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Opportunistic predation by leaf-cutting ants (Hymenoptera: Formicidae) on a wounded Baird's tapir (Mammalia: Perissodactyla: Tapiridae) in Mexico

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Attine ants constitute a monophyletic group that, even when considering adults can use other resources such as sap or extrafloral nectar (Littledyke & Cherrett 1976; Quinlan & Cherrett 1979), are obligately dependent on the cultivation of fungus gardens for food (Mehdiabadi & Schultz 2010; Branstetter et al. 2017). Higher attines of the genera *Acromyrmex*, *Atta*, *Sericomyrmex*, and *Trachymyrmex* (Hymenoptera: Formicidae) are highly selective herbivores, showing preferences in their plant choice for the fungus culture (Masiulionis et al. 2013). However, despite their specialized diet, most species of these genera are polyphagous, and opportunistically forage on temporary resources, from dry plant material to seeds, insect frass, carcasses, or even fungal basidiocarps (De Fine Licht & Boomsma 2010; Masiulionis et al. 2013). The leaf-cutting ants *Acromyrmex* and *Atta*, for example, are recruited to sardine baits (Santos-Junior et al. 2014) and pitfall traps baited with pig or rodent carcasses (Killion 1991; Cruz & Vasconcelos 2006; Moretti et al. 2008; Fonseca et al. 2015), and are often the first arthropods to find and dominate these resources. However, to date, not a single case of attine ants foraging on a living vertebrate has been recorded. Here, we report an atypical observation of *Atta cephalotes* (L.) (Hymenoptera: Formicidae) workers actively foraging on the wounds and scar tissues of a female *Tapirus bairdii* (Gill) (Mammalia: Perissodactyla: Tapiridae), an endangered flagship vertebrate species of Mesoamerica, found injured on communal land within the Municipality of Calakmul (Campeche, Mexico), and propose some hypotheses that could explain such behavior.

Tapirs are primarily nocturnal and crepuscular large mammals; all are strictly herbivorous and classified as endangered or vulnerable (García et al. 2016). Baird's tapir is the largest of the American tapirs, ranging from 1.8 to 2.5 m in length, 0.73 to 1.20 m height, and 150 to 300 kg in weight (Reid 1997; Foerster & Vaughan 2002). With the exception of humans, who despite protective laws, still hunt them in various regions (Matola et al. 1997), their primary predators are jaguars, pumas, and crocodiles (Naranjo 2009). On 26 May 2017, inhabitants of the Nueva Vida ejido (communities in Mexico that share communally farmed land) in the Calakmul Municipality, Campeche, found a female Baird's tapir seriously injured (most probably due to the attack of a jaguar) and contacted one of us (JPF). The female was lethargic and possessed several wounds in different stages of healing on both sides of the muzzle, neck, flanks, and rump. Wounds were variable in depth and shape, with some releasing a purulent secretion. The tapir was transported to the facilities of the Mexican National Commission of Natu-

ral Protected Areas located in the ejido of "Zoh Laguna" (18.5963°N, 89.4135°W) and kept in a handling pen for approximately 20 d. The animal was fed predominantly with Maya nut (*Brosimum alicastrum* Swartz) (Moraceae), trumpet tree (*Cecropia peltata* L.) (Urticaceae), chaya (*Cnidoscolus aconitifolius* (Miller) IM Johnston) (Euphorbiaceae), papaya (*Carica papaya* L.) (Caricaceae), and chaca (*Bursera simaruba* (L.) Sargent) (Burseraceae), which also were foraged by ants present at this site. Unexpectedly, on 30 and 31 May, numerous workers of the leaf-cutting ant *A. cephalotes* were observed exploring the body of the injured animal, foraging upon the scars, cutting small pieces of the hypertrophied scar tissue, and taking them back to their nest. Up to 7 workers were observed foraging simultaneously on the scars for approximately 10 min (Fig. 1 and Supplementary video [online]). Ant samples were brought to the lab for species identification; however, as the tapir was transferred to a zoological institution until its complete physical recovery, no follow-up studies were undertaken.

The capacity of ants to skeletonize vertebrate carcasses has been long considered to be common knowledge, and reports on ants feeding on vertebrate carcasses as an opportunistic food source are quite

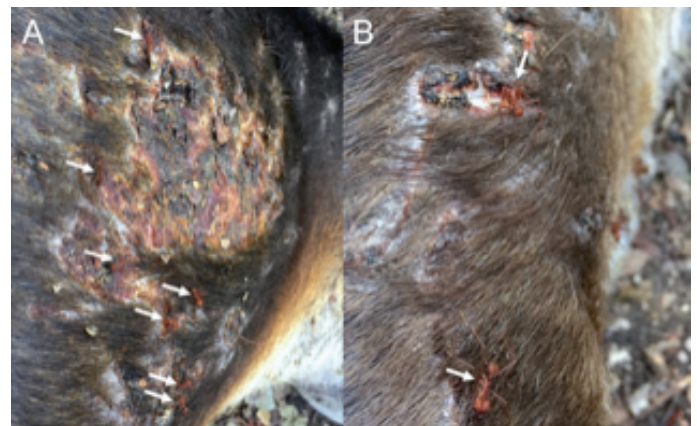


Fig. 1. Workers of the leaf-cutting ant *Atta cephalotes* foraging on a wounded living *Tapirus bairdii* female: (A) 7 workers (see arrows) on the scar tissues of a wound on the right flank of the tapir female; (B) Close up of 2 *Atta cephalotes* (see arrows) foraging on the scar tissues of the female Baird's tapir. In the upper part of the picture, a worker is cutting small pieces of the hypertrophied scar tissue.

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common (Moretti et al. 2008, 2013; Facure & Giaretta 2009; Maciel et al. 2015, 2016; Paula et al. 2016). However, some ant species also are known for their predatory behavior on small living vertebrates, and can constitute a real threat for some species. This is the case for various invasive species such as the fire ant *Solenopsis invicta* Buren (Hymenoptera: Formicidae), which has had negative impact on numerous ground dwelling vertebrates such as birds, amphibians, and turtles (Wojcik et al. 2001; Allen et al. 2004; Wetterer & Moore 2005; Thawley & Langkilde 2016). Conversely, predation by ants on large, living vertebrates is almost unknown; the only observed cases refer to army ants and, even here, there are very few reliable reports, and these refer only to immobile injured and trapped animals (Moffett 2010). Our observations regarding the foraging of *A. cephalotes* workers on scar tissues of *T. bairdii* were quite remarkable for 3 reasons. First, because foraged material gathered by *A. cephalotes* usually consists essentially of plant materials that are used as substrate for the growth of symbiotic fungus; second, because foraging on scar tissues by *A. cephalotes* involved a large, living mammal; and finally, because tapirs do not usually tolerate ants and, in most cases, stop feeding on any food that is subject to ant invasion. It is worth noting that the foraging behavior recorded here occurred in semi-captivity and concerned an individual in a lethargic state. We cannot guarantee whether this behavior would be repeated under natural conditions, or have any real impact on the endangered Baird's tapir. However, cutaneous wounds are one of the most frequent medical problems reported for captive and free-ranging tapirs (Mangini et al. 2012) and could represent a naturally available resource for ant foraging.

Foraging plasticity and diet flexibility in ants are not uncommon, and can result in such drastic changes as those reported for the seed-eating *Brachyponera sennaarensis* (Mayr) (Hymenoptera: Formicidae), which can shift from an essentially granivorous to carnivorous diet, depending on the particular nature of the environmental constraints (Lachaud & Dejean 1994). According to De Fine Licht & Boomsma (2010), nutritional constraints of ants or their fungus may select for diversified diet, which is exhibited occasionally by attine ants. For example, it is known that during the dry season, when the preferred plant items are not available, attine ants tend to diversify the items retrieved and carried to their nest, and this can include insect corpses (Leal & Oliveira 2000). In the case of the genera *Cyphomyrmex*, *Mycetophylax*, *Mycocepurus*, and *Myrmicocrypta* (Hymenoptera: Formicidae), which have been reported to collect insect carcasses, De Fine Licht & Boomsma (2010) suggest that such items may not be used as a direct substrate for fungal growth, but as a resource for rare essential nutrients. In addition, vertebrate carcasses can serve as a source of humidity, or as an indirect or direct food source; furthermore, they are rich in sodium, a limiting nutrient particularly sought by herbivorous species such as leaf-cutting ants (O'Donnell et al. 2010; Pizarro et al. 2012). An alternative hypothesis that would explain the diversified diet of some attine species, not precluding the search for essential nutrients, is the search for different items that might provide ants with different strains of their associated bacteria, and we suggest this might be the explanation of the atypical behavior reported here.

Fungus-growing ants are involved in a very specialized tripartite mutualism with the symbiotic fungi they culture and antimicrobial-producing actinomycete bacteria that reside on their cuticle (Currie et al. 1999). They accumulate complex, dynamic biofilms on their cuticle, carrying a diversity of actinobacteria that may play a role in protection against ant diseases and in their gardens (Mueller 2012). Until recently it was thought that the fungus-attine ants-actinobacteria tripartite mutualism was a very co-evolved symbiosis with both the fungus and the bacteria vertically transmitted (Currie et al. 1999). However, recent studies show that leaf-cutting ants also have windows of op-

portunity for horizontal fungal symbiont transmission during colony founding (Poulsen et al. 2009), and evidence of recruitment of useful antibiotic-producing actinomycetes from the environment is growing, suggesting that ants might select and maintain only those species that make useful antibiotics (Mueller 2012). A combination of co-evolution and environmental sampling would result in the diversity of actinomycete symbionts and antibiotics associated with attine ants (Barke et al. 2010; Mueller 2012). Such a strategy might allow the ants to take advantage of multiple antimicrobials with diverse activities, enabling defense against different pathogens and helping to restrict the evolution of pathogenic resistance. Actinobacteria are present on the skin and cuticle of many vertebrates and invertebrates, respectively (Miao & Davies 2010), so it is not unlikely that *Atta* ants could obtain different strains of their associated bacteria from insect and vertebrate carcasses. Furthermore, in tissue injury, microbes enter the wound where the physical environment differs from the skin surface in temperature, pH, nutrient availability, and host immune effectors, providing opportunities for commensal microbes to become virulent. Chronic non-healing wounds are host to polymicrobial (mixed fungal-bacterial) communities that can form biofilms and interfere with the healing processes (Kalan et al. 2016), but may also be a source of associated bacteria for ants. Tapir skin bacteriome remains unknown; however, *Actinomyces* (Actinomycetaceae) species have been found already in the purulent exudate drawn from an abscess in *Tapirus terrestris* (L.) (Mammalia: Perissodactyla: Tapiridae) (Alexander 1978), so it is not unlikely that the *T. bairdii*'s scar tissues foraged by *A. cephalotes* could host such polymicrobial communities.

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Summary

Notwithstanding their specialized herbivorous diet, leaf-cutting ants opportunistically exploit temporary resources such as insect or vertebrate carcasses. We report on the first case of attine workers, *Atta cephalotes* (L.) (Hymenoptera: Formicidae), foraging on the scar tissues of a living vertebrate, a wounded female Baird's tapir, *Tapirus bairdii* (Gill) (Mammalia: Perissodactyla: Tapiridae). We put forward 2, not mutually exclusive, hypotheses to explain such behavior: (1) utilization by the leaf-cutting ants of these tissues as a resource that provides rare essential nutrients, and (2) opportunistic sampling of polymicrobial communities associated with the skin of the wounded animal in search of new strains of their associated actinobacteria.

Key Words: actinobacteria; *Atta cephalotes*; essential nutrients; foraging plasticity

Sumario

A pesar de su dieta herbívora especializada, las hormigas cortadoras de hojas aprovechan también de manera oportunística fuentes temporales como carcasas de insectos o de vertebrados. Reportamos el primer caso de hormiga atine, *Atta cephalotes* (L.) (Hymenoptera: Formicidae), forrajeando sobre el tejido cicatricial de un vertebrado vivo, una hembra herida del tapir centroamericano, *Tapirus bairdii* (Gill) (Mammalia: Perissodactyla: Tapiridae). Se proponen 2 hipótesis, no mutuamente exclusivas, para explicar tal comportamiento: (1) el uso por parte de las hormigas cortadoras de hojas de estos tejidos como

fuerza de nutrientes esenciales escasos; (2) el muestreo oportunístico de comunidades polimicrobianas asociadas con la piel de animales heridos, en búsqueda de nuevas cepas de sus actinobacterias asociadas.

Palabras Clave: actinobacteria; *Atta cephalotes*; nutrientes esenciales; flexibilidad del forrajeo

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