

Impacts of Temperature on Behaviour of the Mexican Endangered Black Howler Monkey *Alouatta pigra* Lawrence, 1933 (Primates: Atelidae) in a Fragmented Landscape

John F. Aristizabal¹, Lucile Lévêque², Colin A. Chapman³ & Juan Carlos Serio-Silva^{1*}

¹Red Biología y Conservación de Vertebrados, Instituto de Ecología A.C., Carretera antigua a Coatepec No. 351, El Haya, CP 91070 Xalapa, Veracruz, México; E-mails: johnycay@gmail.com and juan.serio@inecol.mx

²School of Biological Sciences, University of Tasmania, Private Bag 55, 7001, Tasmania, Australia; E-mail: lucile.leveque@utas.edu.au

³Department of Anthropology and McGill School of Environment, McGill University, Montreal, QC, H3A 2T7, Canada, and Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460, USA; E-mail: colin.chapman@mcgill.ca

Abstract: For primates, habitat degradation and loss lead to increases in solar radiation, temperature and wind, and in decrease of humidity. This, in turn, leads to cascading changes in the habitat's plant species composition and the types and quality of available food but these changes could also affect animal thermoregulatory abilities and behaviour. In this study, we aimed (1) to determine the influence of ambient temperature (T) and humidity (H) on activity patterns of black howler monkeys *Alouatta pigra* and 2) to test the hypothesis that as the temperature increases, the duration of time resting and frequency of visits in lower canopy increase. We observed two groups (476h) quantifying behaviour and tree stratum use every 15 min. As predicted, animals rested more as temperature increased, they moved into the middle tree strata to rest and there was an interaction between temperature ranges and stratum (GLM: $df = 2$; $P = <0.0001$). Since animals were spending more time resting, there was less time available for other behaviours that might mean that they were neglecting other biologically important activities, such as feeding or social behaviours. We identified the importance of maintaining extensive forest areas which would help to minimising the impact of solar radiation on this endangered Mexican primate. Our study shows the importance of understanding the fitness consequences of such altered time budgets with respect to fragmentation and climate change.

Key words: resting behaviour, thermoregulation, microclimate conditions, abiotic variables, fragmentation

Introduction

The impact of habitat loss and fragmentation is a major threat to biodiversity (FAHRIG 2003), leading to an increasing number of patches, decreasing habitat patch size and increased isolation. Under such fragmented conditions, the microclimate in the patches is altered and there is an increase in solar radiation, temperature and wind as well as a decrease in humidity (SAUNDERS et al. 1991). This in turn leads to cascading changes in availability, quantity and nutritional content of food and in species composition of the habitat (ESTRADA & COATES-ESTRADA 1996,

STEVENS & O'CONNOR 2006, ARROYO-RODRIGUEZ & DIAS 2010, PRETZLAFF & DAUSMANN 2014). These abiotic variables also impact the patterns of distribution and habitat use of animals and many aspects of the behaviour of the patch inhabitants (e.g., the choice of sleeping sites, see SUCHI & ROTHE 1999, DOMINGUEZ 2002, HILL et al. 2004, ARROYO-RODRIGUEZ & DIAS 2010). Understanding the behavioural effects of fragmentation may provide useful information for the preparation of informed management plans. Researchers have suggested that

*Corresponding author: juan.serio@inecol.mx

involving a careful analysis of abiotic factors and effects on habitat and species will help to identify biodiversity hotspots (VENEVSKY & VENEVSKAIA 2005).

Primate species play important roles in forest regeneration (COWLISHAW & DUNBAR 2000, GILBERT 2003, ARROYO-RODRIGUEZ & DIAS 2010, OMEJA et al. 2016). However, one major effect of the fragmentation is the transformation of the vegetation structure and composition that have negative effects on diversity and availability of food sources for wild primates (ARROYO-RODRÍGUEZ & MANDUJANO 2006, ARROYO-RODRÍGUEZ & DIAS 2010). In addition, environmental abiotic variables like temperature and humidity are affected by fragmentation and may force primates to adopt unfavourable activity patterns negatively affecting populations (STELZNER 1988, SUCHI & ROTHE 1999, HILL et al. 2004, VENTURA et al. 2005, KORSTJENS et al. 2006, GONZÁLEZ-ZAMORA et al. 2011). Temperature affects the ability of primates to thermoregulate (SUCHI & ROTHE 1999, HILL et al. 2004, DONATI & BORGOGNINI-TARLI 2006) and may force primates to alter their activity patterns. For instance, to deal with high temperatures and/or low humidity, many primates rest more (STELZNER 1988, BICCA-MARQUES & CALEGARO-MARQUES 1998, KORSTJENS et al. 2010, GONZÁLEZ-ZAMORA et al. 2011). In addition, travelling and feeding are energetically costly (DUNBAR 1992, KORSTJENS et al. 2006) and reducing them when temperature is high allows primates to minimise energy costs (DUNBAR et al. 2009). Primates could also be expected to reduce time devoted to social activities (CONRADT et al. 2000; CLARKE et al. 2002).

It is reasonable to expect that an increase in solar radiation and temperature would encourage primates to move down into the canopy during hot periods of the day to seek shade and cooler temperatures (BICCA-MARQUES & CALEGARO-MARQUES 1998). Therefore, to survive and persist in highly fragmented landscapes, arboreal primates must exhibit flexibility in their diet and behaviour (CHAVES & BICCA-MARQUES 2012). If fragmentation and the corresponding changes in temperature, wind and humidity alter primate behaviours, understanding the ability of species to adapt will be key for developing management plans for primates in general. Such information will also be vital to predict the consequences of accelerating global climate change and to take conservation actions that are pro-active, not just responsive (ANDERSON et al. 2008; DUNBAR et al. 2009; GONZÁLEZ-ZAMORA et al. 2011).

In this study (1) we explored the influence of ambient temperature (T) and humidity (H) on activ-

ity patterns of black howler monkeys *Alouatta pigra* Lawrence, 1933 and (2) tested the hypothesis that as temperature increases, the duration of time resting and frequency of visits in the lower canopy increase. This information could be used to design conservation and management plans about the black howler monkeys *Alouatta pigra* in the region of Balancán, Mexico.

Materials and Methods

The study was conducted at “Estación de Investigación Primatológica y Vida Silvestre”, located in the settlement of Josefa Ortiz de Domínguez near the city of Balancán, Tabasco, Mexico. The climate is hot and humid, with three seasons: a “rainy” season (May – October, mean rainfall = 178 mm), “nortes” season (November – January, mean rainfall = 137 mm) characterised by strong northern winds and a “dry” season (February – April, mean rainfall = 57 mm). The annual average temperature ranges between 21.7 and 33.5°C (CONAGUA 2013). Rainforest, semi-deciduous tropical forest and spiny evergreen bloodwood (*Haematoxylum campechianum*) forest originally dominated the region (LÓPEZ-MENDOZA 1980). However, the colonisation in the 1960’s resulted in forest loss and fragmentation as forests were converted to pasture and agricultural lands (REYES-CASTILLO 1978; TUDELA 1989).

We observed two groups of howler monkeys and recorded their behaviour using focal animal sampling from November 2012 to March 2013, covering the nortes season (290 hr) and dry season (187 hr). Group 1 included two adult males and two adult females (235 hr), and Group 2 consisted of one adult male, three adult females and 4 juveniles (242 hr). The groups inhabited different forest fragments separated by a 400 m pasture (Fragment 1: 2.68 ha; Fragment 2: 3.89 ha). We followed the monkeys from 7:00 to 17:00 and recorded four behavioural categories: resting, feeding, travelling and social activities (playing, vocalisations, agonistic behaviour) and their position in the tree stratum during resting periods: Ground = 0 m, Low < 2 m, Medium: 2-15 m, High > 15 m. In general, trees’ height from forest fragments varied slightly, showing a similar tree size (average height = 8.84 ± 3.9 m SD; Max = 22.8; Min = 2.5), allowing a comparison of stratum positions between trees. The trees with height less than 3m were actually bush and palms and were barely used by the monkeys. The ambient temperature (°C) and humidity (%) data were recorded every 15 minutes with a Datalogger (Extech RHT 10) positioned under the canopy in Fragment 1.

We use Linear Models (LMs) to predict the time allocated in each behavioural category, using temperature and humidity as predictors and Generalized Linear Models (GLMs) to understand if the frequency and duration of resting in each stratum (medium and high) were a function of temperature and humidity categories for each season. Humidity and temperature were strongly correlated ($r_s = -0.78$, $S = 77365.0$, $df = 2962$, $P < 0.001$), thus only temperature was used in the GLMs. Temperature was divided into three categories using the minimum and maximum value and the average temperatures of the zone as follows: Temperature: Low = 20-25 °C, Medium = 26-30 °C, High = 30-36 °C. For all models, appropriate error distributions were specified and transformations or weight structures applied, where necessary, following ZUUR et al. (2009). To determine the best models, we used the Akaike's information criterion (AIC). We performed LMs and GLMs with the R package *nlme* (PINHEIRO et al. 2014; version 3.2.0, R Core Team, 2015).

Results

Howler monkeys' activity was characterised by long periods of resting (76.1% ± SD 21.7), followed by feeding (16 % ± SD 8.7), travelling (6.2 % ± SD 3.3) and social activities (1.7% ± SD 0.8; Fig. 1).

We did not find evidence of the influence of temperature and humidity on the time allocated for feeding, travelling or social behaviours. Only an influence of temperature over the resting time was found (LM: $P = 0.004$; Table 1).

Howler monkeys visited the medium tree stratum more frequently than the other strata when they were resting (Table 2) and this was influenced by the temperature (GLM: $df = 2$; $P = <0.0001$), the stratum (GLM: $df = 1$; $P = <0.0001$) and the interaction between temperature ranges and stratum (GLM: $df = 2$; $P = 0.025$). Furthermore, we found that the frequency of visits was affected by the high temperature range (GLM: $Z = 11.41$; $P = <0.0001$), medium temperature range (GLM: Z

$= 2.29$; $P = 0.02$), medium tree stratum (GLM: $Z = 4.13$; $P = <0.0001$) and the interaction between low temperature range and medium tree stratum (GLM: $Z = -2.67$; $P = 0.007$). The duration of time of resting was different across the tree stratum (LM: $df = 1$; $P = 0.03$; High = 4024 min, Medium = 5431 min) and the temperature ranges (LM: $df = 2$; $P = 0.03$). No differences were found in the time resting by season.

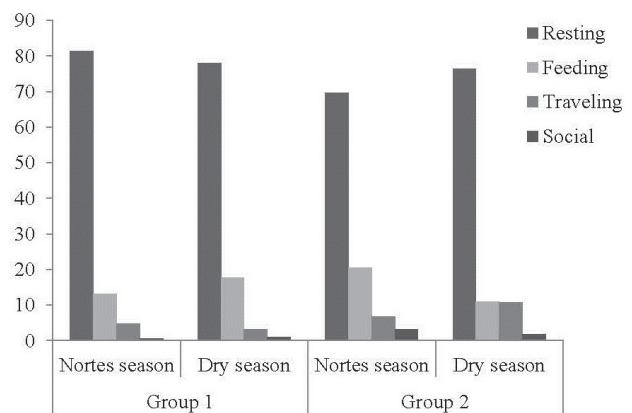


Fig. 1. Activity patterns (% time) for the two groups of black howler monkeys (*Alouatta pigra*).

Table 1. LM analysis of abiotic variables that influence activity patterns of *Alouatta pigra*.

Predictor variables	df	F-value	P-value
Resting			
Humidity	1	0.99	0.32
Temperature	1	9.19	0.004
Feeding			
Humidity	1	3.79	0.06
Temperature	1	0.3	0.58
Traveling			
Humidity	1	2.28	0.14
Temperature	1	1.12	0.29
Social activities			
Humidity	1	3.51	0.08
Temperature	1	0.18	0.67

All models included season as a predictor variable; however, in all cases it had not effect on behaviour.

Table 2. Frequencies of *Alouatta pigra* in each tree stratum divided per temperature ranges and humidity ranges.

Tree stratum	Temperature ranges			Humidity ranges		
	20-25°C	26-30°C	31-35°C	40-60%	61-80%	81-100%
High	31	47	27	23	50	32
Medium	32	88	69	54	104	31
Low	3	9	6	8	8	2

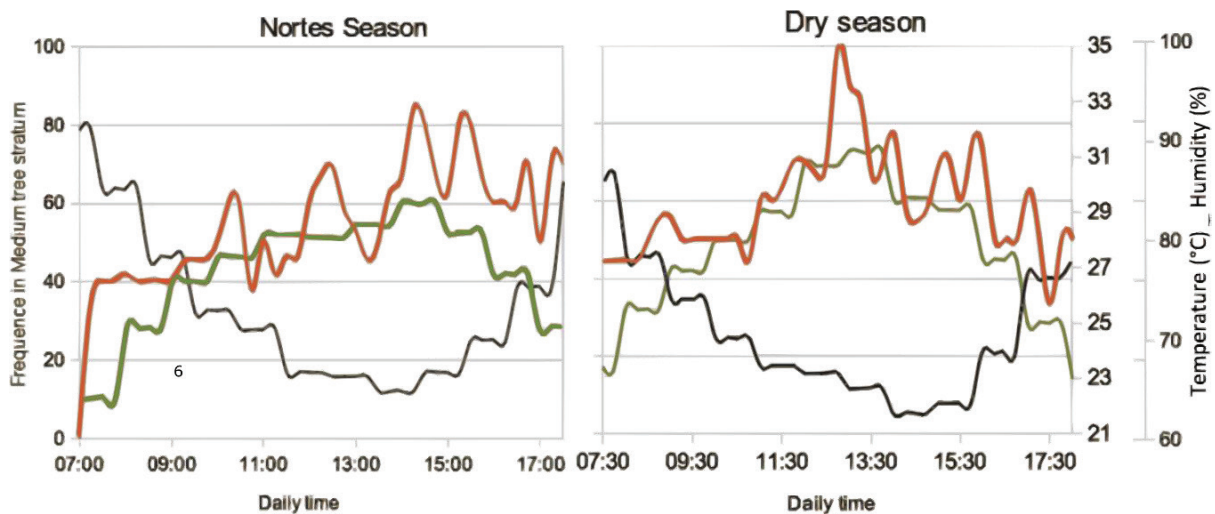


Fig 2. Frequency of use of the medium tree stratum in resting behaviour of black howler monkeys (*Alouatta pigra*) during day-time. Red line: frequency in medium tree stratum; Green line: ambient temperature; Blue line: humidity.

Discussion

We found changes in the frequency and duration of resting of Black howler monkeys in fragments in the Balancán Region only as a function of temperature. As an example, the frequency of use of the medium tree stratum in resting behaviour increased during the day-time when it was hotter (Fig 2).

A number of studies have found relations between primates' activity patterns and temperature or humidity (FERNANDEZ-DUQUE 2003, HILL et al. 2004, VENTURA et al. 2005, KORSTJENS et al. 2010, GONZÁLEZ-ZAMORA et al. 2011). We found an association between temperature and resting time but not with other activities. During the extreme hot conditions of the dry season, howler monkeys are known to spend more time resting and less time feeding or engaging in social activities (CROCKETT et al. 1987, CONRADT et al. 2000). Rest has often been found to be related to temperature (*Alouatta caraya*: BICCA-MARQUES & CALEGARO-MARQUES 1998; primates: KORSTJENS et al. 2010, GONZÁLEZ-ZAMORA et al. 2011) but not always as in mantled howler monkeys *Alouatta palliata* (WILLIAMS-GUILLEN 2003). In contrast, we found no evidence that feeding time was influenced by temperature as opposed to previous suggestions of temperature effect on feeding in both frugivores and folivores.

When the temperature is low and so the percentage of humidity is high, the black howler monkeys rest equally throughout the canopy, but when the temperature increases (above 25°C) and the humidity goes down, the monkeys rest preferentially in middle of the tree (medium stratum) in the shade (see also HILL et al. 2004). In contrast, when tem-

peratures are cool, a number of monkey species tend to rest in sunny places, likely gaining heat from the sunlight (BICCA-MARQUES & CALEGARO-MARQUES 1998, HARRIS & CHAPMAN 2007). In this way, the cost of endothermy can be behaviourally minimised by taking advantage of the solar radiation (SCHMIDT-NIELSEN 1990). Thermoregulation seems to be particularly important for folivores, who need to develop strategies to save energy because of their energy-poor diet (DASILVA 1992). In parallel, during the hot periods of the day, they need to move down in the shade, likely to avoid exposure to solar radiation (BICCA-MARQUES & CALEGARO-MARQUES 1998).

According to the world climate-change models, there will be an increase in temperature and a decrease in humidity and conditions in forest fragments are likely to become more extreme (HILL et al. 2004; POZO-MONTUY & SERIO-SILVA 2007). As a result, the behaviour of species like the black howler monkeys will have to change in order to cope with the new conditions and the related serious time-budgeting problems; it is likely that resting would increase and the time available for other biological demands will decrease (KORSTJENS et al. 2010). The effects of deforestation (less tall trees and more scattered) and edge effects (greater wind penetration, increased dryness and temperature) will make conditions even harsher for many howler monkey populations. This demonstrates the importance of preserving large vegetation fragments (KORSTJENS et al. 2010).

Conclusions

Our results highlight the importance of maintaining extensive vegetation and, thus, minimising exces-

sive solar radiation for arboreal primates and require better understanding of the fitness consequences of such altered time budgets with respect to fragmentation and climate change.

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References

- ANDERSON E. R., CHERRINGTON E. A., FLORES A. I., PEREZ J. B. & CARRILLO R. E. 2008 Potential Impacts of Climate Change on Biodiversity in Central America, Mexico, and the Dominican Republic. Panama City, Panama: CATHALAC / USAID. 105 p.
- ARROYO-RODRÍGUEZ V. & MANDUJANO S. 2006. Forest fragmentation modifies habitat quality for *Alouatta palliata*. *International Journal of Primatology* 27 (4): 1079–1096.
- ARROYO-RODRÍGUEZ V. & DIAS P. A. 2010. Effects of habitat fragmentation and disturbance on howler monkeys: a review. *American Journal of Primatology* 72 (1):1–16.
- BICCA-MARQUES J. C. & CALEGARO-MARQUES C. 1998. Behavioral thermoregulation in a sexually and developmentally dichromatic neotropical primate, the black-and-gold howling monkey (*Alouatta caraya*). *American Journal of Physical Anthropology* 106 (4): 533–546.
- CHAVES O. M. & BICCA-MARQUES J. C. 2012. Dietary flexibility of the Brown howler monkey throughout its geographic distribution. *American Journal of Primatology* 75 (1): 16–29.
- CONAGUA. 2013. Comisión Nacional de Agua. Available at: <http://smn.cna.gob.mx/>, accessed on 01 July 2017
- CONRADT L., CLUTTON-BROCK T. H. & GUINNESS F. E. 2000. Sex differences in weather sensitivity can cause habitat segregation: red deer as an example. *Animal Behavior* 59(5): 1049–1060.
- COWLISHAW G. & DUNBAR R. I. M. 2000. *Primate Conservation Biology*. Chicago: The University of Chicago Press. 498 p.
- CLARKE M. R., CROCKETT C. M., ZUCKER E. L. & ZALDIVAR M. 2002. Mantled howler population of hacienda La Pacifica, Costa Rica, between 1991 and 1998: Effects of deforestation. *American Journal of Primatology* 56 (3): 155–163.
- CROCKETT C. M. & EISENBERG J. F. 1987. Howlers: variations in group size and demography. In: SMUTS B., CHENEY D. L., SEYFARTH R. M., WRANGHAM R. W. & STRUHSAKER T. T. (Ed.) *Primate Societies*. Chicago: The University of Chicago. pp. 54–68.
- DASILVA G. L. 1992. The western black-and-white colobus as a low-energy strategist: activity budgets, energy expenditure and energy intake. *Journal of Animal Ecology* 61 (1): 79–81.
- DOMÍNGUEZ J. 2002. Biotic and abiotic factors affecting the feeding behavior of the black-tailed Godwit. *Waterbirds* 25 (4): 393–520.
- DUNBAR R. I. M. 1992. Time: a hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology* 31 (1): 35–49.
- DUNBAR R. I. M., KORSTJENS A. H. & LEHMANN J. 2009. Time as an ecological constraint. *Biological Reviews*, 84 (3): 413–429.
- DONATI G. & BORGOGNINI-TARLI S. M. 2006. Influence of abiotic factors on cathemeral activity: the case of *Eulemur fulvus collaris* in the littoral forest of Madagascar. *Folia Primatologica* 77 (1–2): 104–122.
- ESTRADA A. & COATES-ESTRADA R. 1996. Tropical rain forest fragmentation and wild populations of primates at los Tuxtlas, Mexico. *International Journal of Primatology* 17 (5): 759–783.
- FAHRIG L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics* 34 (1): 487–515.
- FERNANDEZ-DUQUE E. 2003. Influences of moonlight, ambient temperature, and food availability on the diurnal and nocturnal activity of owl monkeys (*Aotus azarai*). *Behavioral Ecology and Sociobiology* 54 (5): 431–440.
- GILBERT K. A. 2003. Primates and fragmentation of the Amazon forest. In: MARSH L. (Ed.) *Primates in Fragments*. New York: Kluwer Academic/Plenum Publishers. pp. 145–157.
- GONZÁLEZ-ZAMORA A., ARROYO-RODRÍGUEZ V., CHAVES O. M., SÁNCHEZ-LÓPEZ S., AURELI F. & STONER K. E. 2011. Influence of climatic variables, forest type, and condition on activity patterns of geoffroy's spider monkeys throughout Mesoamerica. *American Journal of Primatology* 73 (11): 1189–1198.
- HARRIS T. R. & CHAPMAN C. A. 2007. Variation in the diet and ranging behavior of black-and-white colobus monkeys: implications for theory and conservation. *Primates*, 48 (3): 208–221.
- HILL R. A., WEINGRILL T., BARRETT L. & HENZI S. P. 2004. Indices of environmental temperatures for primates in open habitats. *Primates* 45 (1): 7–13.
- KORSTJENS A. H., VERHOECKX I. L. & DUNBAR R. I. M. 2006. Time as a constraint on group size in spider monkeys. *Behavioral Ecology and Sociobiology* 60 (5): 683–694.
- KORSTJENS A. H., LEHMANN J. & DUNBAR R. I. M. 2010. Resting time as an ecological constraint on primate biogeography. *Animal Behavior* 79 (2): 361–374.
- OMEJA P., LAWES M. J., CORRIVEAU A., VALENTA K., SARKAR D., PAIM F. P. & CHAPMAN C. A. 2016. Recovery of the animal and plant communities across large scales in Kibale National Park, Uganda. *Biotropica* 48 (6): 770–729.
- PINHEIRO J., BATES D., DEBROY S. & SARKAR D. R. 2017. NLME: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131, Available at: <https://CRAN.R-project.org/package=nlme> accessed on 13 February 2017
- POZO-MONTUY G. & SERIO-SILVA J. C. 2007. Movement and resource use by a group of *Alouatta pigra* in a forest fragment in Balancán, Mexico. *Primates* 48 (2): 102–107.
- PRETZLAFF I., RAU D. & DAUSMANN K. H. 2014. Energy expenditure increases during the active season in the small, free-living hibernator *Muscardinus avellanarius*. *Mammalian Biology* 79 (3): 208–214.
- R CORE TEAM. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org/> accessed on 10 February 2017
- REYES-CASTILLO P. 1978. La fauna silvestre en el Plan Balancán-

- Tenosique. Veracruz, México: INIREB. Biblioteca del Instituto de Ecología A.C. Xalapa, 45 p.
- SAUNDERS D. A., HOBBS R. J. & MARGULES C. R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5 (1): 18–32.
- SCHMIDT-NIELSEN K. 1990. *Animal Physiology: Adaptation and Environment*. Fourth Edition. Cambridge: Cambridge University Press. 613 p.
- STELZNER J. K. 1988. Thermal effects on movement patterns of yellow baboons. *Primates* 29 (1): 91–105.
- STEVENS N. J. & O'CONNOR P. M. 2006. Abiotic and biotic factors as predictors of species richness on Madagascar. In: LEHMAN S. M. & FLEAGLE J. G. (Eds.). *Primate Biogeography: progress and prospects*. New York: Springer. pp. 269–300.
- SUCHI S. & ROTHE H. 1999. The influence of abiotic factors on the onset and cessation of activity of semi-free *Callithrix jacchus*. *American Journal of Primatology* 47 (3): 241–253.
- TUDELA F. 1989. *Modernización forzada del trópico mexicano*. Mexico: Colegio de México. Mexico, DF. 475 p.
- VENEVSKY S. & VENEVSKAIA I. 2005. Hierarchical systematic conservation planning at the national level: Identifying national biodiversity hotspots using abiotic factors in Russia. *Biological Conservation* 124 (2): 235–251.
- VENTURA R., MAJOLO B., SCHINO G. & HARDIE S. 2005. Differential effects of ambient temperature and humidity on allogrooming, self-grooming, and scratching in wild Japanese macaques. *American Journal of Physical Anthropology* 126 (4): 453–457.
- WILLIAMS-GUILLEN K. 2003. *The behavioral ecology of mantled howling monkeys (Alouatta palliata) living in a Nicaraguan shade coffee plantation*. Ph.D. Dissertation. New York University. 259 p.
- ZUUR A., LENO E. N. & MEESTERS E. 2009. *A beginner's guide to R*. New York, NY: Springer. 218 p.

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