Veterinary Parasitology: Regional Studies and Reports 22 (2020) 100476

Contents lists available at ScienceDirect

Veterinary Parasitology: Regional Studies and Reports

journal homepage: www.elsevier.com/locate/vprsr

Short Communication

Island and Riverine populations of *Alouatta belzebul* from the Brazilian Amazon parasitized by *Pediculus mjobergi*

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ARTICLE INFO

Keywords:
Wild howler
Microscopy
Louse infestation
Parasite ecology
Amazon basin

ABSTRACT

Mammalian lice are obligate hematophagous ectoparasites that remain on the host throughout the life cycle. This study showed an endangered wild howler species (*Alouatta belzebul*) parasitized by *Pediculus mjobergi*. Twenty-seven primates were rescued during wildlife rescue activities in the process of vegetation suppression at the Belo Monte Hydroelectric Power Plant (UHE), located on the lower Xingu River, in the Brazilian Amazon basin. Among the 27 primates examined from two vegetal formations (alluvial rainforest and liana-infested forest) areas, 13 (48.15%) were parasitized by lice with all positive primates being from alluvial rainforest. Optical and scanning electron microscopy allowed the visualization of the structures and the diagnostic characters of the lice species in greater detail expanding the current description. These results highlight the importance of considering ecological and regional features to provide a better understanding of the factors that promote parasitism.

1. Introduction

The Red-Handed Howler monkey (*Alouatta belzebul*, Linnaeus, 1766) is an endemic species of Brazil with distribution mainly over the eastern Amazon, (Emmons and Feer, 1990). The International Union for Conservation of Nature (IUCN) and the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) have classified this species as *Vulnerable* on a national and global scale (MMA, 2014). Although hunting pressure must not be ignored, the fragmentation and loss of natural habitat caused by deforestation and recent installation of hydroelectric power plants have strongly contributed to the decline in this specific populations of *A. belzebul* (Crockett, 1998; Valença-Montenegro et al., 2012).

The Belo Monte Hydroelectric Power Plant was built on the lower Xingu River, in the Amazon region of northern Brazil, and has caused severe impacts to the river ecosystem (Latrubesse et al., 2017). Environmental changes, such as loss of forest and habitat due to anthropogenic pressure, may cause an overall shift in the host-parasite dynamics (Gillespie and Chapman, 2008; Sures, 2004). A few studies have argued that the prevalence of some parasite species tends to increase in habitat disturbance conditions, caused by fragmentation, deforestation, and climate change (Chapman et al., 2005a; Crockett, 1998). A study in Uganda showed that the environmental change may lead to nutritional stress and a consequent increase in the occurrence of diseases in most primates (Chapman et al., 2005b).

Mammalian lice are obligate hematophagous ectoparasites that remain on the host throughout the life cycle (Scholl et al., 2012). Some authors claim that lice have high host-specificity, even though some species may affect two or more phylogenetically close host species (Veracx and Raoult, 2012).

Previously, the genus *Pediculus* (Linnaeus 1758) was first represented by *Pediculus humanus* which was differentiated in *Pediculus humanus capitis* and *Pediculus humanus corporis* by De Geer in 1778, both of them parasitizing humans. The New World Monkey lice was initially

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https://doi.org/10.1016/j.vprsr.2020.100476
Received 19 March 2020; Received in revised form 28 September 2020; Accepted 4 October 2020
Available online 06 October 2020
2405-9390/ © 2020 Published by Elsevier B.V.

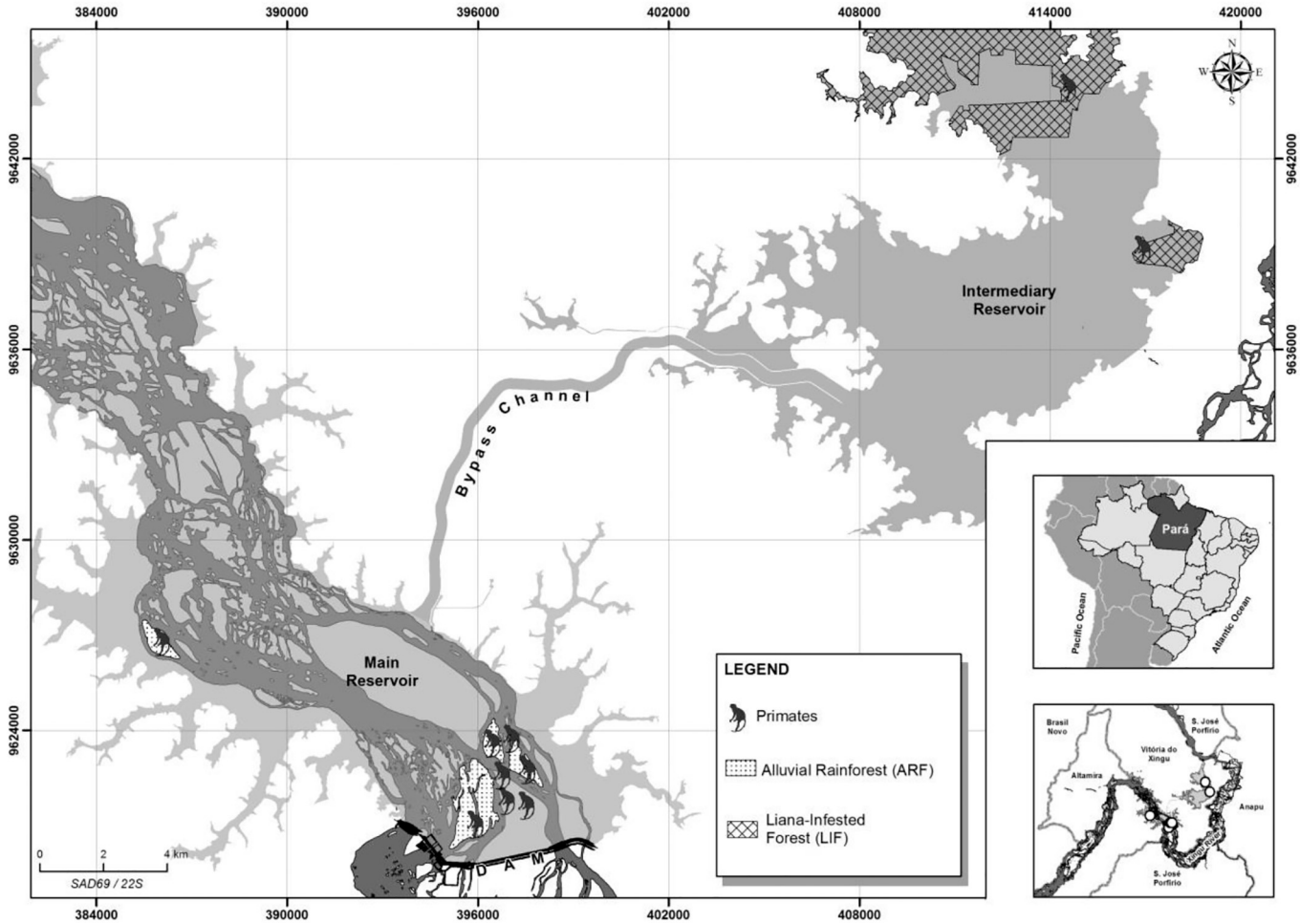

Fig. 1. Map of the sampling area with the respective capture points.

described on *Ateles* spp. as *Pediculus affinis* (Mjöberg, 1910) and renamed as *Pediculus mjobergi* by Ferris (1916). However, according to Ewing (1938), the morphological differences found by Mjöberg on the monkeys' *Pediculus* were not enough to distinguish it from *P. humanus*. For many years there was disagreement regarding the taxonomic status of this louse until Ferris (1951) recognized *P. mjobergi* as a different species from those lice that parasitize humans. A genetic study developed to analyze the relationship between *P. humanus* and *P. mjoberg* lice found a phylogenetic proximity between the two species and indicated that there was a human lice transmission to monkeys caused by genetic and geographic proximity (Maunder, 1983; Drali et al., 2016).

Recent reports have confirmed that *Pediculus mjobergi* has been identified in 11 primate species of the families Cebidae, Atelidae, and Pitheciidae (Drali et al., 2016). There are records in Neotropical species such as *A. belzebul*, *A. caraya*, *A. palliata*, *A. pigra*, *Ateles belzebuth*, *A. fusciceps*, *A. geoffroyi*, *Cebus apela*, *C. capucinus*, *Cacajao calvus*, and *Pithecia monachus* (Durden and Musser, 1994; Stuart et al., 1998).

The morphology of *Pediculus mjobergi* closely resembles the human louse species, and previous studies in South America have presented information only from Argentina, French Guiana, and Costa Rica. The current study aimed to present new morphological features of *Pediculus mjobergi* and its geographical distribution in wild populations of *Alouatta belzebul* from the Brazilian Amazon Basin. Furthermore, we provide preliminary data on the potential relationship of lice infestations with habitat disturbances.

2. Material and methods

This field study was conducted during the Amazonian rainy winter (from February to June) in 2016 during wildlife rescue activities initiated due to deforestation. The lice were collected from *A. belzebul* rescued from the area of influence of the Belo Monte Hydroelectric Power Plant (UHE), located on the lower Xingu River, between the cities of Altamira and Vitoria do Xingu, Pará State, Brazil. Twenty-seven *A. belzebul* were captured, (n = 16 females and n = 11 males) from two different forest formations: alluvial rainforest (ARF) and liana-infested forest (LIF), located on the left bank and islands of the lower Xingu River (Fig. 1).

The wild-caught primates were sedated with tiletamine hydrochloride in association with zolazepam hydrochloride (Zoletil ® 50, Virbac - São Paulo, Brazil), at 3.6 mg/kg body weight for clinical examination prior to relocation in protected areas. All lice seen during the examination were removed and stored in 70% ethanol, and then sent for further identification at the Laboratório de Enfermidades Parasitárias dos Animais of the FCAV/Unesp, in Jaboticabal, São Paulo state, Brazil. The lice were morphologically identified according to descriptions published by Serra-Freire and Mello (2006).

The lice specimens were submitted to clarification in 30% KOH solution and subsequently compressed between microscope slides for morphological examination. Photomicrographs were obtained by light microscopy (Leica®, DM 5000B) with the aid of image capture software (LAS V3 Leica Application Suite®, Wetzlar, Germany) to view the morphological structures with taxonomic relevance.

The best lice specimens were also scanned by electron microscopy

Table 1
Stratification of *Alouatta belzeul* captured in the field and the presence of ectoparasites.

Age	Sex	Vegetal Type	Site	Louse
Adult	Male	ARF	Pimental (Island)	Absent
Juvenile	Male	ARF	Pimental (Island)	Absent
Juvenile	Female	ARF	Pimental (Island)	Absent
Adult	Female	ARF	Pimenta (Island)	Absent
Adult	Female	ARF	Pimental (Island)	Absent
Juvenile	Male	ARF	Pimental (Island)	Absent
Juvenile	Female	ARF	Pimental (Island)	Absent
Adult	Female	ARF	Pimental (Island)	Absent
Adult	Male	ARF	Pimental (Island)	Present
Adult	Male	LIF	Left Bank	Present
Adult	Female	LIF	Left Bank	Absent
Juvenile	Male	LIF	Left Bank	Absent
Adult	Male	LIF	Left Bank	Absent
Adult	Male	LIF	Left Bank	Absent
Adult	Male	ARF	Do Meio (Island)	Absent
Juvenile	Female	ARF	Grande (Island)	Absent
Adult	Male	ARF	Do Meio (Island)	Present
Adult	Female	ARF	49 (Island)	Present
Adult	Female	ARF	Maravilha (Island)	Present
Adult	Female	ARF	Maravilha (Island)	Present
Adult	Female	ARF	Maravilha (Island)	Present
Juvenile	Female	ARF	Maravilha (Island)	Present
Juvenile	Female	ARF	Maravilha (Island)	Present
Adult	Male	ARF	Maravilha (Island)	Present
Juvenile	Female	ARF	Maravilha (Island)	Present
Adult	Female	ARF	Do Meio (Island)	Present
Adult	Female	ARF	Do Meio (Island)	Present

ARF – Alluvial Rainforest; LIF – Liana-Infested Forest;

(SEM). Initially, lice were cleaned by shaking them in preservative solution, post-fixed in osmium tetroxide 2% at 23 °C for 12 h, and then dehydrated in a series of graduated ethanol and liquid CO_2 until dried to a critical point.

After drying, the lice specimens were mounted on SEM suitable bases using a stereoscopic microscope. After the metallization step, they were examined under an electronic microscope (Quanta 200, FEI Company) operating at 12.5 kV, located in the Electronic Microscopy Center, at the Instituto de Biociências de Botucatu - Unesp, in Botucatu, São Paulo state, Brazil.

3. Results and discussion

Most of the captured animals (81.48%) came from islands with "ARF-type" vegetation, while all other animals came from the left bank of the river ("terra firme"), from LIF area (Salomão et al. de P. Salomão et al., 2007; Tymen et al., 2016). It is important to highlight the non-probabilistic character of sampling because there was no means to predict the number of animals that could be captured, by sex and location. Of the 27 captures, 13 (48.15%) of the primates (four adult males, six adult females, and three juvenile females) were parasitized by lice (Table 1). This prevalence is slightly higher than found by Pope (1966) in a province located in Argentina, where 37% of *Alouatta caraya* were infested by the same lice species.

Sixteen specimens of lice, nine adults and seven nymphs, were collected. Among the adults, six were identified as males and three as females, while five females and two males were still in the nymphal stage. Based on their morphological features, the lice were identified as *Pediculus mjobergi*. This study is the first report of *P. mjobergi* on *A. belzebul*. In Brazil, this species had already been reported in Pará State in *Ateles paniscus* (Werneck, 1937).

The main characteristics that differentiate this species from the others are: the head presents a conical pre-antral region and projected forward; antennae as long as head, with segment I almost twice as long as broad, segment II about one and half times as long as broad, segment III longer than broad and longer than IV segment, segment IV as long as broad, and segment V slightly longer than broad and equal to III in length; small thoracic spiracles; medium legs; presence of eyes, normal abdominal segments, five or six paratergal plates of the abdominal segments (Fig. 2A), a pair of thoracic spiracles located in the dorsolateral region of the mesothorax (Fig. 2A), six pairs of abdominal spiracles (Fig. 2A), single claws with a prominent tibia (tibial spur) and tibiotarsal joint (Fig. 2D). Females present with a broader and longer abdomen than the males, with the thorax more chitinized. Furthermore, females have two well-developed pairs of gonopodia with long lateral bristles and close to opening in the transversal line (Fig. 2C); males present smaller pleural plates. These lice present a modified sucking oral apparatus, used to perforate the skin of their hosts, which is formed by three styli, located in the ventral bag (Fig. 2B).

Drali et al. (2016) found two different genotype clades present in the human lice that indicate the shift between the species. In general, the sucking lice are specific parasites and the intimate contact with their hosts reflected in their morphological characteristics (Reed and Hafner, 1997). They have a short life cycle and spend their lifetime on their hosts requiring morphological adaptations to enable them to survive (Cannon, 2010). The presence of tibiotarsal claws at the end of the paired legs is an essential adaptation of *P. mjobergi*. It allows them to adhere to the hair strand and orient close to the skin to feed (Durden and Musser, 1994).

Females of *A. belzebul* had higher lice prevalence than males in this study, and this may be related to allogrooming behavior. There are different approaches to the role of grooming in primate species, and specifically in the genus *Alouatta (*Thorington et al., 1984*;* Chiarello, 1995*;* Van Belle et al., 2009). For hygiene purposes, and for the "strengthening" of social hierarchies or courtship displays, it is common the females "clean up" the males as a gesture of submission (Hutchins and Barash, 1976; Spruijt et al., 1992; Allen et al., 2007; de P. Salomão et al., 2007). Most of these studies on this "trade-off" have considered plausible males less lice-infested because females manually remove their ectoparasites (Kinzey and Wright, 1982; Sánchez-Villagra et al., 1998; Schino, 2007; Schino and Aureli, 2008).

Regarding habitat, although there is a trend to expect higher parasitic infection in disturbed habitats (Crockett, 1998; Gillespie and Chapman, 2008, 2006; Pope, 1966; Sures, 2004), the most parasitized howlers of this study came from island environments, in better conservation status. In a recent meta-analysis with South American howler monkeys (Kowalewski and Gillespie, 2009; Martínez-Mota et al., 2015), it was demonstrated that primates that inhabit disturbed forests did not have higher parasitic infections than primates living in conserved habitats (Young et al., 2013).

We understand the limitations of providing a "snapshot" from one-time sampling and numerous predictor factors of the lice prevalence in howlers. However, we hope that illustrating and discussing the morpho-functional features of this interaction provide an opportunity to explore general trends of parasitism.

Animal ethics

All the procedures used in this study were approved by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis - IBAMA (n. 473/2014_2), Instituto Chico Mendes de Conservação da Biodiversidade – ICMBio (124/2015), and Animal Use Ethics Committee of the FMVZ/Unesp (no. 49643-1).

Declaration of Competing Interest

The authors declare no conflicts of interest regarding the publication of this paper.

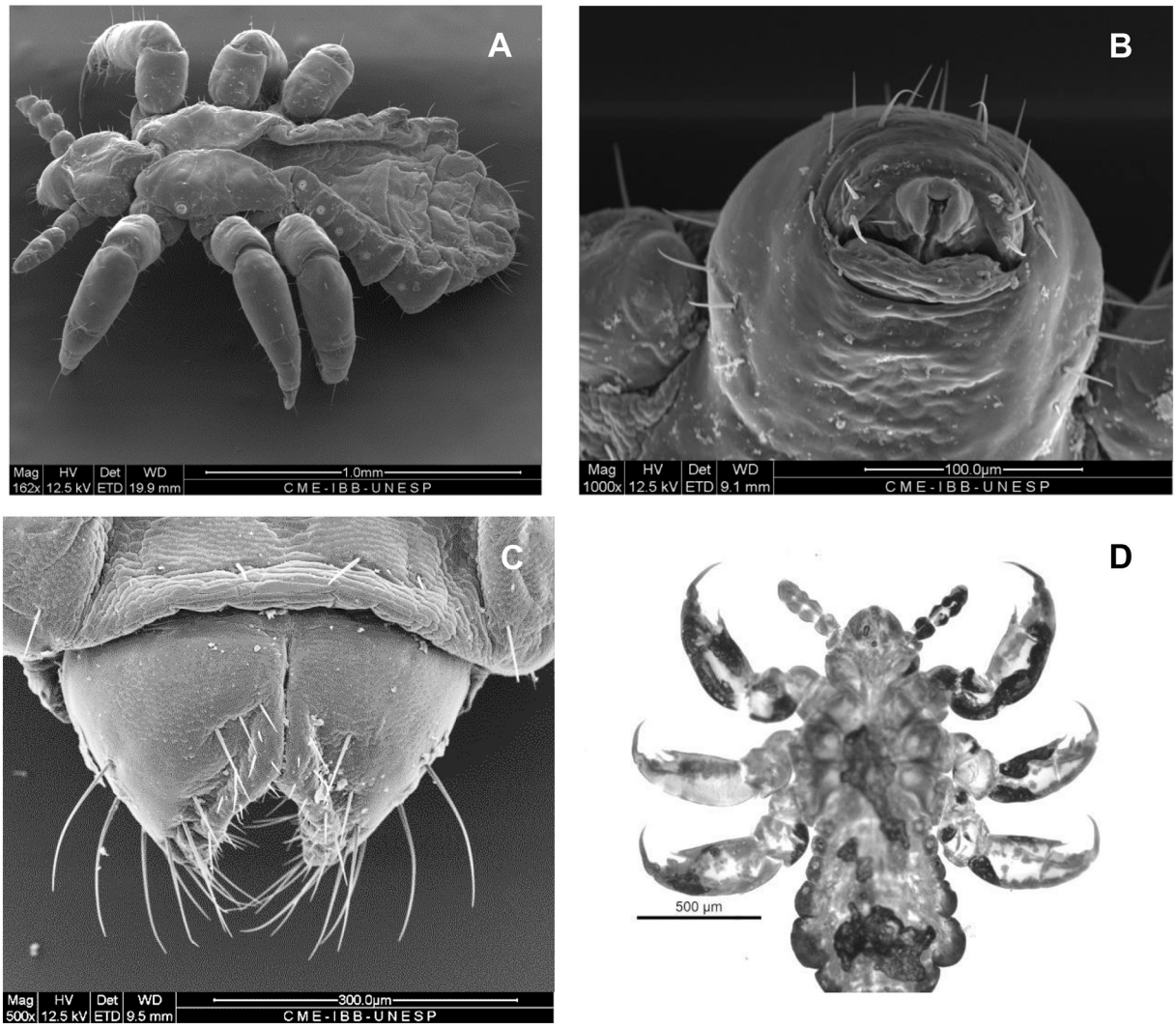

Fig. 2. *Pediculus mjobergi* scanned by electron microscopy: A- Adult female, showing a pair of thoracic spiracles, six pairs of abdominal spiracles; B- Sucking mouthpiece; C- Adult female, dorsal view of gonopodium. Microscopy of light: D- Adult male, claw with the prominence of the tibia.

Acknowledgements

The author would like to thank Norte Energia SA and Biota Projetos e Consultoria Ambiental Ltda. for logistical support during field activities, and to all the biologists that contributed in some way toward this study.

References

Allen, J.M., Reed, D.L., Perotti, M.A., Braig, H.R., 2007. Evolutionary relationships of "*Candidatus riesia* spp.," endosymbiotic Enterobacteriaceae living within hematophagous primate lice. Appl. Environ. Microbiol. 73, 1659–1664. https://doi.org/10.1128/AEM.01877-06.

Cannon, S.M., 2010. Size Correlations between Sucking Lice and their Hosts Including a Test of Harrison' S Rule. Georgia Southern University Electronic Theses and Dissertations. https://digitalcommons.georgiasouthern.edu/etd/764.

Chapman, C.A., Gillespie, T.R., Goldberg, T.L., 2005a. Primates and the ecology of their infectious diseases: how will anthropogenic change affect host-parasite interactions? Evol. Anthropol. 14, 134–144. https://doi.org/10.1002/evan.20068.

Chapman, C.A., Chapman, L.J., Struhsaker, T.T., Zanne, A.E., Clark, C.J., Poulsen, J.R., 2005b. A long-term evaluation of fruiting phenology: importance of climate change. J. Trop. Ecol. 21, 31–45. https://doi.org/10.1017/S0266467404001993.

Chiarello, A.G., 1995. Grooming in brown howler monkeys, *Alouatta fusca*. Am. J. Primatol. 35, 73–81. https://doi.org/10.1002/ajp.1350350107.

Crockett, C.M., 1998. Conservation biology of the genus *Alouatta*. Int. J. Primatol. 19, 549–578. https://doi.org/10.1023/A:1020316607284.

Drali, R., Abi-Rached, L., Boutellis, A., Djossou, F., Barker, S.C., Raoult, D., 2016. Host switching of human lice to new world monkeys in South America. Infect. Genet. Evol. 39, 225–231. https://doi.org/10.1016/j.meegid.2016.02.008.

Durden, L.A., Musser, G.G., 1994. The sucking lice (Insecta, Anoplura) of the world - a taxonomic checklist with records of mammalian hosts and geographical distributions. Bull. Am. Mus. Nat. Hist. 1–90.

Emmons, L.H., Feer, F., 1990. Neotropical Rainforest Mammals, A Field Guide. The University of Chicago Press.

Ewing, H.E., 1938. The sucking lice of American monkeys. J. Parasitol. 24, 13–33.

Ferris, G.F., 1916. Notes on Anoplura and Mallophaga, from Mammals, with Descriptions of Four New Species and a New Variety of Anoplura. Psyche 23 (4), 97–120. https://doi.org/10.1155/1916/10871.

Ferris, G.F., 1951. The Sucking Lice. Mem. Pacif. Coast ent. Soc. 1 (pp.ix + 320 pp. Record Number: 19521000146).

Gillespie, T.R., Chapman, C.A., 2006. Prediction of parasite infection dynamics in primate metapopulations based on attributes of forest fragmentation. Conserv. Biol. 20, 441–448. https://doi.org/10.1111/j.1523-1739.2006.00290.x.

Gillespie, T.R., Chapman, C.A., 2008. Forest fragmentation, the decline of an endangered primate, and changes in host-parasite interactions relative to an unfragmented forest. Am. J. Primatol. 70, 222–230. https://doi.org/10.1002/ajp.20475.

Hutchins, M., Barash, D.P., 1976. Grooming in primates: implications for its utilitarian function. Primates 17, 145–150. https://doi.org/10.1007/BF02382848.

Kinzey, W.G., Wright, P.C., 1982. Grooming behavior in the Titi Monkey (*Callicebus torquatus*). Am. J. Primatol. 3, 267–275. https://doi.org/10.1002/ajp.1350030124.

Kowalewski, M.M., Gillespie, T.R., 2009. South American primates. South Am. Primates. https://doi.org/10.1007/978-0-387-78705-3.

Latrubesse, E.M., Arima, E.Y., Dunne, T., Park, E., Baker, V.R., D'Horta, F.M., Wight, C., Wittmann, F., Zuanon, J., Baker, P.A., Ribas, C.C., Norgaard, R.B., Filizola, N., Ansar, A., Flyvbjerg, B., Stevaux, J.C., 2017. Damming the rivers of the Amazon basin. Nature 546, 363–369. https://doi.org/10.1038/nature22333.

Martínez-Mota, R., Kowalewski, M.M., Gillespie, T.R., 2015. Ecological determinants of parasitism in Howler Monkeys. In: Kowalewski, M.M., Garber, P.A., Cortés-ortiz, L., Urbani, B., Youlatus, D. (Eds.), Howler Monkeys: Adaptive Radiation, Systematics,

and Morphology. Springer, New York, pp. 259–288. https://doi.org/10.1007/978-1-4939-1957-4_10.
Maunder, J., 1983. The appreciation of lice. In: Proceeding of the Royal Institution of Great Britain. Great Britain, pp. 1–31.
Mjöberg, E., 1910. Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia, 1913. pp. 14.
MMA, 2014. Portaria MMA n 444, 17 dezembro de 2014. 39. pp. 1–15. https://doi.org/10.4324/9781315853178.
de P. Salomão, R., Vieira, I.C.G., Suemitsu, C., de A. Rosa, N., de Almeida, S.S., do Amaral, D.D., de Menezes, M.P.M., 2007. As florestas de Belo Monte na grande curva do rio Xingu, Amazônia Oriental. Bol. do Mus. Para. Emílio Goeldi Ciências Nat. 2. pp. 55–153.
Pope, B.L., 1966. Some parasites of the Howler Monkey of northern Argentina. J. Parasitol. 52, 166–168. https://doi.org/10.2307/3276409.
Reed, D.L., Hafner, M.S., 1997. Host specificity of chewing lice on pocket gophers: a potential mechanism for cospeciation. J. Mammal. 78, 655–660. https://doi.org/10.2307/1382916.
Sánchez-Villagra, M.R., Pope, T.R., Salas, V., 1998. Relation of intergroup variation in allogrooming to group social structure and ectoparasite loads in red howlers (*Alouatta seniculus*). Int. J. Primatol. 19, 473–491. https://doi.org/10.1023/A:1020360422305.
Schino, G., 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. Behav. Ecol. 18, 115–120. https://doi.org/10.1093/beheco/arl045.
Schino, G., Aureli, F., 2008. Trade-offs in primate grooming reciprocation: testing behavioural flexibility and correlated evolution. Biol. J. Linn. Soc. 95, 439–446. https://doi.org/10.1111/j.1095-8312.2008.01067.x.
Scholl, K., Allen, J.M., Leendertz, F.H., Chapman, C.A., Reed, D.L., 2012. Variable microsatellite loci for population genetic analysis of old world monkey lice (*Pedicinus* sp.). J. Parasitol. 98, 930–937. https://doi.org/10.1645/ge-3060.1.
Serra-Freire, N.M., Mello, R.D., 2006. Entomologia & acarologia na medicina veterinária. LF Livros. ed, Rio de Janeiro.
Spruijt, B.M., Van Hooff, J.A.R.A.M., Gispen, W.H., 1992. Ethology and neurobiology of grooming behavior. Physiol. Rev. 72, 825–852. https://doi.org/10.1152/physrev.1992.72.3.825.
Stuart, M., Pendergast, V., Rumfelt, S., Pierberg, S., Greenspan, L., Glander, K., Clarke, M., 1998. Parasites of wild howlers (*Alouatta* spp.). Int. J. Primatol. 19, 493–512.
Sures, B., 2004. Environmental parasitology: relevancy of parasites in monitoring environmental pollution. Trends Parasitol. 20, 170–177. https://doi.org/10.1016/j.pt.2004.01.014.
Thorington, R.W., Ruiz, J.C., Eisenberg, J.F., 1984. A study of a Black Howling Monkey (*Alouatta caraya*) population in northern Argentina. Am. J. Primatol. 6, 357–366. https://doi.org/10.1002/ajp.1350060405.
Tymen, B., Réjou-Méchain, M., Dalling, J.W., Fauset, S., Feldpausch, T.R., Norden, N., Phillips, O.L., Turner, B.L., 2016. Evidence for arrested succession in a liana-infested Amazonian forest. J. Ecol. 104, 149–159. https://doi.org/10.1111/1365-2745.12504.
Valença-Montenegro, M.M., Fialho, M.S., Carvalho, A.S., Ravetta, A.L., Régis, T., Melo, F.R., Veiga, L.M., 2012. Processo de avaliação do risco de extinção da fauna Brasileira. ICMBio URL. http://www.icmbio.gov.br/portal/biodiversidade/fauna-brasileira/lista-de-especies/7171-mamiferos-alouatta-belzebul-guariba-de-maos-ruivas.html.
Van Belle, S., Estrada, A., Ziegler, T.E., Strier, K.B., 2009. Sexual behavior across ovarian cycles in wild black Howler Monkeys (*Alouatta pigra*): male mate guarding and female mate choice. Am. J. Primatol. 71, 153–164. https://doi.org/10.1002/ajp.20635.
Veracx, A., Raoult, D., 2012. Biology and genetics of human head and body lice. Trends Parasitol. 28, 563–571. https://doi.org/10.1016/j.pt.2012.09.003.
Werneck, F.L., 1937. Nota sobre *Pediculus mjobergi* Ferris (Anoplura: Pediculidae). Mem. Inst. Oswaldo Cruz 161–163.
Young, H., Griffin, R.H., Wood, C.L., Nunn, C.L., 2013. Does habitat disturbance increase infectious disease risk for primates? Ecol. Lett. 16, 656–663. https://doi.org/10.1111/ele.12094.