then removed to allow other individuals to be tested without interference. Five male and five female *N. narica* were observed interacting with a live spirostreptidan millipede, *Orthoporus ornatus*, (approximately 14 cm long) released on the ground in their enclosure. Millipedes were captured in Val Verde, Texas; *Orthoporus* spp. occur throughout the range of *N. narica*. In each case, a coati approached a crawling millipede, brought its nose down to within a few centimeters away from it, and then rolled the millipede for a mean duration of 34 s (range 8–77 s) by rapid, alternating movements of its forepaws (Fig. 1). Coatis often shuffled

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backward, dragging a millipede 1.5 m or more through the soil in some cases before eating it.

To test the response of *N. narica* to toluquinone, four males and six females were first enticed to approach an 85-cm wooden rod by being offered marshmallows impaled on the end of it. Twenty-five microliters of acetone were applied to the end 3 cm of the rod, and it was allowed to air-dry for 20 s. The treated tip of the rod was held several centimeters away from the nose of the subjects, and they were then observed for 30 s. A 0.4 M solution of toluquinone (Sigma-Aldrich, St. Louis, MO, USA) in acetone was presented the same way. Three males and four females immediately attacked the toluquinone-treated rod tips using rapid, alternating forepaw movements (Fig. 1); none did so to the controls.

To test individual *N. narica* with benzoquinones under more controlled conditions, two males and four females were transferred to separate indoor metal cages (0.9×0.9×1.2 m) and allowed to acclimate for 20 min. They were then randomly presented with 3×10-cm strips of bibulous paper treated with 25 μl of 0.4 M solutions of 1,4-benzoquinone; toluquinone; and MMB in acetone and, for control, acetone alone. 1,4-Benzoquinone and toluquinone were obtained commercially (Sigma-Aldrich); MMB was synthesized, as described by Weldon et al. [15]. Subjects were observed with each paper strip for 2 min, with 5 min between presentations. Four individuals vigorously pawed papers treated with 1,4-benzoquinone (two males, two females) and toluquinone (one male, three females), and five subjects (two males, three females) did so to papers treated with MMB. Subjects responding to 1,4-benzoquinone; toluquinone; and MMB pawed papers for mean durations (range) of 27 s (8–54 s), 49 s (20–81 s), and 27 s (22–33 s), respectively, before papers were abandoned or destroyed. None of the subjects exhibited rapid, alternating pawing when exposed to the acetone-treated papers.

Fig. 1 A *N. narica* rolls a millipede using rapid, alternating movements of its forepaws (*above*). A *N. narica* attacks the tip of a wooden rod treated with toluquinone using rapid, alternating movements of its forepaws

Discussion

A variety of predators refuse to attack millipedes, disgorge them, or reluctantly consume them (see [6, 12]). Free-ranging *N. narica* in Central America, however, often have been observed preying on millipedes [8], and their scats often contain them [11]. In southeastern Brazil, nearly 55% of the scats examined from the brown-nosed coati (*N. nasua*), which also paws and rolls millipedes, contained millipede remains [1]. Prey rolling by *Nasua* spp. may contribute to successful predation on millipedes by applying mechanical cues necessary to maximally stimulate defensive chemical discharge [6], thus depleting glandular reserves, and wiping secretions off of millipedes before they are consumed.

Our tests demonstrate that 1,4-benzoquinone; toluquinone; and MMB elicit prey rolling in *N. narica*. We have observed that *N. nasua* also rapidly paws and rolls paper strips and wooden rods treated with these compounds. Although we have focused on millipedes as a source of benzoquinones, these compounds also are defensively discharged by opilionids, beetles, and other insects [3]; thus, they may elicit prey rolling by coatis in interactions with other arthropods. It is worth noting that the striped skunk (*M. mephitis*) rapidly paws and rolls tenebrionid beetles, e.g., *Eleodes* spp. [9, 13], which are known to secrete benzoquinones, and that this mephitid recognizes these insects by chemical cues [13].

Chemicals elaborated for defense sometimes evolutionarily "backfire," providing cues to predators on the presence or identity of prey [2]. The elicitation of prey-rolling behavior in *Nasua* spp. by benzoquinones illustrates this effect for millipedes (and possibly other arthropods) that defensively discharge these compounds. Benzoquinones also elicit self-anointing behaviors in neotropical capuchin (*Cebus* spp.) [15] and owl monkeys (*Aotus* spp.) [16], which rub millipedes against their fur, appropriating their secretions presumably to deter ectoparasites [4, 14, 15]. The possibility that benzoquinones elicit special prey-handling or self-anointing behaviors in other tetrapods should be considered in future studies.

Acknowledgements B. Harrod, W. Piechocki, J. Roth, and J. Zolonowski (Vanishing Species Wildlife, Davie, FL, USA) permitted access to animals in their care. D. Barker and E. Timaeus (Vida Preciosa International, Boerne, TX, USA) supplied millipedes. J.E. Oliver and A. Weatherwax (USDA, Beltsville, MD, USA) provided synthetic chemicals. A. Hutchinson and D.T. Steere Jr. (Smithsonian Institution Libraries, Washington, DC, USA) provided valuable library services. J. Greff (Tonal Vision LLC, Baltimore, MD, USA) prepared the figure. P. Burchfield, S. Evans, and M. Tebraue extended courtesies in the course of our study. S. Evans, R. Hoffman, S. Krane, and T. Spande commented on the manuscript.

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