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Two new vertebrate prey species in the diet of the agouti, *Dasyprocta punctata*, recorded in the highlands of Costa Rica

Dos nuevas especies de vertebrados en la dieta de la guatusa, *Dasyprocta punctata*, registradas en las tierras altas de Costa Rica

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The Central American agouti, *Dasyprocta punctata*, has traditionally been considered an herbivore, primarily feeding on fruits and seeds. However, there are reports of this rodent consuming 3 vertebrate species: a mouse (in captivity), a bird, and a worm lizard. In this study, we add 2 new vertebrate species to the diet of the agouti: a bird and a mammal. We conducted research and led natural history tours in the Monteverde region of Costa Rica. Monteverde is well-known for its biological reserves and ecotourism activities. The villages of Monteverde and Santa Elena are situated within the Tropical Montane Cloud Forest, a relatively narrow elevational band with frequent cloud cover throughout much of the year. On 2 separate occasions, we observed agoutis preying on vertebrate species in Monteverde. On June 8, 2023, we saw an adult agouti with a juvenile nine-banded armadillo, *Dasypus novemcinctus*, in its mouth. On July 12, 2024, we observed another agouti pursuing and consuming 2 chicks of the black-breasted wood-quail, *Odontophorus leucolaemus*. These 2 new prey items suggest the opportunistic carnivorous tendencies of the agouti. It appears to capture young animals that do not pose a significant threat or require considerable effort to catch, nor do they cause collateral damage. In this way, the agouti obtains some essential nutrients that it does not get from its usual plant-based diet during lean times.

Key words: Birds; mammals; Monteverde; opportunistic; predation.

La guatusa centroamericana, *Dasyprocta punctata*, ha sido tradicionalmente considerada un herbívoro, alimentándose principalmente de frutos y semillas. Sin embargo, existen informes de este roedor consumiendo 3 especies de vertebrados: un ratón (en cautiverio), un ave y una lagartija gusano. En este estudio, añadimos 2 nuevas especies de vertebrados a la dieta de la guatusa: 1 ave y 1 mamífero. Llevamos a cabo investigaciones y guiamos tours de historia natural en la región de Monteverde, Costa Rica. Monteverde es bien conocido por sus reservas biológicas y sus actividades de ecoturismo. Los poblados de Monteverde y Santa Elena están situados dentro del Bosque Nuboso Tropical Montano, una franja altitudinal relativamente estrecha con cobertura de nubes frecuente durante gran parte del año. En 2 ocasiones separadas, observamos guatusas depredando especies de vertebrados en Monteverde. El 8 de junio de 2023, vimos a una guatusa adulta con un armadillo de nueve bandas juvenil, *Dasypus novemcinctus*, en la boca. El 12 de julio de 2024, observamos a otra guatusa persiguiendo y consumiendo 2 polluelos de la codorniz serrana pechinegra, *Odontophorus leucolaemus*. Estos 2 nuevos ítems de presa sugieren tendencias carnívoras oportunistas de la guatusa. Parece ser que este roedor captura animales jóvenes que no representan una amenaza significativa ni requieren un esfuerzo considerable para ser capturados, ni causan daños colaterales. De esta manera, la guatusa obtiene algunos nutrientes esenciales que no obtiene de su dieta habitual basada en plantas durante tiempos de escasez.

Palabras clave: Aves; depredación; mamíferos; Monteverde; oportunista.

The diets of animals reveal their adaptations and ecological roles, making dietary analysis crucial for ecological, evolutionary, and paleo-biological research (Verde Arregoitia and D'Elía 2021). While trophic levels offer a broad perspective on diet, detailed dietary data at a finer scale are essential for a deeper understanding of ecology and natural history (Verde Arregoitia and D'Elía 2021).

Rodents are the most diverse order of mammals, with over 2,600 species described (ASM 2024). This order spans a wide spectrum of body sizes and showcases remarkable diversity in feeding ecology (Verde Arregoitia and D'Elía 2021). Rodents, in fact, constitute the most diverse group of mammals, exhibiting extraordinary ecomorphological diversification that is closely tied to their varied diets and locomotor behaviors (Kay and Hoekstra 2008).

Most rodents have a diet that combines vegetation, seeds, and arthropods (Landry 1970). Strictly carnivorous diets are rare among this order (Merritt 2010). For instance, while murids are generally opportunistic feeders, some have developed specialized carnivorous diets, such as the amphibious Indo-Pacific water-rats, *Hydromys* (Fabre *et al.* 2017). In the Americas, grasshopper mice (3 species of *Onychomys*) are obligate carnivores, primarily feeding on arthropods but also preying on lizards and other rodents like *Perognathus*, *Peromyscus*, and *Microtus* (Rosas Zaragoza and Hernández Canchola 2024).

Larger rodents predominantly rely on vegetation. For example, all Hystricomorphs are primarily or mainly herbivorous, although some may opportunistically include insects and other animal items in their diet (Wilson *et al.* 2016). While most Echimyidae feed on fruits, some, like *Proechimys*, include fungi in their diet, and others, like *Thrichomys*, primarily feed on arthropods but also include plant parts (Fabre *et al.* 2016). Some Hutias, such as *Capromys pilorides*, eat mollusks, insects, shoals of dead seafood including crustaceans and fish, and even lizards (Fabre *et al.* 2016). Lizards, therefore, are one of the few vertebrates reported as food for Hystricomorphs. However, Dasyproctidae have been reported to exhibit a high degree of omnivory (Gilbert and Lacher Jr. 2016). Despite this, a preference for fruit consumption is widespread among Neotropical rodents (Fabre *et al.* 2016).

The Central American agouti, *Dasyprocta punctata* Gray, 1842 (Dasyproctidae), is found from southern México to northern and western Colombia, western Venezuela, and northwestern Ecuador (Mora 2000). In Costa Rica, it is distributed throughout most of the country, primarily in warm forests on both the Pacific and Caribbean slopes up to 2,743 m (Mora 2000; Marín *et al.* 2020). The agouti inhabits a variety of environments, including dry, gallery, humid, and secondary forests, as well as orchards, gardens, and plantations (Emmons 2016; Reid and Gómez Zamora 2022).

The Central American agouti primarily has an herbivorous diet, consisting mainly of seeds, fruits and seedling cotyledons (Jansen *et al.* 2012; Gilbert and Lacher Jr. 2016). Occasionally, it also consumes flowers, leaves, fungi, and insects, especially when fruit supplies are low (Emmons 2016). The agouti's diet is diverse, occasionally including flowers, leaves, fungi, and insects, especially when fruits are scarce (Emmons 2016). It may browse on leaves when fruit availability is low, and in captivity, it has been observed eating carrots, potatoes, and cassava (Smythe 1978). The agouti does not show strong dietary selectivity, likely optimizing foraging efficiency by remaining flexible in its food choices (Eberhart 2006). However, food seasonality influences its home range and social behaviors, with larger ranges observed in response to fluctuating food availability (Aliaga-Rossel *et al.* 2008; Emsens *et al.* 2013).

Additionally, there are reports of agoutis preying on a mouse in captivity in Panamá (reported as *Heteromys pictus* by Smythe 1978), a clay-colored thrush, *Turdus grayi*, in the wild in Costa Rica (Ramírez Calvo *et al.* 2018), and a worm lizard, *Amphisbaena alba*, in Colombia (Cáceres-Martínez *et al.* 2020). While its primary diet includes fruits and seeds, its role as both a seed disperser and seed predator is well-recognized and has significant implications for the regeneration and succession processes of Neotropical forests (Smythe 1978; Hallwachs 1986; Wright and Duber 2001; Jansen *et al.* 2012; Patton and Emmons 2015; Cáceres-Martínez *et al.* 2020).

Despite extensive research on mammals, diet data for specific species can vary significantly in detail and coverage (Verde Arregoitia and D'Elía 2021). In this study, we present 2 new vertebrate species identified as prey for the Central American agouti.

During our routine ecotourism and research activities in the Monteverde region of the Tilarán mountain range, Costa Rica, we observed 2 predation events involving the Central American agouti. During a casual walk, we observed an agouti preying on a small mammal on the property of Hotel El Establo, Monteverde (10° 18' 49" N, 84° 48' 56" W; 1,415 m; Figure 1). During a birdwatching tour, we found another agouti feeding on a bird along the Alondra trail in the Curi-Cancha Reserve, Monteverde (10° 18' 30" N, 84° 48' 13" W; 1,500 m; Figure 1).

Monteverde is a well-known area for ecotourism in Costa Rica (Nadkarni and Wheelwright 2000). The villages of Monteverde and Santa Elena are located within the Tropical Montane Cloud Forest, a relatively narrow elevational zone with frequent cloud cover throughout much of the year (Nadkarni and Wheelwright 2000). The vegetation in Monteverde consists of an evergreen forest with a few deciduous species, particularly on the Pacific slope, and is noted for its moderate epiphyte diversity and abundance (Haber 2000).

On June 8, 2023, we observed an agouti walking with an animal hanging from its mouth. We followed the agouti and took photographs. After the agouti dropped the prey, we inspected it closely and identified it as a young nine-banded armadillo, *Dasypus novemcinctus* (Linnaeus, 1758; Figure 2a). The armadillo was dead and showed wounds inflicted by the agouti's teeth (Figure 2c).

On July 12, 2024, at 08:47 hr, we heard the alarm call of the black-breasted wood-quail, *Odontophorus leucolaemus* Salvin, 1867. A female and 4 chicks were seen running from an agouti that was chasing them, but we lost sight of them as they moved into the forest. However, a few minutes later, we spotted the agouti again. This time, the agouti was consuming a chick, with only the feet visible (Figure 2b). After finishing the first chick, it grabbed another one that was beside it and consumed it as well.

We identified 2 new animal prey items in the diet of the Central American agouti: chicks of the black-breasted wood-quail and a juvenile nine-banded armadillo. Traditionally, the food habits of the Central American agouti have been described as primarily herbivorous, with a diet consisting mainly of seeds and fruits (Jansen *et al.* 2012; Cáceres-Martínez *et al.* 2020). When fruit supplies are low,

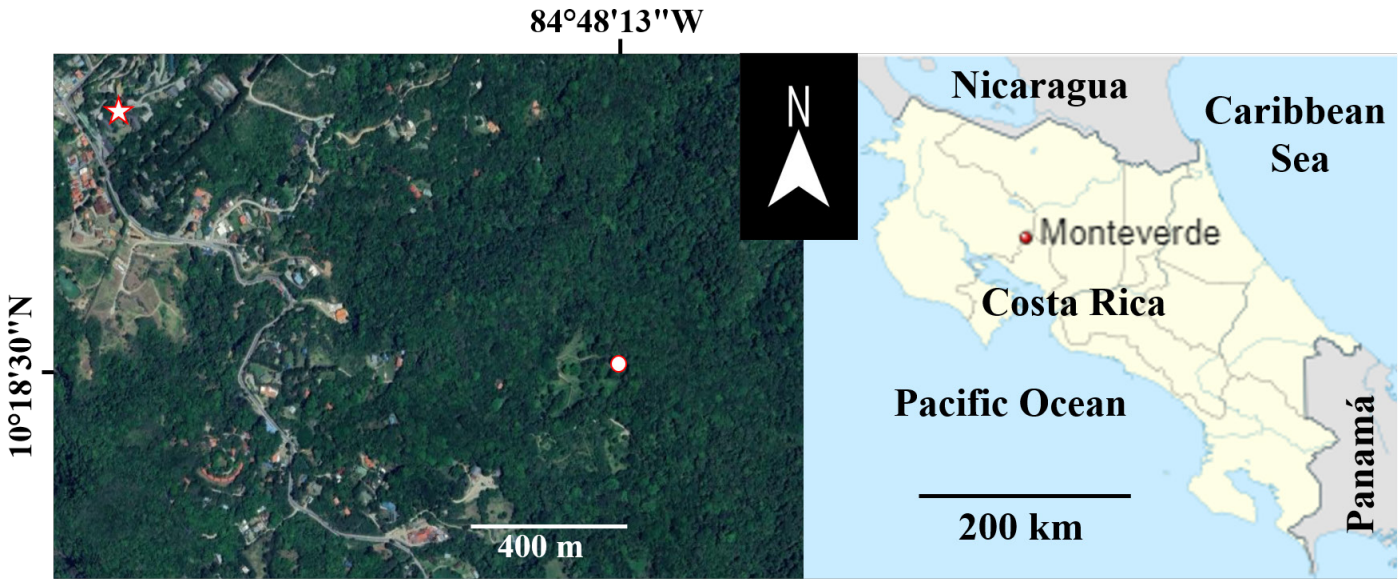

Figure 1. Locations where 2 Central American agoutis, *Dasyprocta punctata*, were observed preying on a juvenile nine-banded armadillo, *Dasypus novemcinctus* (white star), and a black-breasted wood-quail, *Odontophorus leucolaemus* (white dot), in Monteverde (indicated by the red dot on the map of Costa Rica). The figure is based on Google Earth (left section) and Wikipedia, under the Creative Commons Attribution-ShareAlike 3.0 license (right section).

small amounts of plant material and fungi are also included (Emmons 2016). However, there are reports of this rodent preying on and consuming animal prey, including a mouse in captivity, a clay-colored thrush, and an amphisbaenian (Smythe 1978; Ramírez Calvo *et al.* 2018; Cáceres-Martínez *et al.* 2020). This further illustrates that the diets of terrestrial mammals are often more complex than the simple classifications of herbivore, omnivore, or carnivore (Pineda-Munoz and Alroy 2014).

Notably, the clay-colored thrush, like the black-breasted wood-quail chicks and the juvenile nine-banded armadillo, was a young individual. This type of prey (young animals) does not pose a significant threat or require considerable effort to capture, nor does it result in collateral damage (Ramírez Calvo *et al.* 2018). The ease of capture is often a critical factor for small vertebrates that are not specialized in preying on other vertebrates when deciding whether to exploit predation opportunities (Acosta and Morún 2014; Ramírez Calvo *et al.* 2018).

The reported cases suggest that the Central American agouti actively pursues and captures animal prey. For instance, a male agouti, after moving stealthily, suddenly pounced on a clay-colored thrush chick, capturing it with its front paws and then killing it with its incisors (Ramírez Calvo *et al.* 2018). In the case of the amphisbaenian, the agouti paused, then swiftly snapped at the ground, detecting and capturing the worm lizard with its mouth (Cáceres-Martínez *et al.* 2020). Although we did not observe the agouti capturing the armadillo, its cadaver showed signs of incisor marks (Figure 2c). The agouti definitely pursued and killed the quail chicks.

These predation events may reflect the agouti's opportunistic behavior, taking advantage of available food resources (Ramírez Calvo *et al.* 2018). These last authors noted that the agouti follows monkey troops to consume the fruits they drop, as reported by Smythe (1978). While animal prey might be difficult to obtain given the agouti's primarily terrestrial and herbivorous habits, such prey would represent a valuable source of protein and fats, as they are known to consume in captivity (Ramírez Calvo *et al.* 2018).

During season of fruit scarcity, the Central American agouti consume roots and crabs (Smythe 1978). During fruiting seasons, the diet comprises around 37 % fruit pulp and 44 % seeds, supplemented with other plant and animal matter (McWilliams 2009). In the off-season, it relies on cached seeds, roots, and various plant and animal sources (McWilliams 2009). Agoutis may take advantage of easy preys during these fruit shortage times, explaining its predatory behavior.

Some species also exhibit specific behaviors to counteract the metabolic loss of sodium, chloride, and potassium ions (Denton 1982). This phenomenon is particularly evident among herbivores, as the naturally low sodium content in plant tissues often fails to meet their nutritional needs (Lundquist and Varnedoe Jr. 2006). For instance, Hoffmann's two-toed sloth, *Choloepus hoffmanni*, ingests sand for salt (Durán-Apuy and Mora 2023), and the herbivorous mountain tapir, *Tapirus pinchaque*, in Colombia drinks mineral-rich water at salt licks (Lizcano and Cavelier 2004). Some primates also occasionally consume small vertebrates and bird eggs to obtain additional nutrients (Nowak 1999).

Understanding the dietary habits of species is crucial for assessing functional diversity, evolutionary patterns, and the ecological roles they play (Verde Arregoitia and D'Elía 2021). The diet data of vertebrates, including

those from species previously considered strictly herbivorous, offer valuable insights into their niches and can significantly inform conservation and management strategies (González-Maya *et al.* 2017; Grossnickle *et al.* 2019). Despite the challenges inherent in characterizing diets due to complex foraging patterns (Ungar 2010; Nielsen *et al.* 2018), recent findings on the Central American agouti reveal its opportunistic feeding behaviors, including predation on small vertebrates. Such observations underscore the importance of considering cryptic trophic traits in herbivorous species and contribute to a more comprehensive understanding of their ecological roles (Cáceres-Martínez *et al.* 2020).

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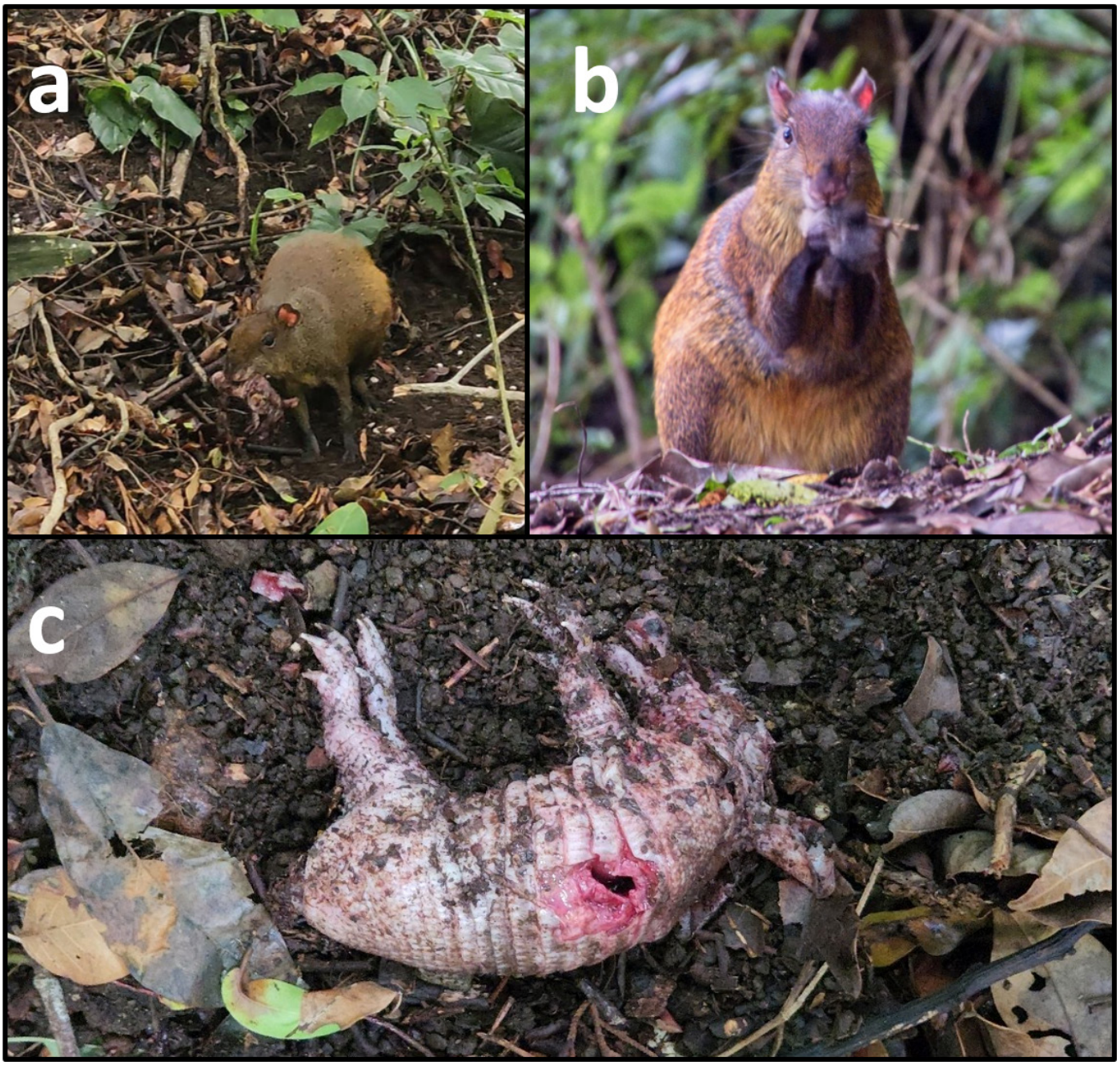

Figure 2. a) A Central American agouti, *Dasyprocta punctata*, with a young nine-banded armadillo, *Dasypus novemcinctus*, in its mouth. b) A Central American agouti consuming a chick of the black-breasted wood-quail, *Odontophorus leucolaemus* (photo by N. Gupte). c) The young armadillo dropped by the agouti. Images available at josemora07@gmail.com.

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