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NEWS AND PERSPECTIVES

Factors affecting the drinking behavior of black howler monkeys (*Alouatta pigra*)

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Abstract Water is essential for animals, and is particularly critical for thermoregulation. Animals obtain water from three main sources, free water, water contained in food, and water produced in the body during metabolism. Howler monkeys (*Alouatta* spp.) spend a small proportion of their time drinking water and some populations have not been observed drinking, suggesting they obtain most of their water requirements in food or by metabolism. However, when howler monkeys have been observed drinking there is evidence suggesting the drinking is associated with low precipitation, temperature, and fruit consumption, and high mature leaf consumption, although it remains unclear which factors determine drinking by this genus. In this study we tested the hypothesis that drinking by howler monkeys results from increased hydration requirements in drier climates and from lower consumption of foods rich in water (e.g., new leaves, fruit). We tested this hypothesis by comparative analysis of 14 groups of Yucatán black howler monkeys (*A. pigra*) living under different climatic conditions. From April 2005 to November 2008 we collected a total of 3,747.2 focal observation hours of the feeding and drinking behavior of 60 individuals, with data on ambient temperature and rainfall. Individuals spent more time drinking when they lived in habitats with higher maximum temperature and when they consumed more mature leaves. For this species, therefore, drinking seems to be linked to heat stress and a low availability of water in ingested food.

P. A. D. Dias (✉) · A. Rangel-Negrín · A. Coyohua-Fuentes · D. Canales-Espinosa
Instituto de Neuroetología, Universidad Veracruzana, Industrial Animas, Av. Dr. Luis Castelazo Ayala S/N, 91190 Xalapa, Veracruz, Mexico
e-mail: paddias@hotmail.com

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Introduction

Water is essential for animals, because it is involved in numerous functions, including hydrolytic reactions, temperature control, and excretion (Barboza et al. 2009). Water is particularly critical for thermoregulation. Under hot conditions, water absorbs heat with little body temperature rise and dissipates it, whereas under cold conditions body fluids may be redistributed to maintain high temperature in core areas that are critical for survival (Oddershede and Elizondo1980; Müller et al. 1985). Animals obtain water from three main sources: free water, present, for instance, in lakes, rain, or snow; water contained in food; and water produced during metabolism by oxidation of organic compounds containing hydrogen (National Research Council 2003). Howler monkeys (*Alouatta* spp.) spend a small (<1 %; Dias and Rangel-Negrín 2013) proportion of their foraging time drinking water, suggesting they obtain most of their water requirements either from food or by metabolism. Furthermore, in several studies howler monkeys have never been observed drinking (Carpenter 1934; Baldwin and Baldwin 1972).

In some studies, however, howler monkeys have been observed drinking rainwater accumulated in flowers, epiphytic bromeliads (Bonvicino 1989; Steinmetz 2001; Miranda et al. 2005), pools, and holes in trunks (Glander 1978; Bicca-Marques 1992; Silver et al. 1998; Giudice and Mudry 2000; Miranda et al. 2005; Pozo-Montuy and Serio-Silva 2007), and from ponds and rivers (Gilbert and Stouffer 1989; Almeida-Silva et al. 2005; Miranda et al. 2005). There is indirect evidence suggesting that drinking by howler monkeys is associated with low precipitation, low temperature, and low fruit consumption, and with high consumption of mature leaves (Glander 1978; Bonvicino 1989; Gilbert and Stouffer 1989; Steinmetz 2001; Miranda et al. 2005). Nevertheless, drinking by a group of black-and-gold howler monkeys (*A. caraya*) increased with increasing rainfall, suggesting that it depends more on water availability than on physiological requirements (Bicca-Marques 1992). Therefore, it remains unclear which factors determine drinking by howler monkeys.

In this study we tested the hypothesis that drinking by howler monkeys results from increased hydration requirements in drier climates and lower consumption of foods rich in water (e.g., new leaves, fruit). We tested this hypothesis by comparative analysis of 14 populations of Yucatán *A. pigra* (hereafter, black howler monkeys) that lived in different climatic conditions.

Methods

Study sites and subjects

The study was conducted between April 2005 and November 2008 in the Mexican state of Campeche, located in the Yucatan Peninsula. In Campeche the climate is hot and humid (Vidal-Zepeda 2005), and mean annual rainfall is 1,300 mm, with a drier season from November to May (mean monthly rainfall $\pm$ SD $=$ 43.7 $\pm$ 25.8 mm), and a wetter period between June and October (218.9 $\pm$ 14.1 mm). Mean annual temperature is 26 °C. We studied 14 groups of black howler monkeys that lived in different locations (described in Dias et al. 2011). Mean ($\pm$SD) group size was 6.1 $\pm$ 2.3 individuals, of which 1.8 $\pm$ 0.7 were sexually mature males, 2.3 $\pm$ 0.9 were sexually mature females, and 2.1 $\pm$ 1.2 were immature (i.e., <30 months of age).

Behavioral observations

We used focal-animal sampling with continuous recording (1-h samples; Altmann 1974) to study feeding and drinking behavior. When focal animals fed or drank we noted the duration of this behavior; during feeding we noted the plant parts consumed: mature leaves, young leaves, fruit, or flowers. Observations were performed during complete days (i.e., 6:00–17:00 or 7:00–18:00, depending on daylight during the year), and all individuals were identified on the basis of their natural anatomical and physiognomic characteristics, for example body size and proportions, scars, broken fingers, and genital morphology and pigmentation. Focal animals were selected on a pseudorandom basis, such that no individual was sampled twice until all were sampled once, and focal samples of each animal were evenly distributed throughout the day. We sampled only adult individuals ($N = 60$; 32 females and 28 males). We collected a total of 3,747.2 focal hours, with a mean ($\pm$SD) observation time of 62.5 $\pm$ 19.8 h per individual and 267.7 $\pm$ 39.71 h per group. Each group was sampled for approximately one month in each season (i.e., dry and wet seasons).

Climate data

We collected the climatic data total monthly rainfall, monthly maximum ambient temperature, and monthly mean ambient temperature for each group. These data were available from a network of weather stations managed by CONAGUA-SMN (Mexican National Water Committee-National Weather Service) that covers the entire territory of Campeche State. For each study group, we located the nearest station (mean $\pm$ SD distance between weather stations and study sites $=$ 7.3 $\pm$ 5.1 km) and obtained the data corresponding to the dates in which we sampled the groups.

Data organization and analysis

The time each individual spent feeding from each plant part and drinking was converted to the proportion of total feeding time per focal sample, and then transformed to the square root of the arcsine. To determine whether drinking depended on the types of food consumed and on climate we ran a linear mixed model (LMM) with time drinking as response variable and feeding, climate, group, season, and sex as fixed predictive variables. We used Akaike's information criterion (AIC) to determine the model that best explained variation among groups in time spent drinking (Burnham and Anderson 2002). In this test we specified seasons within individuals and individuals within groups as hierarchical random effects to account for the repeated sampling of several individuals belonging to the same group through time. This test was two-tailed and statistical significance was set at $P < 0.05$.

Results

All observed instances of drinking corresponded to use of water in tree holes. Howler monkeys directly drank water from the holes or licked water from their hands after immersing them in the water. Drinking behavior occurred in all groups except one, and 38 % of all focal individuals drank during observations. Across all groups, the mean percentage of time spent drinking per individual was 0.5 $\pm$ 1.3 % (median $=$ 0; range $=$ 0–7.2 %). At the group level, the proportion of individuals that drank varied from 0 to 100 %, with a mean (±SD) percentage of 43.0 ± 29.4 % individuals drinking per group.

Overall, individuals spent 30.5 ± 23.7 % of their feeding time eating fruit, 48.4 ± 26.1 % eating young leaves, 9.8 ± 11.6 % eating mature leaves, and 10.6 ± 17.7 % eating flowers. Mean rainfall was 133.5 ± 107.5 mm, mean temperature was 25.8 ± 2.2 °C and maximum temperature was 36.7 ± 2.5 °C. On the basis of AIC values, the most parsimonious model explaining variation among groups in drinking behavior included maximum temperature and the proportion of time spent consuming mature leaves (Table 1). This model was significant ($R^2 = 0.78$, $F_{2,21.96} = 18.1$, $P < 0.001$) and indicated that individuals spent more time drinking when living in habitats with higher maximum temperatures ($F_{1,22.08} = 10.6$, $P < 0.001$; Fig. 1a) and when they consumed more mature leaves ($F_{1,67.35} = 8.9$, $P < 0.01$; Fig. 1b).

Table 1 Models evaluated during investigation of variation in drinking behavior of *Alouatta pigra*

Model	Delta AIC (Δ_i)*
Maximum temperature + mature leaves	0
Maximum temperature + mature leaves + mean temperature	2.2
Maximum temperature + mature leaves + group	3.5
Maximum temperature	5.1
Mean temperature + group + mature leaves + rainfall	6.9

* Only models with $\Delta_i < 7$ (i.e., those receiving high to moderate support: Burnham and Anderson 2002) are presented

Discussion

In this study, variation of the time spent drinking among groups of black howler monkeys depended on maximum ambient temperature and time spent eating mature leaves. Groups that faced higher temperatures and consumed more mature leaves spent more time drinking, and these relationships were independent of variation in sex or season. These results suggest that for black howler monkeys drinking is important to maintain water balance when the likelihood of dehydration increases.

High air temperatures and aridity increase water loss, requiring individuals to adjust their water balance (Barboza et al. 2009). For primates, maintenance of thermal balance at high temperatures is mainly achieved by evaporative heat loss (Elizondo 1977). Greater heat stress leads to increased water loss by evaporation and, ultimately, loss of thermoregulatory ability if the animal becomes dehydrated (Brain and Mitchell 1999). Our results indicate that high ambient temperatures may oblige black howler monkeys to drink. Under such conditions drinking is a rapid and effective way of reducing body temperature and recovering water homeostasis (Barboza et al. 2009). In the group that faced the driest conditions (>40 °C and <40 % humidity on four consecutive days) we observed several individuals

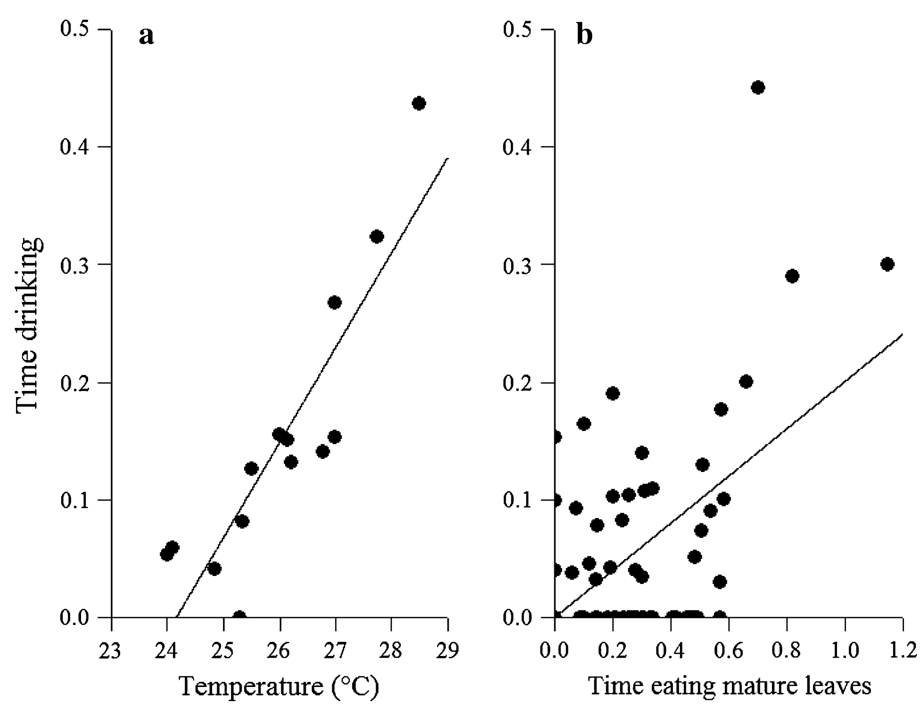

Fig. 1 The relationship between the proportion of time spent drinking (transformed to the square root of the arcsine) and both maximum temperature (**a** represented as mean group values) and the percentage of time spent eating mature leaves (**b**)

panting, behavior that has been reported for other primate species (Hiley 1976) and that enables dissipation of excess heat (National Research Council 2003). For this group the rate of drinking was the third highest in our sample. Because drinking was associated with variation in climate and diet but not with group or season, access to water sources (which should be more abundant in the wet season) was not a determinant factor explaining drinking in this study (cf. Bicca-Marques 1992). To corroborate the importance to howler monkeys of drinking for thermoregulation and water balance, future research could include measurement of physiological indicators of the hydration status of individuals, for example vasopressin hormone (Bossingham et al. 2005), which can be monitored non-invasively (Diederich et al. 2001).

Water in food varies from less than 30 % of mass in some seeds to more than 80 % in some fruits (Barboza et al. 2009). There is evidence that the water content of mature leaves consumed by black howler monkeys is lower than that of other plant parts (Silver et al. 1999), so it is possible that, as observed for other howler monkeys (*A. guariba clamitans*: Steinmetz 2001; *A. palliata*: Glander 1978), when mature leaf consumption increases, water supply in the food decreases, and howler monkeys drink as a response to this decrease. In addition, coarse residues from fibrous leaf diets result in more feces with a greater water-holding capacity than the dense residues from more digestible foods, increasing water loss (Barboza et al. 2009). Detoxification of secondary components, which are more abundant in mature leaves than other plant parts, may increase water requirements (Freeland and Janzen 1974). In conclusion, drinking by black howler monkeys is linked to heat stress and a decrease of water ingested in food.

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