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Anointing behavior with millipedes by a wild group of Caribbean night monkeys (*Aotus griseimembra*) in Colombia

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ABSTRACT
Anointing occurs when animals rub substances on their own or other individuals' bodies for various purposes. Although this behavior has been described in several species, it has only been observed in captivity in night monkeys. We present the first report of anointing (self and allo-anointing) in wild night monkeys, occurring specifically in the Caribbean night monkey (*Aotus griseimembra* Elliot, 1912). The event involved three of the five individuals in the group writhing, closing their eyes, and salivating. Anointing in wild night monkeys may be related to auto-medication or may serve as an insect repellent, or both, considering the chemical characteristics of millipedes.

Keywords: allo-anointing, medicinal, nocturnal primates, repellent, self-anointing

RESUMEN – Comportamiento de unción con milpiés por un grupo del mono nocturno caribeño (*Aotus griseimembra*) en vida silvestre en Colombia
La unción ocurre cuando los animales frotan sustancias sobre su cuerpo o el de otros individuos con diferentes propósitos. Aunque este comportamiento se ha descrito para varias especies, en el caso de monos nocturnos, solo se ha observado en cautiverio. Presentamos el primer reporte de unción (autounción y alounción) en monos nocturnos silvestres ocurrido específicamente en el mono nocturno caribeño (*Aotus griseimembra* Elliot, 1912). En el evento participaron tres de los cinco individuos del grupo, quienes se retorcían, cerraban los ojos y salivaban. La unción en los monos nocturnos silvestres puede estar relacionada con la automedicación o puede servir como repelente de insectos, o ambas cosas, teniendo en cuenta las características químicas de los milpiés.

Palabras clave: alo-unción, auto-unción, bosque tropical, medicinal, primates nocturnos, repelente

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Anointing, a behavior in which individuals actively apply scent-bearing substances on their own or other individuals' bodies has been recorded in several mammals (Weldon et al. 2003; Jefferson et al. 2014; Gasco et al. 2016; Charlton et al. 2020) and birds (Morozov 2015; Coulson 2023; Perin & Perin 2023). It has been suggested that anointing may influence social relationships and dynamics, communication, or act as a medicine or repellent for ectoparasites and other disease vectors (Baker 1996; Valderrama et al. 2000; Laska et al. 2007; Lynch-Alfaro et al. 2012). This behavior has been observed in several non-human primates including lemurs (genus *Eulemur*) (Birkinshaw 1999), apes (genus *Pan* and *Pongo*) (Morrogh-Bernard 2008; Fruth et al. 2014), capuchin monkeys (genus *Cebus* and *Sapajus*) (Weldon et al. 2003; Lynch-Alfaro et al. 2012; Messer et al. 2022), spider monkeys (genus *Ateles*) (Campbell 2000; Laska et al. 2007; Cortés-Vesga & Link 2022), titi monkeys (genus *Plecturocebus*) (Souza-Alves et al. 2018) and night monkeys (genus *Aotus*) (Zito et al. 2003; Jefferson et al. 2014). Anointing behaviors have been classified into [1] self-anointing: when application of substances is performed by a single individual on its own body and with no physical contact with others; and [2] allo-anointing: when more than one individual participates in anointing and involves the application of scent-bearing substances from one individual to another one (Baker 1996; Leca et al. 2007; Lynch-Alfaro et al. 2012; Jefferson et al. 2014; Gasco et al. 2016).

Anointing has been proposed to serve as self-medication potentially helping to treat, control, or prevent diseases, parasites, ectoparasites, and act as a repellent against invertebrates (Baker 1996; Laska et al. 2007; De la Fuente et al. 2022). In great apes, different plants have been proposed to serve in self-medication. For example, in bonobos *Pan paniscus* Schwarz, 1929 and orangutans *Pongo pygmaeus* Linnaeus, 1760 the use of the leaves of *Manniophyton fulvum* Müll, 1864 (Fruth et al. 2014) and *Dracaena cantleyi* Baker, 1981 (Morrogh-Bernard et al. 2017) are used in self-medication, respectively. In platyrrhines, anointing has been observed in wild populations of spider monkeys (Campbell 2000; Laska et al. 2007) and capuchin monkeys (Lynch-Alfaro et al. 2012), as individual monkeys rub plants in their bodies, probably related to sexual attraction and social communication. In captivity, anointing with plants has also been observed in capuchin monkeys (Messer et al. 2022), spider monkeys (Cortés-Vesga & Link 2022) and titi monkeys (Souza-Alvez et al. 2018).

The anointing of primates with various arthropods, such as millipedes, has led to the assumption that the use of various compounds found in these invertebrates may have a deterrent effect on parasites (Blum 1981; Baker 1996; Valderrama et al. 2000; Weldon et al. 2003; Zito et al. 2003). Millipedes of some families secrete toxic compounds from repellent glands containing volatile substances such as benzoquinones, which have been described as highly toxic to parasites and pathogens (Arab et al. 2003). In fact, experimental studies have shown that benzoquinone can reduce the load of ticks and other parasites over long periods of time (Weldon et al. 2003; Carroll et al. 2005). For example, anointing behavior in wild *Eulemur rufifrons* Bennet, 1833 using millipedes of the genus *Sechelleptus* (Spirostreptidae) on the perianal area and tail, followed by consumption of the arthropod, has been suggested to act as a thera-

peutic and prophylactic against nematodes (Peckre et al. 2018). In addition, anecdotal self-anointing by a female using a millipede (*Charactopygus* sp.; Spirostreptidae) has been recorded in *Eulemur macaco* Linnaeus, 1766; in this case, the anointing was performed on the ventral body and tail, and there was no consumption of the arthropod (Birkinshaw 1999). Similarly, Valderrama et al. (2000) reported this behavior in individuals of different sexes and ages of *Cebus olivaceus* Schomburgk, 1848 during the rainy season using a millipede of the genus *Orthoporus* (Spirostreptidae family).

Other studies, especially in night monkeys have recorded the application of garlic, onion, millipedes, and plant material for both self-anointing and allo-anointing, mostly applied on the head, limbs, and upper dorsolateral parts of the body (Zito et al. 2003). The functions of anointing behaviors are currently unknown, and especially for night monkeys, information is only available from captive individuals. Here, we describe the first report self-anointing and allo-anointing using millipedes, in wild Caribbean night monkeys *Aotus griseimembra* Elliot, 1912 as part of a long-term study on their ecology and social behavior at San Juan del Carare in the lowland tropical forests of Central Colombia.

The study site is the Hacienda San Juan del Carare (latitude 6.716389; longitude -74.139444) (hereafter San Juan), a cattle ranch located in the Inter Andean lowland forests, in the municipality of Cimitarra, department of Santander, in Colombia. This study site comprises a mosaic of pastures for cattle-ranching, gallery forests, and forest fragments of tropical rainforest that are seasonally flooded by the San Juan River (Fig. 1) (Link et al. 2010). Long term research on all four sympatric primates at San Juan has been going on for more than 15 years by Fundación Proyecto Primates (NGO). Different studies on the ecology, behavior, and genetics of red howler monkeys *Alouatta seniculus* Linnaeus, 1766 (Link et al. 2010; de Luna et al. 2017), brown spider monkeys *Ateles hybridus* Geoffroy, 1829 (Link et al. 2010; Abondano & Link 2012; Rimbach et al. 2012, 2014; de Luna et al. 2017), varied white-fronted capuchin monkeys *Cebus versicolor* Pucheran, 1845 (Link et al. 2010; de Luna et al. 2017), and Caribbean night monkeys *A. griseimembra* (Montilla et al. 2021; Muñoz-Delgado et al. 2021) have been conducted since the onset of the research and conservation project at San Juan.

Since 2018, the "Proyecto Aotus" was launched, focusing on the study of the ecology, behavior, genetics, and other aspects of the natural history of night monkeys in both highland and lowland forests of Colombia. At San Juan, a total of five groups have been habituated and studied since the beginning of the project, and three of them are currently being monitored ("Búfalo" group, "Casa" group, and "Caño 0" group). The home ranges of most groups overlap and the vegetation structure and plant composition in the forest is similar for every study group (Montilla et al. 2021).

As part of the long-term study of *A. griseimembra* at San Juan, nocturnal follows are performed several nights per week, starting at the sleeping site of one of our study groups (Montilla et al. 2021). The record of the anointing behavior took place in the "Búfalo" group which contains five individuals: an adult male and adult female, plus three offspring of unknown sex, including a juvenile with no subcaudal patch development, a subadult with a weakly developed subcaudal patch and a subadult with a de-

veloped subcaudal patch in the process of natal dispersal. During the direct observation of the individuals of the group, we were able to differentiate their age and sex categories through their body size, scars, marks, and the development of the subcaudal patch, which becomes more developed as the age of the individuals increase (Montilla et al. 2021). To differentiate the sex of the two adult individuals in the "Búfalo" group, we consider the subtle development of the testes in the male and the swelling of the nipples in the female, which were present due to the suckling of the juvenile brood. The "Búfalo" group uses a small home range (less than two ha), located in a seasonally flooded forest fragment with a canopy height of approximately 10 to 30 m (Fig. 1).

During the observation of the anointing behavior, we recorded the beginning and end time of the event, the identities of all individuals involved in anointing, the body parts anointed, and other activities associated with their behavior. We also obtained a video recording of the anointing event. *Ad libitum* data categories followed the ones suggested in the ethogram described by Jefferson et al. (2014).

During the date we recorded the anointing event, the study area was experiencing a strong El Niño Southern Oscillation (ENSO) phenomenon with a significant reduction in rainfall. On the night of the observation of the anointing behavior, the moon was in the waning phase with an illumination percentage of 79%.

From the photographs and video taken during the anointing behavior, we identified the millipede used for anointing by individuals of *A. griseimembra* to the family taxonomic category using taxonomic keys such as Sierwald (2008) (Milli-PEET) from the Field Museum.

Observation of the anointing took place on March 28th and began close to midnight, exactly at 23:15:30 h with the adult male self-anointing for approximately 20 s. First, we observed the adult male bite the millipede on its back, followed immediately by body twisting movements (described as writhing by Jefferson et al. 2014), while closing the eyes with pressure and opening the mouth, showing obvious salivation (described as drooling by Jefferson et al. 2014). Approximately 5 s later, the adult male began rubbing the millipede throughout his body, starting at the lower dorsum, lower limbs, and tail. Immediately after, the adult male was approached by the subadult with the weakly developed subcaudal patch. This second individual adopted a similar posture to the adult male, closing his eyes, opening his mouth with salivation, and writhing as he moved his head closer to the body of the adult male (Fig. 2A). The adult male then positioned himself on top of him and continued to hold and bite the millipede on its dorsal area. At this point, the adult male and subadult individual maintained a synchronized writhing behavior with their eyes closed and mouths open for approximately 10 s.

Then, at 23:16:45 h, the adult male began allo-anointing behaviors (using his hands to rub an object on the fur of another individual, according to Jefferson et al. 2014) and rubbed the body of the millipede over the head of the subadult individual with his left hand, moving down to the mid dorsum and tail for approximately 15 s while holding it (Fig. 2B). During this time, both individuals continued to writhe, eyes closed, mouth open, and salivate. The adult male also repeatedly bit the dorsum of the millipede while allo-anointing the subadult.

At 23:17:04 h, a third individual (the adult female) approached, who observed the adult male allo-anointing the subadult individual for 7 s (Fig. 2C) and then displayed the same behavior as the subadult, bringing her head close to the adult male´s body with her eyes closed and mouth open. The adult female positioned herself in between the adult male (who continued to hold the millipede with his right hand) and the subadult, which was positioned at the bottom in contact with the branch (Fig. 2D). At this point, and exactly in the same location, the adult male began to rub the millipede over the head, upper dorsum, and middle dorsum of the adult female for approximately 35 s. While this allo-anointing was taking place, all three individuals continued to writhe, eyes closed, mouth open, salivating and placed in the same position, and occasionally the adult male would bite the millipede on its dorsum.

The three individuals then climbed approximately 20 cm up in the tree and positioned themselves horizontally from right to left, with the subadult on the far right, the adult male in the middle self-anointing over his entire body, and the adult female on the far left (Fig. 2E). Soon after, at 23:19:23 h, the adult male bit the millipede again, and all three individuals simultaneously writhed, closed their eyes, and opened their mouths while salivating for approximately 20 s as the male continued to self-anoint (Fig. 2F). At this point, both the subadult on the right and the female on the left oriented their heads toward the body of the adult male where he was holding the millipede (Fig. 2G). The adult male rubbed the millipede on his body alone for approximately 39 s, while the subadult and adult female rubbed their heads and hands on the body of the adult male while the adult female was begging for the millipede (possible recipient extending hand or mouth toward the millipede held by the possessor, according to Jefferson et al. 2014) (Fig. 2H).

At 23:20:12 h only the adult male climbed about 40 cm up in the tree and 20 s later the subadult and the adult female approached him. At 23:20:45 h they switched positions (from right to left, subadult, adult female and adult male) and the millipede was held for the first time by the adult female, who continued to bite it on the dorsum while they all writhed, eyes closed and mouth open, salivating. As this occurred, the subadult and adult male moved his head and body closer to the millipede and the body of the adult female (see Fig. 2I), who held it for approximately 23 s more, biting and anointing it all over his body, from his lower limbs and tail to his head. Finally, the adult female released the millipede, and the three individuals climbed to the top of the canopy, approximately 15 m above the ground. In total, the anointing event lasted approximately six min and involved only three of the five individuals in the study group. The youngest offspring with the undeveloped subcaudal patch never approached during anointing episode and remained vigilant about one meter away from the other individuals, while the older subadult offspring with the developed subcaudal patch and in the process of natal dispersal was not observed near the rest of the group members at the time of the anointing. During the anointing event, no vocalization was recorded from any of the individuals involved or from individuals who did not participate in the event.

Finally, we were unable to find the millipede used in the anointing event after it was released by the adult female. Although we were unable to recover the millipede

used during the anointing event, by analyzing the photographs, the video, and another millipede found days later in the same study site with the same characteristics of size, color, and shape, we can assume that it likely belongs to the order Spirobolida and specifically to the family Rhinocricidae.

After several years of intensive study of groups of *A. griseimembra* in San Juan and other locations where we have studied night monkeys, we recorded the first event of millipede anointing (including self-anointing and allo-anointing) by these primates in the wild. This observation builds on information on wild individuals of *A. azarae* Humboldt, 1812 that have been reported self-anointing with flowers or fruits of *Fagara* spp. and other unknown objects in Argentina (Spence-Aizenberg et al. 2023). Under captive conditions, anointing behavior has been widely reported in several species of night monkeys with various elements, including onion, garlic, chives, cinnamon, *Piper marginatum* Jacq, 1790 leaf extract, moths, and both live millipedes and the benzoquinones they produce (Zito et al. 2003; Jefferson et al. 2014). Self-anointing has been reported in captivity in individuals of the species *A. azarae, A. griseimembra, A. nancymaae* Hershkovitz, 1983, and *A. nigriceps* Dollman, 1909, and even in hybrids between *A. griseimembra* and *A. azarae*, and *A. nigriceps* and *A. trivirgatus* Humboldt, 1811. In turn, allo-anointing behavior has been reported in *A. nancymaae*, *A. azarae*, and a hybrid between these two species (Zito et al. 2003; Jefferson et al. 2014).

Under more controlled captive conditions, each anointing event is considered independent when researchers intentionally provide night monkeys with different anointing elements (Zito et al. 2003; Jefferson et al. 2014). In these studies, self and allo-anointing behaviors have been also examined independently (Jefferson et al. 2014). In our case, we consider that our observation in wild individuals of *A. grisiemembra* with a single millipede, corresponds to a single anointing event composed of several self-anointing events performed by the male and adult female and several allo-anointing events involving the male and adult female and the subadult.

Since there are no previous reports of millipede anointing in wild night monkeys, here we provide some comparisons between our observations and those reported in captivity. With respect to the time that night monkeys invest in anointing, in captivity there is a wide variability in the duration of self-anointing events (between 2 s and 14.1 min) with an average of 3.7 min, and in allo-anointing events (between 5 s and 5.3 min) with an average time of 1.2 min. In our observations of both self and allo-anointing events, the time spent in the wild was within the proposed ranges and did not exceed 45 s, as did the general anointing event, which lasted approximately 6 min. In captive studies (Zito et al. 2003; Jefferson et al. 2014), anointing events occurred when researchers supplemented night monkeys with millipedes, which coincides with the initial peak of activity of these primates, which corresponds to the first part of the night (Fernandez-Duque & Erkert 2006; Fernandez-Duque et al. 2010; Erkert et al. 2012; Muñoz-Delgado et al. 2021). However, our observation in the wild took place near midnight, just when the activity of the same population of *A. griseimemebra* tends to be lower and when they reduce the time spent traveling through the forest (Montilla et al. 2021; Muñoz-Delgado et al. 2021; Link et al. 2023).

However, our observation occurred on a night with a high percentage of moonlight (79%), when night monkeys are potentially more active because they are likely to have fewer visual limitations, which may facilitate finding items to anoint, such as millipedes (Fernandez-Duque 2003; Fernandez-Duque et al. 2010; Muñoz-Delgado et al. 2021; Link et al. 2023). In captivity, researchers perform a detailed zonation of the body parts where anointing occurs in night monkeys (19 body parts), with the lower back, base/tail length, and outer thigh being the most common sites for self-anointing behaviors. Allo-anointing behaviors include the dorsolateral trunk, head, base and tip of the tail, hands and hind legs, limbs, and proximal shoulder and hip areas (Zito et al. 2003; Jefferson et al. 2014). Although we were not able to observe each part in detail in the wild, self and allo-anointing were evident in the most common parts reported for captive night monkeys. In captivity, millipedes were only offered to adult or subadult night monkeys (older than one year), and therefore, data on self and allo-anointing are only available for this age category (Jefferson et al. 2014). In our study, only the adult male and female performed self-anointing, and of the three offspring in the group, only one of the two subadults (the one with weakly developed subcaudal patch) participated in allo-anointing without handling the millipede. Finally, with respect to behaviors performed during anointing, in captivity, during self and allo-anointing, the night monkeys writhed, closed their eyes, and opened their mouths, drooled and gnashed their teeth, and emitted gurgles and trills (Zito et al. 2003; Jefferson et al. 2014). Of all these behaviors, the only ones we did not record during our observations in the wild were teeth grinding and the emission of gurgles and trills (likely vocalizations such as squeaks and low trills according to Erazo et al. (2023)).

Although different explanations have been proposed to explain anointing behaviors, it is still unclear what its main function is, and it could depend on the context of the behavior and the organisms that perform it (Brockie 1976; Lynch-Alfaro et al. 2012; Charlton et al. 2020). First, it has been proposed that anointing could have a medicinal or insecticidal function, considering that it is mainly performed with plants known to present secondary compounds or with arthropods presenting substances with deterrent properties such as benzoquinones (Blum 1981; Baker 1996; Valderrama et al. 2000; Weldon et al. 2003; Zito et al. 2003). In fact, under captive conditions, benzoquinones (2-methoxy-3-methyl-1,4-benzoquinone) extracted directly from the segmental gland secretions of millipedes and known for their insecticidal properties have been given to night monkeys, which were used by these primates in self-anointing behaviors (Zito et al. 2003; Carroll et al. 2005). The use of millipedes for medicinal or insecticidal purposes could explain the anointing behavior of individuals of *A. griseimembra* in San Juan, where these primates have recently been reported to be infected with both protists such as *Blastocystis* sp. and *Plasmodium* sp. and myiasis-causing flies of the species *Cuterebra baeri* Shannon & Greene, 1926 (Rondón et al. 2019; Rondón et al. 2023a, b). Additionally, in comparison to other study sites of the "Proyecto Aotus", where we have long-term monitoring of night monkeys and have not observed anointing behavior or infections in them, the forests of the San Juan are characterized by high humidity and abundant rainfall (Montilla

et al. 2021). These environmental conditions are associated with an increase in the abundance of insects and pathogen vectors (Baker 1996). However, if the function of anointing was medicinal or insecticidal, and for this reason it was only recorded in the locality where there were reports of infections and climatic conditions favorable to vectors, it is questionable why captive individuals (Zito et al. 2003; Jefferson et al. 2014), who theoretically are not exposed to vectors or adverse climatic conditions, would also exhibit anointing behavior.

Second, it has been proposed that the specific behavior of self-anointing may be related to some form of social communication, because in some primates, such as *Ateles geoffroyi* Kuhl, 1820 and *A. fusciceps* Gray, 1866, males perform this behavior significantly more than the females (Laska et al. 2007; Cortés-Vesga and Link 2022). However, no differences were observed between males and females in the onset or duration of anointing in captive night monkeys (Jefferson et al. 2014), nor did we observe marked differences between adult male and adult female when performing this behavior in the wild. The social complexity hypothesis of communicative complexity proposes that more complex social systems require more complex communication systems with a greater number of signals (Freeberg et al. 2012). Therefore, species with multi-male/multi-female social systems, such as *Ateles*, are likely to exhibit more complex communication systems (Aureli et al. 2022) that include behaviors such as anointing, but for species with apparent monogamy, pair-living and small social groups, such as night monkeys (Huck et al. 2014; Garcia de la Chica et al. 2023), more evidence is needed to link anointing to aspects of communication. A third explanation suggests that anointing behavior may be related to the strengthening of social bonds within the group (Baker 1996). However, more data are needed to confirm this for monogamous primates living in pairs and in small groups. In addition, our observations showed that only three of the five individuals in the group engaged in anointing behavior. If this behavior were intended to strengthen social relationships, one would expect all individuals, including the youngest offspring, to participate.

Among the elements used for anointing primates, the use of millipedes stands out (Medeiros et al. 2000; Valderrama et al. 2000; Zito et al. 2003; Jefferson et al. 2014; Peckre et al. 2018). These animals are characterized by the use of hydrogen cyanide, quinazolinones, benzoquinones and cresols as a defense mechanism, which are produced by a large number of segmental glands located throughout the body (Eisner et al 1978; Fairhurst 1993; Birkinshaw 1999; Valderrama et al. 2000; Carroll et al. 2005) and can cause writhing and salivation in night monkeys when bitten. Individuals from the family Rhinocricidae, which we consider to be the taxonomic group of millipedes used by the San Juan *A. griseiembra*, have been identified in previous research as one of the elements commonly used in primate anointing events (Jefferson et al. 2014; Medeiros et al. 2020). Characteristics that define the Rhinocricidae family, and that were present in the other specimen found in the study area, are a broad column with a broad, rounded ventrolateral aspect, as well as a generally triangular sternite with a transverse proximal section and tapering distally (Hoffman 1998; Marek et al. 2003).

In conclusion, our report of anointing with millipedes by individuals of wild *A. gri-*

seimembra provides new information on this behavior, which until now has only been observed under captive conditions. This report of anointing in the wild complements previous findings in captivity, showing similarities in terms of body parts involved, individuals and duration, and providing new insights into the timing and circumstances under which this behavior occurs in the wild. Although the exact function of anointing behavior is still poorly understood, our report tends to understand this behavior as a medicinal and insecticidal measure, without ruling out its function in communicative or social aspects, for which a larger amount of data is needed. Finally, these reports emphasize the importance of understanding animal behavior in its natural environment in order to obtain a complete picture of its functions and meanings.

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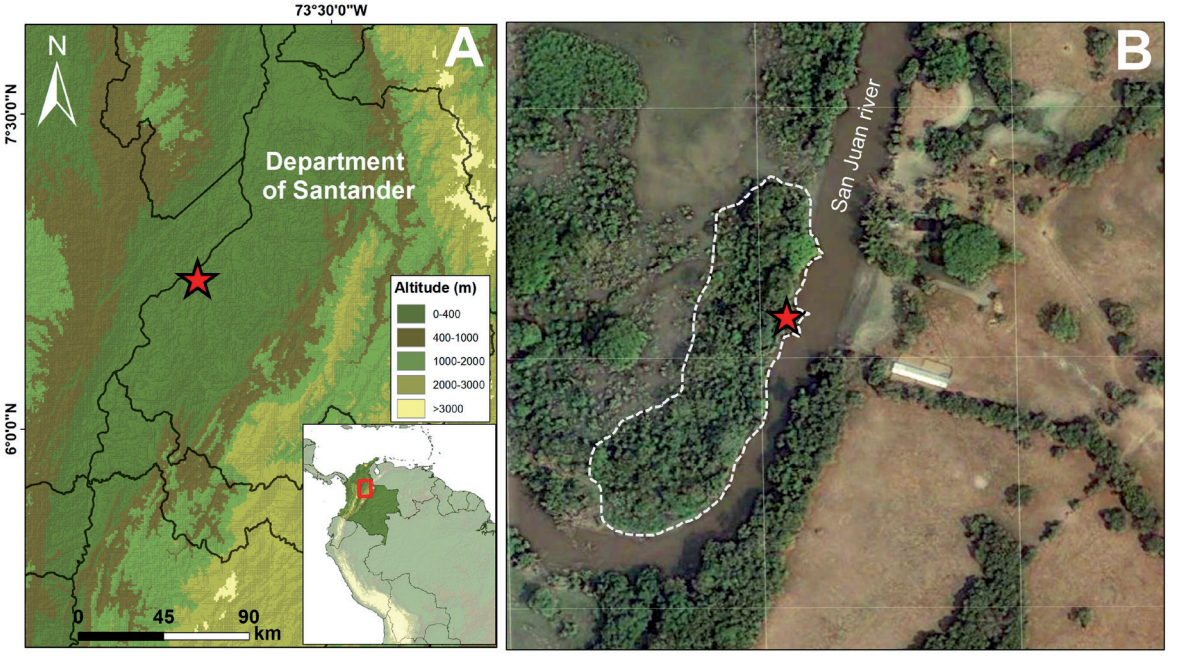

Figure 1. A) Geographic location of the Hacienda San Juan del Carare where we report the anointing event of night monkeys with millipedes; B) Satellite image of the home range white outline) of the "Búfalo" Caribbean night monkey (*Aotus griseimembra*) group and the location of the anointing event (red star).

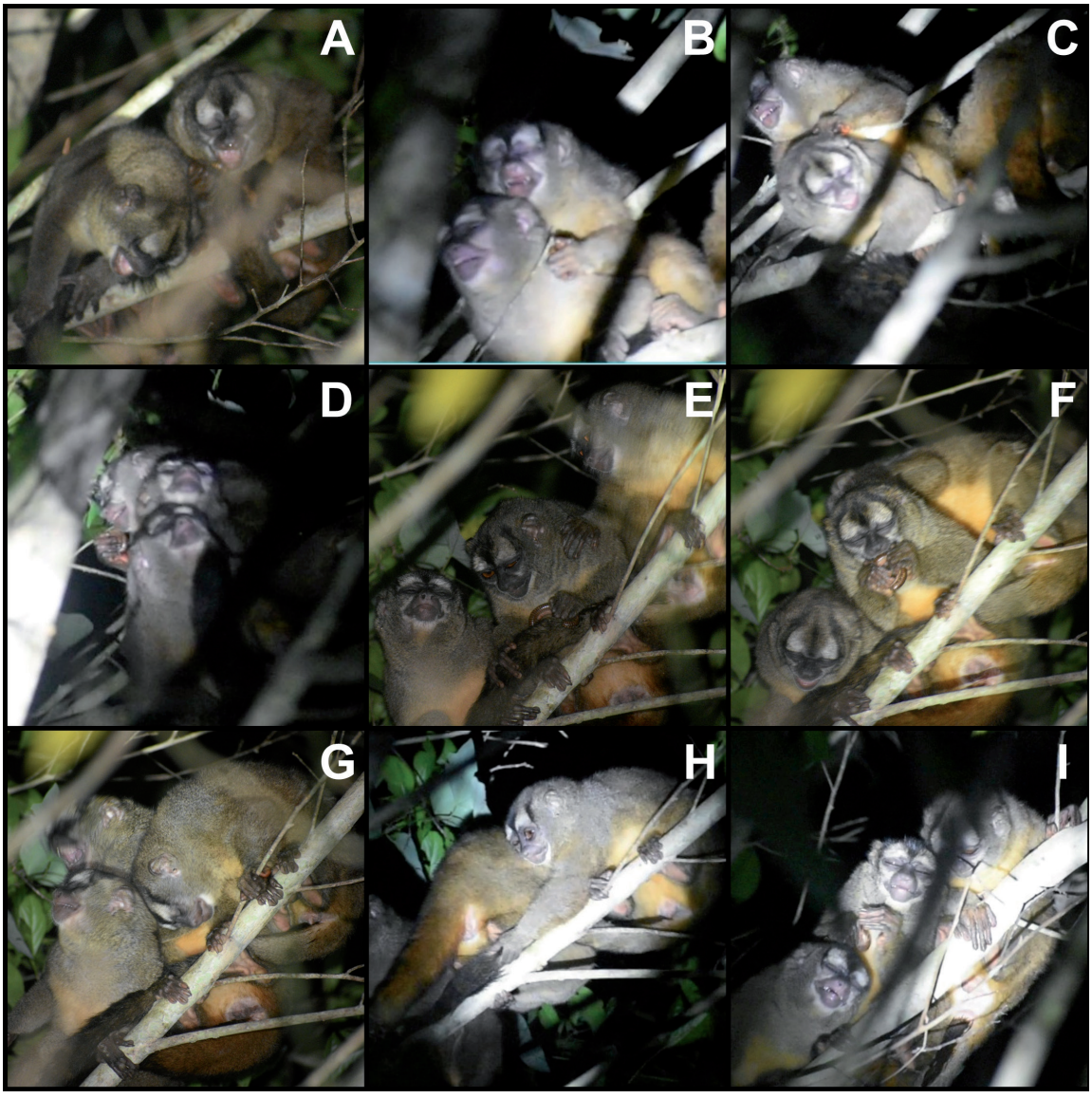

Figure 2. Anointing behavior by a group of Caribbean night monkey (*Aotus griseimembra*) in Colombia. A) Adult male and subadult individual writhing synchronously with eyes closed and mouth open and salivating; B) Allo-anointing of the adult male to the subadult individual while standing on it; C) Adult female observing allo-anointing from adult male to subadult individual; D) Adult male bites the millipede and positions himself on top of the female, who is on top of the subadult, while all individuals writhe their bodies and present their eyes closed and mouth open; E) From right to left, subadult individual, adult male anointing millipede on tail, and adult female; F) From right to left, subadult individual, adult male biting millipede, and adult female; G) Subadult individual on the right and adult female on the left pushing her head toward the adult male holding the millipede; H) Adult female begging for millipede by extending her hand to the body of the adult male who owns it; I) Subadult individual on the right and adult male on the left pushing her head toward the adult female holding the millipede.

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