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HYPOTHESIS

Why sloths defecate on the ground: rejection of the mutualistic model

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ABSTRACT. Introduction: Sloths are arboreal mammals that defecate on the ground, increasing the risk of predation. There are several hypotheses that try to explain why they undergo this risk. **Objective:** To critically review all the hypotheses and to propose a new hypothesis that is compatible with all known data. **Methods:** I verified the assumptions and implications of five hypotheses against the literature available February, 2021. **Results:** Previous hypotheses either lack reliable supporting data, or are contradicted by published data. Here I propose that defecation on the ground is an ancestral behavior that persists in all sloth species because there has not been enough natural selection against it. **Conclusions:** Current knowledge of sloth biology is compatible with the hypothesis that there has not been enough selective pressure for sloths to abandon defecation on the ground.

Keywords: Evolution of sloth behavior, natural selection and defecation, algae, mutualism, moths, arboreal mammal evolution.

RESUMEN. "Por qué los perezosos defecan en el suelo: rechazo del modelo mutualista". **Introducción:** Varias hipótesis intentan explicar por qué los perezosos, siendo mamíferos arbóreos, defecan en el suelo, aumentando el riesgo de depredación. **Objetivo:** Revisar críticamente todas las hipótesis y proponer una nueva, compatible con todos los datos conocidos. **Métodos:** Verifiqué las bases e implicaciones de cinco hipótesis con la literatura disponible en febrero de 2021. **Resultados:** Las hipótesis anteriores carecen de datos confiables o son incompatibles con datos publicados. Aquí propongo que la defecación en el suelo es un comportamiento ancestral que persiste en todas las especies de perezosos porque no ha habido suficiente presión selectiva en contra. **Conclusiones:** Lo que se sabe actualmente de la biología de los perezosos calza con la idea de que no ha habido suficiente presión selectiva para que los perezosos abandonen la defecación en el suelo.

Palabras clave: Evolución del comportamiento de los perezosos, selección natural y defecación, algas, mutualismo, polillas, evolución de mamíferos arbóreos.

Sloths are arboreal mammals that harbor a complex community of organisms in their fur, including moths and algae (Aiello, 1985; Vaughan, Ramírez, Herrera, & Guries, 2007; Ramírez, Vaughan, Herrera, & Guries, 2011). Some sloths descend to defecate and urinate on the ground, increasing the risk of predation by ground animals. At least, five hypotheses have been proposed to explain this behavior: to fertilize trees, because feces are deposited at the tree base (Montgomery & Sunquist, 1975); to avoid predation, by covering the feces and reducing smells, as occurs in some other mammals (see Bailey, 1974; Liberg, 1980; Pauli et al., 2014); to communicate with chemical messages because direct interactions among individuals are rare, as implied by Chiarello (2008); to pick trace nutrients from the ground when they lick mud from their claws, as observed by Voirin, Kays, Wikelski, & Lowman (2013); and to increase moth populations, a mutualistic model (Voirin et al., 2013) for which Pauli et al. (2014) published some experimental support.

The current version of the mutualistic model states that sloths of the species *B. variegatus* lick and digest algae from their hair to obtain nutrients (algae might be fertilized by

sloth fur moths, Voirin et al., 2013; Pauli et al., 2014). This model proposes that sloths defecate on the ground, and cover their feces to benefit moth larvae; these larvae develop inside fecal pellets in the "latrines". Pauli et al. (2014) add that *B. variegatus* descends to the ground, with higher risk of falling prey to predators. According to those authors, another species, *C. hoffmanii*, is less affected by predation because it defecates from the relative safety of branches, and has less algae and moths.

Here I summarize scientific reports that contradict the mutualistic hypothesis and propose a different explanation for why some sloths defecate on the ground.

The mutualistic model is contradicted by the scientific literature: The key aspect of the mutualistic hypothesis is that sloths lick and digest the algae from their hair to obtain nutrients. However, *Bradypus variegatus* do not lick themselves, or each other (Aiello, 1985). Additionally, no noticeable algal remains are found in their digestive systems (Dünner & Pastor, 2017) and they cannot reach most of their own fur because of their short tongues and necks (Dünner & Pastor, 2017). Pauli et al. (2014) reported that 83 % of their *B. variegatus* digesta samples did *not* have any algal remains, but explained this absence, which is lethal to the mutualistic hypothesis, as the result of rapid digestion. The same algae may also grow on the leaves that sloths eat (Suutari et al., 2010) and this can explain why Pauli et al. (2014) detected some algal remains in a few stomachs. Furthermore, the test with cow ruminal inoculum, used to propose that sloths can digest fur algae, does not take into account differences in cow and sloth digestive systems (Clauss, 2004; Dünner & Pastor, 2017).

Secondary aspects of the mutualistic model lacking evidence in the scientific literature: Like Aiello (1985), I could not find any reports that sloth algae are fertilized by sloth moths, either through any secretions, or through their corpses as proposed by Pauli et al. (2014). Pauli et al. (2014) also stated that *B. variegatus*, which descends to the ground, suffers more predation than *C. hoffmanii*, which often drops feces from the canopy. However, a study in Costa Rica reported the opposite: 5.5 times less predation of *B. variegatus* than of *C. hoffmanni* (see Table 2 in Peery & Pauli, 2014).

Recommendation for new studies: The following hypotheses could be studied in captive sloths: that algae are fertilized by the sloth fur moths (by keeping algae in cultures with and without the moths); that algal nutrients might be absorbed through the sloth skin (by chemical analysis of skin samples from areas with and without algae), and that moths feed on secretions from the sloth skin (by keeping moths in small containers attached to living sloths, with bottoms with or without holes allowing contact with the fur).

New hypothesis: The new hypothesis that I propose here is that *sloths defecate on the ground because they maintain their ancestral defecation behavior and there has been no selective pressure for them to defecate from the canopy*.

Supporting references for the new hypothesis: The six extant species of sloths are the only surviving descendants of a much larger group of mammals that defecated on the ground (Slater et al., 2016; Hunt & Lucas, 2018). Both families adapted independently to life on trees, and instead of convergently evolving ground defecation to increase their moth populations as proposed by, among others, Pauli et al. (2014); or by habit and to obtain additional nutrients, as proposed by Voirin et al. (2013); I propose that they retained the ancestral behavior of ground

defecation in *all* species, as reported in the literature (Sunquist & Montgomery, 1973; Waage & Best, 1985; Hayssen, 2009; Hayssen, 2011; Slater et al., 2016; Dünner & Pastor, 2017), because there was no natural selection pressure (significant predation pressure or other) to stop defecating in the ground.

Maybe we should pay more attention to *B. tridactylus*, which sometimes defecates from the canopy (Waage & Best, 1985; Hayssen, 2009), and may be in the process of evolving a more fully arboreal life.

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ETHICAL, CONFLICT OF INTEREST AND FINANCIAL STATEMENTS

The author declares that he has fully complied with all pertinent ethical and legal requirements, both during the study and in the production of the manuscript; that there are no conflicts of interest of any kind; that all financial sources are fully and clearly stated in the acknowledgements section; and that he fully agrees with the final edited version of the article. A signed document has been filed in the journal archives.

The statement of each author's contribution to the manuscript is as follows: J.M.N.: is the sole author.

REFERENCES

Aiello, A. (1985). Sloth hair: unanswered questions. In G. G. Montgomery (ed). *The Evolution of Armadillos, Sloths, and Vermilinguas* (pp. 213-218). Washington, D.C., USA: Smithsonian Institution Press.

Bailey, T. N. (1974). Social organization in a bobcat population. *The Journal of Wildlife Management*, *38*(3),435-446.

Chiarello A.G. (2008) Sloth ecology: an overview of field studies. In S. Vizcaíno & W. Loughry (eds.). *The biology of the Xenarthra* (pp. 269–280). Gainesville, FL: University Press of Florida.

Clauss, M. (2004). The potential interplay of posture, digestive anatomy, density of ingesta and gravity in mammalian herbivores: Why sloths do not rest upside down. *Mammal Review*, *34*(3), 241-245.

Dünner, C., & Pastor, G. (2017). *Manual de manejo, medicina y rehabilitación de perezosos.* Chile: Fundación Huálamo.

Hayssen, V. (2009). *Bradypus tridactylus* (Pilosa: Bradypodidae). *Mammalian Species*, 839, 1-9. DOI: 10.1644/839.1

Hayssen, V. (2011). *Choloepus hoffmanni* (Pilosa: Megalonychidae). *Mammalian Species*, *43*(873), 37-55. DOI: 10.1644/873.1

Hunt, A. P., & Lucas, S. G. (2018). The Record of Sloth Coprolites in North and South America: Implications for Terminal Pleistocene Extinctions. *New Mexico Museum of Natural History and Science Bulletin*, *79*, 277-298.

Liberg, O. (1980). Spacing patterns in a population of rural free roaming domestic cats. *Oikos*, *32*(3),336-349.

Montgomery, G. G., & Sunquist, M. E. (1975). Impact of Sloths on Neotropical Forest Energy Flow and Nutrient Cycling. *Ecological Studies*, 69–98. DOI:10.1007/978-3-642-88533-4_7

Pauli, J. N., Mendoza, J. E., Steffan, S. A., Carey, C. C., Weimer, P. J., & Peery, M. Z. (2014). A syndrome of mutualism reinforces the lifestyle of a sloth. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1778), 20133006. DOI: 10.1098/rspb.2013.3006

Peery, M. Z., & Pauli, J. N. (2014). Shade-grown cacao supports a self-sustaining population of two-toed but not three-toed sloths. *Journal of Applied Ecology*, *51*(1), 162-170. DOI: 10.1111/1365-2664.12182

Ramírez, O., Vaughan, C., Herrera, G., & Guries, R. (2011). Temporal and spatial resource use by female three-toed sloths and their young in an agricultural landscape in Costa Rica. *Revista de Biologia Tropical*, *59*(4), 1743-1755.

Slater, G. J., Cui, P., Forasiepi, A. M., Lenz, D., Tsangaras, K., Voirin, B., ... & Greenwood, A. D. (2016). Evolutionary relationships among extinct and extant sloths: the evidence of mitogenomes and retroviruses. *Genome Biology and Evolution*, *8*(3), 607-621. DOI: 10.1093/gbe/evw023

Sunquist, M. E., & Montgomery, G. G. (1973). Activity patterns and rates of movement of two-toed and three-toed sloths (*Choloepus hoffmanni* and *Bradypus infuscatus*). *Journal of Mammalogy*, *54*(4), 946-954. DOI: 10.2307/1379088

Suutari, M., Majaneva, M., Fewer, D. P., Voirin, B., Aiello, A., Friedl, T., ... & Blomster, J. (2010). Molecular evidence for a diverse green algal community growing in the hair of sloths and a specific association with *Trichophilus welckeri* (Chlorophyta, Ulvophyceae). *BMC Evolutionary Biology*, *10*(1), 1-12. DOI: 10.1186/1471-2148-10-86

Vaughan, C., Ramírez, O., Herrera, G., & Guries, R. (2007). Spatial ecology and conservation of two sloth species in a cacao landscape in Limón, Costa Rica. *Biodiversity and Conservation*, *16*(8), 2293-2310. DOI: 10.1007/s10531-007-9191-5

Voirin, B., Kays, R., Wikelski, M., & Lowman, M. (2013). Why Do Sloths Poop on the Ground? In M. Lowman, S. Devy, & T. Ganesh (eds). *Treetops at Risk* (pp. 195-199). Springer, New York, NY.

Waage, J. K., & Best, C. (1985). Arthropod associates of sloths. In G. G. Montgomery (ed). *The Evolution of Armadillos, Sloths, and Vermilinguas* (pp. 297-311). Washington, D.C., USA: Smithsonian Institution Press.

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