American Journal of Primatology

WILEY

AMERICAN JOURNAL OF PRIMATOLOGY

RESEARCH ARTICLE

Impact of Botfly Parasitism on the Behavior of Mantled Howler Monkeys

Ricardo J. Ortíz-Zárate[1] | Jurgi Cristóbal-Azkarate[2] | Ariadna Rangel-Negrín[1] | Alejandro Coyohua-Fuentes[1] | Pedro A. D. Dias[1]

[1]Primate Behavioral Ecology Lab, Instituto de Neuro-etología, Universidad Veracruzana, Xalapa, México | [2]Department of Basic Psychological Processes and their Development, University of the Basque Country, Donostia, Spain

Correspondence: Ricardo J. Ortíz-Zárate (ricardojesus.ortiz@upaep.mx) | Pedro A. D. Dias (pedroaddias@gmail.com)

Received: 4 July 2024 | **Revised:** 4 November 2024 | **Accepted:** 3 January 2025

Funding: The study was financed by Consejo Nacional de Ciencia y Tecnología (CONAHCyT grant 1147976), Posgrado en Neuroetología, Instituto de Neuroetología (Universidad Veracruzana), and the Leakey Foundation.

Keywords: activity budgets | *Cuterebra* | foraging | grooming | sickness behaviors

ABSTRACT

Parasitism, a widespread nutrient acquisition strategy among animals, results from a long evolutionary history where one species derives its metabolic needs from another. Parasites can significantly reduce host fitness, affecting reproduction, growth, and survivability. Vertebrate hosts exhibit defensive strategies against parasites, including "sickness behaviors" such as lethargy and self-grooming to remove ectoparasites. In addition, social animals may engage in "helping sick animals" behaviors, such as social grooming, to aid parasitized group members. Mantled howler monkeys (*Alouatta palliata*) parasitized by botfly larvae (*Cuterebra baeri*) exhibit subdermal nodules, which can be fatal under nutritional stress. This study investigates whether mantled howler monkeys display sickness behaviors or helping behaviors in response to *C. baeri* parasitism. Observations from July 2022 to April 2023 in La Flor de Catemaco, Mexico, revealed that parasitized individuals did not increase the frequency of self-directed (rub, scratch, and touch) nor received helping behaviors (social scratch and social touch) compared to non-parasitized ones. However, parasitized monkeys were more active, spending more time feeding and moving, likely to compensate for the metabolic costs of parasitism. This shift from energy conservation to energy acquisition strategies suggests a complex response to parasitism, emphasizing the need for further research on the energetic impacts of parasitism in this species. These preliminary findings suggest behavioral flexibility by mantled howler monkeys in coping with infection, indicating potential adaptive strategies to mitigate the adverse effects of parasitism.

1 | Introduction

Parasitism is the result of a long evolutionary history between one species whose metabolic requirements are provided by another one (Roberts, Janovy, and Nadler 2013), being the most common nutrient acquisition strategy among animals (de Meeûs, Michalakis, and Renaud 1998; de Meeûs and Renaud 2002). Parasites can decrease the fitness of hosts and cause damage to them (Goater, Goater, and Esch 2014), through impacts on reproductive rates (Schwanz 2008), growth (Gorrell and Schulte-Hostedde 2008), and survivability (Robar, Burness, and Murray 2010).

Hosts defend against parasites (Kuris, Blaustein, and Alio 1980), and in vertebrates, parasitized individuals may display two main types of defensive behavioral strategies (Hart 1990). The first, are "sickness behaviors," and pertain to behavioral differences between parasitized and healthy individuals. Such behaviors contribute to recovery from illness, remove parasites, and mitigate the effects of parasites, suggesting they are

American Journal of Primatology, 2025; 87:e23731
https://doi.org/10.1002/ajp.23731

Summary

- Botfly parasitism does not influence self-directed behaviors.
- Botfly parasitism does not influence "helping to sick animals" behaviors.
- Parasitized individuals are more active and spend more time feeding and moving.

adaptive (Hart 1990; Moore 2002). Examples of sickness behaviors include self-directed behaviors and lethargy (Hart 1988, 1990). Self-grooming (preening in birds) plays an important role in eliminating ectoparasites, cleaning, and conditioning the coat (Kakuma et al. 2003) and has been documented, for instance, in rodents (Murray 1987), cats (Eckstein and Hart 2000), cattle (Snowball 1956), and impala (*Aepyceros melampus*: Mooring, McKenzie, and Hart 1996). In primates, there is evidence that self-grooming and scratching are used by parasitized individuals to cope with ectoparasites (e.g., Duboscq et al. 2016; Thatcher, Downs, and Koyama 2021). Because parasites consume host resources, hosts must likely compensate for metabolic deficits by modifying their activity budgets (Smith 1978). For example, eastern chipmunks (*Tamias striatus*) parasitized by botfly larvae of the *Cuterebra* genus reduce activity time (Bennett 1973) and parasitized deer mice (*Peromyscus maniculatus*) reduce strenuous activities, such as running, but spend more time engaging in non-strenuous activities, such as eating, drinking, and grooming (Smith 1978). Furthermore, at early parasitization, deer mice slightly decrease food intake, but by days 5–6 of being parasitized, increase food intake (Hunter and Webster 1974). Contrary to deer mice, eastern chipmunks heavily parasitized by botfly larvae of the *Cuterebra* genus reduce food intake but increase water consumption up to 10 times more than those not parasitized (Bennett 1973). In the context of having a disease, in primates, eastern chimpanzees (*Pan troglodytes schweinfurthii*) with influenza-like illness take longer to leave their nests in the morning, which results in an increase in resting time (Huffman and Seifu 1989; Krief et al. 2005; Takasaki and Hunt 1987).

The second behavioral strategy to cope with parasites is "helping sick animals" (Hart 1990). For animals living in groups, there may be some advantages for healthy animals, as well as for sick and parasitized animals, in displaying behaviors of helping sick, injured, or parasitized animals in their recovery. Some of the benefits for healthy animals involved in these behaviors could be the obtention of extra nutrients via social grooming (e.g., consuming ectoparasites; Ewing 1935; Ramanantsalama et al. 2018). This strategy is observed in several primate species (Hart 1990). There is evidence that social grooming promotes the elimination of ectoparasites (Tanaka 1995). For example, chimpanzees (*Pan troglodytes*) have been observed removing lice from conspecifics (Assersohn et al. 2004; Zamma 2002), and baboons (*Papio cynocephalus*) that receive more social grooming have fewer ticks (Akinyi et al. 2013). In addition, chimpanzees tend to do removal movements more frequently while giving social grooming than during self-grooming. This may be because there is no restriction on using both hands for social grooming, whereas in self-grooming, some parts of the body can only be groomed with one hand (e.g., it is impossible to groom an arm with both hands; Zamma 2011).

FIGURE 1 | An adult mantled howler monkey male parasitized by the botfly *Cuterebra baeri*. Two subdermal nodules with open pores can be observed in the neck. Photo by Josef Stulz.

The botfly *Cuterebra baeri* parasitizes mantled howler monkeys in its larval stages (Dunn 1934; Zeledón, Otto Jiménez, and Brenes 1957). It produces myiasis in the thoracic region and around the neck of parasitized individuals (Cristobal-Azkarate et al. 2012; Hopkins and Milton 2016; Milton 1996), which is reflected in the form of subdermal nodules (Pastor-Nieto 2015; Figure 1). Fundamental aspects of this parasitic relationship, such as oviposition sites of adult flies (Catts 1982; Colwell and Milton 1998; Dudley and Milton 1990) and mode of access to hosts (Catts 1982), are unknown.

Glander (1975) reported observing a single instance of grooming in the area of the body where an oestrid nodule was present, but howler monkeys frequently repel flying insects, including flies, with their hands (Dudley and Milton 1990). This behavior was estimated to account for an average of 4.6% and a maximum of 24% of daily active energy expenditure (i.e., energy expenditure after accounting for basal metabolism: Dudley and Milton 1990), suggesting that parasite deterrence may be energetically costly for howler monkeys. Parasitism by botfly larvae may also be energetically costly for mantled howler monkeys due to myiasis (Catts 1982), in which the larvae feed on living and dead host tissues, body fluids, or ingested food (Hall and Wall (1995); Sandeman 1996; Zumpt 1965). Mantled howler monkeys tend to increase their feeding effort in response to decreases in food availability (Dunn, Cristóbal-Azkarate, and Veà 2010). If botfly larvae consume enough resources from the host, they will likely need to alter these behaviors to meet their energy needs and those of the parasites. This scenario could have negative consequences for parasitized mantled howler monkeys, particularly because howler monkeys minimize energy expenditure through the consumption of low-calorie foods and fermentative digestion (Milton and McBee 1983), which are associated with long rest periods (Milton 1980).

Parasitization by botfly larvae has a direct energetic cost to hosts, as they consume host resources to develop and grow

(Nilssen 1997). It has been suggested that individuals parasitized by botfly larvae may die when hosts are under nutritional stress, supporting the idea that this parasitization is energetically costly for howler monkeys (Arroyo-Rodríguez, Asensio, and Cristóbal-Azkarate 2008; Milton 1996), and Milton (1996) argued that bot flies exert a regulatory effect on the howler monkey population of Barro Colorado Island, Panama. In Los Tuxtlas, Mexico, three peaks of nodule prevalence and abundance were recorded during a 10-month follow-up (February, April, and September), while nodule intensity peaked in February, April, and August. Regarding the effect of climate variables on nodule appearance, the likelihood of nodule appearance increases when both mean and minimum temperature decrease in the 24–21 days before nodule appearance. Nodule appearance also increases as rainfall decreases in the 5–2 days preceding nodule appearance (Ortíz-Zárate et al. 2024).

Parasite burden and serum albumin level are negatively related in parasitized mantled howler monkeys (Milton 1996). It has been suggested that some albumin may be ingested by botfly larvae, which may lead to a reduction in the albumin/globulin ratio (Payne et al. 1965). Low albumin levels are indicative of a disruption of protein metabolism due to different causes, including starvation, protein malnutrition, infections, or the decreased synthesis of albumin in the liver (Coles 1980; Małkowski 2013). Also, mantled howler monkeys parasitized by *C. baeri* synthesize immunoglobulin G (IgG) antibodies against larval antigens during the first and third stages of development of the larva. Antibodies persist after the parasites leave the host, although it is unknown for how long (Baron, Colwell, and Milton 1996). Furthermore, parasitized mantled howler monkeys have 54.5% lower levels of thyroid hormone metabolites than non-parasitized individuals (Dias et al. 2017). The basal metabolic rate of thyroid hormone decreases when organisms are under nutritional stress (Cristóbal-Azkarate et al. 2016; Eales 1988; Hulbert and Else 2004). Therefore, being parasitized by *C. baeri* has a negative energetic impact on mantled howler monkeys, which must be compensated.

The larvae of *Dermatobia hominis* (a member of the Subfamily Cuterebrinae, to which *C. baeri* belongs) cause itching just a few hours after the entrance into the host. The larvae have been reported to cause itching and pain during their development, but there is no pain when mature larvae exit the host (Dunn 1930). If the same applies to *C. baeri*, it should be expected that parasitized mantled howler monkeys will display symptom-relieving behaviors (e.g., touching and scratching).

Given the potential biological impacts of *C. baeri* on mantled howler monkeys and the paucity of information on the behavior of individuals infected by this parasite, our study aimed to examine the occurrence of sickness behaviors and helping sick animals by mantled howler monkeys in relation to being parasitized by *C. baeri*. We tested two hypotheses. In the first, we posed that, if mantled howler monkeys use sickness behaviors to cope with being parasitized by *C. baeri*, then, compared to non-parasitized individuals, parasitized individuals should have increased frequency of self-directed coping behaviors against parasitism (self-groom, rub, scratch, and touch) and lethargy. In the second hypothesis, we proposed that, if mantled howler monkeys help sick animals to cope with being parasitized by *C. baeri*, then, compared to non-parasitized individuals, parasitized individuals should receive an increased frequency of coping behaviors against parasitism (social groom, social scratch, and social touch).

2 | Methods

2.1 | Study Site and Subjects

Our study was conducted at La Flor de Catemaco, a forest fragment of approximately 100 ha situated in Los Tuxtlas, Mexico (coordinates: 18°26′43″ N, 95°02′49″ W). The vegetation within this area primarily consists of tropical evergreen forest, though some regions have undergone transformation due to the introduction of palm plantations (mainly *Chamaedorea* spp.), replacing the original understory and forest floor vegetation. The climate is hot and humid, and during this study, the monthly mean ambient temperature was 24.4°C ± 2.0°C (ranging from 21.4°C in December to 27.2°C in May), and the mean monthly rainfall was 375.7 ± 206.4 mm (ranging from 114 mm in March to 674 mm in September; annual rainfall = 4509 mm).

We have been observing mantled howler monkeys residing in La Flor de Catemaco since 2002, and all subjects have become habituated to human presence (Dias et al. 2023). We focused on the adult members of two groups, totaling 17 subjects, consisting of 10 females and 7 males (Table 1). We identified individuals based on unique natural markings on their fur and other physical characteristics, including scars, broken fingers, and distinctive facial features.

2.2 | Parasitism Observation

Between July 2022 and April 2023, we conducted extensive observations to track the presence of *C. baeri* nodules in study subjects. Our observation protocol involved following each group continuously for five consecutive days (which we defined as an observation period; mean ± SD duration of observation periods was 4.8 ± 4.0 days), carrying out a total of 36 periods and 127 observation days during the study. Each day, we meticulously examined individuals using Bushnell 10 × 42 mm binoculars to assess the presence of *C. baeri* nodules, and we recorded individual identity, date of observation, number, and precise location of the parasitic nodules.

2.3 | Behavioral Observations

We used focal-animal sampling with continuous recording for 1-h periods (Altmann 1974) to assess all occurrences of self-directed behaviors (behaviors emitted by the focal animal: self-groom, rub, self-scratch, and self-touch) and social interactions (behaviors that the focal animal received: social groom, social scratch, and social touch; Table 2). It should be noted that we only recorded these behaviors when they were directed at any area of the body from the chest up, where nodules are usually located (Ortíz-Zárate et al. 2024). We focused on behaviors that have been previously reported as potentially associated with

TABLE 1 | Number of botfly nodules and behavioral sampling effort per mantled howler monkey observed in this study.

Subject	Sex	Group	#Nodules	Sampling effort in hours Without nodules	 With nodules
MT	Male	1	0	24.4	0.0
MM	Male	1	2	22.7	2.7
ML	Male	1	2	16.5	2.5
M2	Male	1	1	21.4	1.0
HF	Female	1	5	13.3	6.7
HB	Female	1	3	11.5	10.6
H1	Female	1	1	12.1	1.6
HS	Female	1	1	13.3	0.0
HN	Female	1	2	11.1	2.9
HSP	Female	1	6	5.4	10.6
MJ	Male	2	3	28.7	0.6
MP	Male	2	1	33.0	4.7
MCN	Male	2	1	34.2	4.6
HPG	Female	2	2	26.4	8.0
HPM	Female	2	0	34.1	0.0
HA	Female	2	2	22.8	3.3
HCC	Female	2	2	19.1	5.7
Total	—	—	34	350	65.5

TABLE 2 | Mantled howler monkey behaviors sampled in this study.

Behavior[a]	Description
Groom	The actor touches its (self-grooming) or another individual's (social grooming) body with the fingers from one or the two hands, delicately splitting apart the fur while paying visual attention to this action.
Rub	The actor rubs its body with some substrate in the environment (branches and leaves).
Scratch	The actor moves its fingers repetitively against its (self-directed) or another individual's (social scratch) fur/skin.
Touch	Contact between a hand and any body part, either own (self-touching) or from another individual (social touch).

[a] All recorded behaviors were directed at any area of the body from the chest up.

behavioral coping with ectoparasites in primates and other animals (e.g., scrathing and grooming, Alexander 1986; Clayton et al. 2010; Duboscq et al. 2016; Dunbar 1991; Hart 1990). During focal-animal samples, we also continuously recorded the behavioral state of subjects considering the following classification: rest (sleep or static without interaction), feed (inspection of food, bringing food to mouth, chewing and swallowing, moving while feeding within a food patch), moving (movement to a new area or tree), and other behavior (remaining activities not categorized as resting, feeding or moving, e.g., socializing; Dunn, Cristóbal-Azkarate, and Veà 2009). We collected 415.5 h of focal-animal recordings, with a mean ± SD of 24.4 ± 8.2 h observation hours per individual.

2.4 | Data Organization and Analysis

We classified individuals as parasitized (i.e., with at least one nodule) or non-parasitized in each focal-animal sample. We then summed the counts of each behavior per individual per condition (i.e., parasitized/non-parasitized). We similarly summed the duration of all state behaviors observed per individual per condition across all focal samples. We never observed self-grooming. The frequencies of social interactions with potential antiparasitic functions (social groom, social scratch, and social touch) directed at any area of the body were very low, so we combined them into a single category for statistical analysis (helping behaviors). To analyze how the occurrence of botfly parasitism affected behavioral frequencies (i.e., rub, scratch, and touch as self-directed behaviors and helping behaviors) we used generalized mixed models with negative binomial distribution and log link function to handle the overdispersion in our count data. The rub and the helping behaviors models were, in addition, adjusted for zero-inflation due to many zeros in data (Table S1). We calculated an activity index by dividing the sum of time spent feeding, moving, and in other behaviors by resting time (Cavigelli 1999; Dunn, Cristóbal-Azkarate, and Veà 2010). We then used a linear mixed model (identity link function) to investigate variation in this index as a function of the occurrence of parasitism. We further examined variation in activity by analyzing time spent feeding and moving with binomial generalized mixed models and logit link function, in which the response was a two-vector variable composed of time spent and time not spent in each behavior. In all models we added total observation time per individual per condition as an offset variable and individual identity as a random factor. Given previous evidence of behavioral variation between sexes in this species (e.g., Ho et al. 2014) we also added sex as a fixed control variable in all models.

We diagnosed residual distribution (with Q-Q plots), overdispersion, and zero inflation and found that all models met statistical assumptions. We also assessed the contribution of the fixed predictor (parasitized/non-parasitized) relative to fixed control (sex) and random (identity) factors with likelihood ratio tests, which in all cases indicated a low influence of the latter (i.e., $p < 0.001$ in all tests). We calculated pseudo coefficients of determination to assess model goodness-of-fit. We performed all analyses in R (R Core Team 2024).

3 | Results

We observed 15 of the 17 study subjects with botfly nodules (Table 2) and a total of 34 nodules (24 in females and 10 in males). Neither self-directed nor helping behaviors varied between parasitized and non-parasitized individuals (Table 3; Table S1). Activity levels were higher in parasitized than in non-parasitized individuals (Figure 2a), and this difference was also observed in time spent feeding (Figure 2b) and moving (Figure 2c).

4 | Discussion

In this study, we examined if mantled howler monkeys display sickness behaviors and "helping sick animals" behaviors in the context of botfly parasitism. We specifically expected to observe increases in self-directed behaviors, lethargy, and received helping behaviors in parasitized individuals but found none of the predicted trends. In contrast, parasitized subjects were more active, which resulted from increases in time spent feeding and moving. Therefore, there is no evidence that mantled howler monkeys display behaviors aimed at relieving the symptoms of being parasitized (e.g., itch, pain) to themselves or to other group members, but adjust their activity budgets. This evidence should be considered preliminary, given the limited behavioral sampling that could be conducted. For example, individual data had to be pooled per condition (i.e., parasitized/non-parasitized), which precluded assessing the effects of female reproductive state and climate on the relationship between parasitism and activity. Despite these limitations, this study lays the groundwork for future research on how botfly parasitism affects the behavior of mantled howlers.

Behaviors such as self-grooming and scratching allow animals to relieve itching and remove ectoparasites (Hart 1990; Moore 2002). Even if removal is not possible, scratching may

TABLE 3 | Mixed model results on the influence of botfly (*Cuterebra baeri*) parasitism on mantled howler monkey behavior.

				95% CI			
Behavior	**R^2[a]**	**Estimate**	**SE**	**Lower**	**Upper**	**χ^2**	***p***
Scratch	0.10	−0.13	0.14	−0.41	0.15	0.82	0.366
Touch	0.02	−0.03	0.20	−0.44	0.37	0.02	0.873
Rub	0.08	−0.22	0.33	−0.91	0.38	0.45	0.502
Activity	0.59	1.59	0.24	1.13	2.05	42.6	< 0.001
Feed	0.36	0.83	0.08	0.67	0.99	110.4	< 0.001
Move	0.74	1.55	0.11	1.32	1.77	183.2	< 0.001
Helping behaviors	0.25	0.33	0.34	−0.34	1.00	0.93	0.336

[a] Marginal pseudo-coefficients of determination, which correspond to the effect of fixed factors on dependent variables.

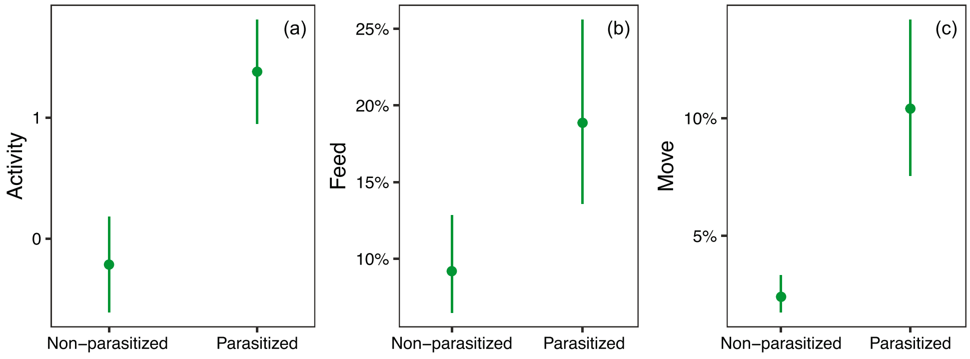

FIGURE 2 | Estimates (and 95% confidence intervals) of mixed models relating parasitism of mantled howler monkeys by the botfly *Cuterebra baeri* with (a) activity levels, (b) time spent feeding, and (c) time spent moving.

damage the parasite, thus halting its development (Clayton et al. 2010). The absence of an increase in grooming, scratching, and touching frequencies in parasitized mantled howler monkeys may be interpreted in three ways. First, it is possible that the presence of the parasite does not produce discomfort, although this is unlikely given the reddening and increase in temperature of the skin surrounding the nodules (Milton 1996). Second, maybe howler monkeys do not possess the manual dexterity and strength necessary to remove botfly larvae from the subdermal nodules (Milton 1996). Therefore, if these behaviors do not offer benefits in terms of mitigating and/or eliminating the parasites, mantled howler monkeys should not invest time and energy in displaying them. Third, the observed trends in helping sick animals may result from the overall rarity of the recorded behaviors in the behavioral repertoire of howler monkeys (Di Fiore and Campbell 2007; Jones 1979). Regardless of which explanation accounts for the observed trends, our study demonstrates that mantled howler monkeys do not cope with botfly parasitism with self-directed behaviors or help from others.

Mantled howler monkeys parasitized by botfly larvae were more active. This result contrasts with the behavior reported for other sick and parasitized animals, which tend to be more inactive, lethargic, drowsy, and disinterested in the environment (Bennett 1973; Hart 1988, 1990; Smith 1978). For example, eastern chipmunks decrease the frequency of activity when parasitized by *C. emasculator* (Bennett 1973). Among primates, decreased activity has been reported in several species infected with gastrointestinal parasites, including Barbary macaques (*Macaca sylvanus*, Müller-Klein et al. 2019), red-capped mangabeys (*Cercocebus torquatus*, Friant, Ziegler, and Goldberg 2016), and red colobus monkeys (*Procolobus rufomitratus tephrosceles*, Ghai et al. 2015). This may be due to trade-offs of the energetic costs of parasite infections. Decreasing activity, as a characteristic of sickness behavior (Hart 1988, 1990), may lead to maintaining energy balance. Notwithstanding, feeding time does not vary among red-capped mangabeys (*Cercocebus torquatus*) prior and after antiparasitic treatment (Friant, Ziegler, and Goldberg 2016). Also, not all activities show the same time reduction. In red colobus monkeys (*Piliocolobus tephrosceles*), the most energetically expensive behaviors, such as copulating and grooming, show the greatest reduction during infection (Ghai et al. 2015). Similar to red colobus monkeys, parasitized deer mice are more active in terms of non-strenuous activities (Smith 1978) and increase food intake (Hunter and Webster 1974). Also, heavily parasitized eastern chipmunks increase water consumption (Bennett 1973).

It is possible that mantled howler monkeys parasitized by botfly larvae have higher activity levels because of a negative association between being parasitized and food availability, with the latter determining an increase in foraging effort. In Los Tuxtlas, fruit availability decreases between November and March, and the period of resource abundance occurs between April and May (Cristóbal Azkarate et al. 2017; Dunn, Cristóbal-Azkarate, and Veà 2010). However, in our population, only one peak of botfly nodule prevalence coincided with the period of lower food availability (January–February), with the other two peaks occurring within the period of greater resource abundance and in the intermediate period (Ortíz-Zárate et al. 2024). Therefore, it is unlikely that increased activity time in parasitized subjects results from higher foraging effort due to food scarcity.

Increased activity may be associated with a metabolic compensation of the effects of being parasitized. Parasitization by oestrid larvae has a direct energetic cost for hosts, as they consume host resources to develop and grow (Nilssen 1997). In this context, the increased activity time of parasitized mantled howler monkeys could be explained by the need to invest in activities that allow them to meet their energetic demands and those of the parasites, that is, foraging. Such a coping strategy against botfly larvae parasitism converges with that observed in deer mice, in which the activity of infected individuals is linked to energy-acquisition activities (Hunter and Webster 1974; Smith 1978). Howler monkeys follow an energy-minimizing ecological strategy based on consuming low-calorie foods and long resting times (Milton 1980). Under this strategy, even small increases in energy expenditure associated with parasitism may lead to readjustments in activity budgets, resulting in shifts from energy conservation to energy acquisition strategies (Dunbar, Korstjens, and Lehmann 2009). Such flexibility has been observed in mantled howler monkeys in other contexts, such as under resource scarcity and during energy-demanding reproductive stages (e.g., Dias et al. 2017; Dunn, Cristóbal-Azkarate, and Veà Cristóbal-Azkarate, and Veà 2009, 2010, 2013; Rangel Negrín et al. 2021). If parasitism by botfly larvae results in energetic unbalances, it could represent a contributing factor to mortality of mantled howler monkeys (Milton 1996). Future research on the energetic condition of parasitized mantled howler monkeys (e.g., noninvasive monitoring of C-peptide concentrations) should allow for further understanding of the role of changes in activity levels for coping with botfly larvae parasitism.

Finally, we highlight that in our study, the increase in time spent active, feeding, and moving by parasitized mantled howler monkeys was observed at very low nodule intensity (1–1.5 parasites per individual: Ortíz-Zárate et al. 2024). This may indicate that a single *C. baeri* larva demands enough resources from the hosts that a shift to an energy acquisition strategy is necessary to compensate for metabolic deficits.

In sum, we did not find evidence that mantled howler monkeys cope with botfly parasitism via self-directed behaviors and "helping sick animals" behaviors. However, parasitized individuals were more active and spent more time moving and feeding. It is thus possible that mantled howler monkeys try to offset the metabolic costs of parasitism by increasing energy acquisition.

Author Contributions

Ricardo J. Ortíz Zárate: Formal analysis (equal), investigation (equal), software (equal), visualization (equal), writing–original draft (equal). **Jurgi Cristóbal Azkarate:** Conceptualization (equal), investigation (equal), methodology (equal), supervision (equal), validation (equal), writing–original draft (equal). **Ariadna Rangel Negrín:** Conceptualization (equal), formal analysis (equal), funding acquisition (equal), project administration (equal), resources (equal), supervision (equal), writing–original draft (equal). **Alejandro Coyohua Fuentes:** Investigation (equal), methodology (equal), writing–review & editing (equal). **Pedro A. D. Dias:** Conceptualization (equal), data curation (equal), formal analysis (equal), funding acquisition (equal), investigation (equal), methodology (equal), project administration (equal), resources (equal), supervision (equal), validation (equal), visualization (equal), writing–original draft (equal).

Acknowledgments

We thank D. Canales Espinosa, Laura Johnson, and Jamie Whewell for their support during fieldwork and Ing. J. L. Ponce Puente for allowing the work at La Flor de Catemaco S.A. We thank Dr. Anthony Di Fiore and two anonymous reviewers for constructive comments on earlier versions of this paper. A. Rangel Negrín and P.A.D. Dias thank Mariana and Fernando for continued inspiration to understand primate behavior. The study was financed by Consejo Nacional de Ciencia y Tecnología (CONAHCyT grant 1147976), Posgrado en Neuroetología, Instituto de Neuro-etología (Universidad Veracruzana), and the Leakey Foundation.

Ethics Statement

Our research was noninvasive and based on the observation of mantled howler monkeys. We conducted our research in accordance with national and international laws regulating the protection of endangered species. All fieldwork took place with permission from landowners and our research protocols were approved by the Secretaría de Medio Ambiente y Recursos Naturales (permit SGPA/DGVS/04015/21). The research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data are included in this article and its supplementary material files. Further inquiries can be directed to the corresponding author.

References

Akinyi, M. Y., J. Tung, M. Jeneby, N. B. Patel, J. Altmann, and S. C. Alberts. 2013. "Role of Grooming in Reducing Tick Load in Wild Baboons (*Papio cynocephalus*)." *Animal Behaviour* 85, no. 3: 559–568. https://doi.org/10.1016/j.anbehav.2012.12.012.

Alexander, J. O. 1986. "The Physiology of Itch." *Parasitology Today* 2, no. 12: 345–351. https://doi.org/10.1016/0169-4758(86)90055-4.

Altmann, J. 1974. "Observational Study of Behavior: Sampling Methods." *Behaviour* 49, no. 3–4: 227–266. https://doi.org/10.1163/156853974x00534.

Arroyo-Rodríguez, V., N. Asensio, and J. Cristóbal-Azkarate. 2008. "Demography, Life History, and Migrations in a Mexican Mantled Howler Group in a Rainforest Fragment." *American Journal of Primatology* 70, no. 2: 114–118. https://doi.org/10.1002/ajp.20463.

Assersohn, C., A. Whiten, Z. T. Kiwede, J. Tinka, and J. Karamagi. 2004. "Use of Leaves to Inspect Ectoparasites in Wild Chimpanzees: A Third Cultural Variant?" *Primates* 45, no. 4: 255–258. https://doi.org/10.1007/s10329-004-0092-x.

Baron, R. W., D. D. Colwell, and K. Milton. 1996. "Antibody Immunoglobulin G (IgG) Response to *Alouattamyia baeri* (Diptera: Cuterebridae) Parasitism of Howler Monkeys, *Alouatta palliata*, in Panama." *Journal of Medical Entomology* 33, no. 6: 946–951. https://doi.org/10.1093/jmedent/33.6.946.

Bennett, G. F. 1973. "Some Effects of *Cuterebra emasculator* Fitch (Diptera: Cuterebridae) on the Blood and Activity of Its Host, the Eastern Chipmunk." *Journal of Wildlife Diseases* 9, no. 1: 85–93. https://doi.org/10.7589/0090-3558-9.1.85.

Catts, E. P. 1982. "Biology of New World Bot Flies: Cuterebridae." *Annual Review of Entomology* 27, no. 1: 313–338. https://doi.org/10.1146/annurev.en.27.010182.001525.

Cavigelli, S. A. 1999. "Behavioural Patterns Associated With Faecal Cortisol Levels in Free-Ranging Female Ring-Tailed Lemurs, *Lemur catta*." *Animal Behaviour* 57: 935–944. https://doi.org/10.1006/anbe.1998.1054.

Clayton, D. H., J. A. H. Koop, C. W. Harbison, B. R. Moyer, and S. E. Bush. 2010. "How Birds Combat Ectoparasites." *Open Ornithology Journal* 3: 41–71.

Coles, E. H. 1980. *Veterinary Clinical Pathology* (3rd ed.). London: Saunders Co.

Colwell, D. D., and K. Milton. 1998. "Development of *Alouattamyia baeri* (Diptera: Oestridae) From Howler Monkeys (Primates: Cebidae) on Barro Colorado Island, Panama." *Journal of Medical Entomology* 35, no. 5: 674–680. https://doi.org/10.1093/jmedent/35.5.674.

Cristobal-Azkarate, J., D. D. Colwell, D. Kenny, et al. 2012. "First Report of Bot Fly (*Cuterebra baeri*) Infestation in Howler Monkeys (*Alouatta palliata*) From Mexico." *Journal of Wildlife Diseases* 48, no. 3: 822–825. https://doi.org/10.7589/0090-3558-48.3.822.

Cristóbal Azkarate, J., J. C. Dunn, C. Domingo Balcells, and J. Veà Baró. 2017. "A Demographic History of a Population of Howler Monkeys (*Alouatta palliata*) Living in a Fragmented Landscape in Mexico." *PeerJ* 5: e3547. https://doi.org/10.7717/peerj.3547.

Cristóbal-Azkarate, J., L. Maréchal, S. Semple, B. Majolo, and A. MacLarnon. 2016. "Metabolic Strategies in Wild Male Barbary Macaques: Evidence From Faecal Measurement of Thyroid Hormone." *Biology Letters* 12, no. 4: 20160168. https://doi.org/10.1098/rsbl.2016.0168.

Dias, P. A. D., A. Coyohua-Fuentes, D. Canales-Espinosa, R. Chavira Ramírez, and A. Rangel-Negrín. 2017. "Hormonal Correlates of Energetic Condition in Mantled Howler Monkeys." *Hormones and Behavior* 94: 13–20. https://doi.org/10.1016/j.yhbeh.2017.06.003.

Dias, P. A. D., A. Coyohua-Fuentes, D. Canales-Espinosa, and A. Rangel-Negrín. 2023. "Demography and Life-History Parameters of Mantled Howler Monkeys at La Flor de Catemaco: 20 Years Post-Translocation." *Primates* 64: 143–152. https://doi.org/10.1007/s10329-022-01030-z.

Duboscq, J., V. Romano, C. Sueur, and A. J. MacIntosh. 2016. "Scratch That Itch: Revisiting Links Between Self-Directed Behaviour and Parasitological, Social and Environmental Factors in a Free-Ranging Primate." *Royal Society Open Science* 3, no. 11: 160571. https://doi.org/10.1098/rsos.160571.

Dudley, R., and K. Milton. 1990. "Parasite Deterrence and the Energetic Costs of Slapping in Howler Monkeys, *Alouatta palliata*." *Journal of Mammalogy* 71, no. 3: 463–465. https://doi.org/10.2307/1381962.

Dunbar, R. I. M. 1991. "Functional Significance of Social Grooming in Primates." *Folia Primatologica* 57, no. 3: 121–131. https://doi.org/10.1159/000156574.

Dunbar, R. I. M., A. H. Korstjens, and J. Lehmann. 2009. "Time As an Ecological Constraint." *Biological Reviews* 84, no. 3: 413–429. https://doi.org/10.1111/j.1469-185X.2009.00080.x.

Dunn, J. C., J. Cristóbal-Azkarate, B. Schulte-Herbrüggen, R. Chavira, and J. J. Veà. 2013. "Travel Time Predicts Fecal Glucocorticoid Levels in Free-Ranging Howlers (*Alouatta palliata*)." *International Journal of Primatology* 34, no. 2: 246–259. https://doi.org/10.1007/s10764-013-9657-0.

Dunn, J. C., J. Cristóbal-Azkarate, and J. J. Veà. 2009. "Differences in Diet and Activity Pattern Between Two Groups of *Alouatta palliata* Associated With the Availability of Big Trees and Fruit of Top Food Taxa." *American Journal of Primatology* 71, no. 8: 654–662. https://doi.org/10.1002/ajp.20700.

Dunn, J. C., J. Cristóbal-Azkarate, and J. J. Veà. 2010. "Seasonal Variations in the Diet and Feeding Effort of Two Groups of Howlers in Different Sized Forest Fragments." *International Journal of Primatology* 31, no. 5: 887–903. https://doi.org/10.1007/s10764-010-9436-0.

Dunn, L. H. 1930. "Rearing the Larvæ of dermatobia Hominislinn., in Man." *Psyche: A Journal of Entomology* 37, no. 4: 327–342. https://doi.org/10.1155/1930/31970.

Dunn, L. H. 1934. "Entomological Investigations in the Chiriqui Region of Panama." *Psyche: A Journal of Entomology* 41, no. 3: 166–183. https://doi.org/10.1155/1934/21960.

Eales, J. G. 1988. "The Influence of Nutritional State on Thyroid Function in Various Vertebrates." *American Zoologist* 28, no. 2: 351–362. https://doi.org/10.1093/icb/28.2.351.

Eckstein, R. A., and B. L. Hart. 2000. "Grooming and Control of Fleas in Cats." *Applied Animal Behaviour Science* 68, no. 2: 141–150. https://doi.org/10.1016/S0168-1591(00)00095-2.

Ewing, H. E. 1935. "Sham Louse-Picking, or Grooming, Among Monkeys." *Journal of Mammalogy* 16, no. 4: 303–306. https://doi.org/10.2307/1374640.

Di Fiore, A., and C. J. Campbell. 2007. "The Atelines: Variation in Eecology, Behavior, and Social Organization." In *Primates in Perspective*, edited by C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, and S. K. Bearder, 155–185. Oxford: Oxford University Press.

Friant, S., T. E. Ziegler, and T. L. Goldberg. 2016. "Changes in Physiological Stress and Behaviour in Semi-Free-Ranging Red-Capped Mangabeys (*Cercocebus torquatus*) Following Antiparasitic Treatment." *Proceedings of the Royal Society B: Biological Sciences* 283, no. 1835: 20161201. https://doi.org/10.1098/rspb.2016.1201.

Ghai, R. R., V. Fugère, C. A. Chapman, T. L. Goldberg, and T. J. Davies. 2015. "Sickness Behaviour Associated With Non-Lethal Infections in Wild Primates." *Proceedings of the Royal Society B: Biological Sciences* 282, no. 1814: 20151436. https://doi.org/10.1098/rspb.2015.1436.

Glander, K. E. 1975. Habitat and Resource Utilization: An Ecological View of Social Organization in Mantled Howling Monkeys (PhD dissertation, The University of Chicago). http://pi.lib.uchicago.edu/1001/cat/bib/44099.

Goater, T. M., C. P. Goater, and G. W. Esch. 2014. *Parasitism: The Diversity and Ecology of Animal Parasites* (2nd ed.). Cambridge: Cambridge University Press.

Gorrell, J. C., and A. I. Schulte-Hostedde. 2008. "Patterns of Parasitism and Body Size in Red Squirrels (*Tamiasciurus hudsonicus*)." *Canadian Journal of Zoology* 86, no. 2: 99–107. https://doi.org/10.1139/Z07-123.

Hall, M., and R. Wall. 1995. "Myiasis of Humans and Domestic Animals." *Advances in Parasitology* 35: 257–334. https://doi.org/10.1016/S0065-308X(08)60073-1.

Hart, B. L. 1988. "Biological Basis of the Behavior of Sick Animals." *Neuroscience and Biobehavioral Reviews* 12, no. 2: 123–137. https://doi.org/10.1016/s0149-7634(88)80004-6.

Hart, B. L. 1990. "Behavioral Adaptations to Pathogens and Parasites: Five Strategies." *Neuroscience and Biobehavioral Reviews* 14, no. 3: 273–294. https://doi.org/10.1016/S0149-7634(05)80038-7.

Ho, L., L. Cortés-Ortiz, P. A. D. Dias, D. Canales-Espinosa, D. M. Kitchen, and T. J. Bergman. 2014. "Effect of Ancestry on Behavioral Variation in Two Species of Howler Monkeys (*Alouatta pigra* and *A. palliata*) and Their Hybrids." *American Journal of Primatology* 76, no. 9: 855–867. https://doi.org/10.1002/ajp.22273.

Hopkins, M. E., and K. Milton. 2016. "Adverse Effects of Ball-Chain Radio-Collars on Female Mantled Howlers (*Alouatta palliata*) in Panama." *International Journal of Primatology* 37, no. 2: 213–224. https://doi.org/10.1007/s10764-016-9896-y.

Huffman, M. A., and M. Seifu. 1989. "Observations on the Illness and Consumption of a Possibly Medicinal Plant *Vernonia amygdalina* (DEL.), by a Wild Chimpanzee in the Mahale Mountains National Park, Tanzania." *Primates* 30, no. 1: 51–63. https://doi.org/10.1007/bf02381210.

Hulbert, A. J., and P. L. Else. 2004. "Basal Metabolic Rate: History, Composition, Regulation, and Usefulness." *Physiological and Biochemical Zoology* 77, no. 6: 869–876. https://doi.org/10.1086/422768.

Hunter, D. M., and J. M. Webster. 1974. "Effects of Cuterebrid Larval Parasitism on Deer-Mouse Metabolism." *Canadian Journal of Zoology* 52, no. 2: 209–217. https://doi.org/10.1139/z74-025.

Jones, C. B. 1979. "Grooming in the Mantled Howler Monkey, *Alouatta palliata* GRAY." *Primates* 20, no. 2: 289–292. https://doi.org/10.1007/bf02373380.

Kakuma, Y., Y. Takeuchi, Y. Mori, and B. L. Hart. 2003. "Hormonal Control of Grooming Behavior in Domestic Goats." *Physiology & Behavior* 78, no. 1: 61–66. https://doi.org/10.1016/S0031-9384(02)00942-3.

Krief, S., M. A. Huffman, T. Sévenet, et al. 2005. "Noninvasive Monitoring of the Health of *Pan troglodytes schweinfurthii* in the Kibale National Park, Uganda." *International Journal of Primatology* 26, no. 2: 467–490. https://doi.org/10.1007/s10764-005-2934-9.

Kuris, A. M., A. R. Blaustein, and J. J. Alio. 1980. "Hosts as Islands." *American Naturalist* 116, no. 4: 570–586. https://doi.org/10.1086/283647.

Małkowski, P. 2013. "Human Albumin: Old, New, and Emerging Applications." *Annals of Transplantation* 18: 205–217. https://doi.org/10.12659/AOT.889188.

de Meeûs, T., Y. Michalakis, and F. Renaud. 1998. "Santa Rosalia Revisited: Or Why Are There So Many Kinds of Parasites in 'The Garden of Earthly Delights'?" *Parasitology Today* 14, no. 1: 10–13. https://doi.org/10.1016/S0169-4758(97)01163-0.

de Meeûs, T., and F. Renaud. 2002. "Parasites Within the New Phylogeny of Eukaryotes." *Trends in Parasitology* 18, no. 6: 247–251. https://doi.org/10.1016/S1471-4922(02)02269-9.

Milton, K. 1980. *The Foraging Strategy of Howler Monkeys*. New York: Columbia University Press.

Milton, K. 1996. "Effects of Bot Fly (*Alouattamyia baeri*) Parasitism on a Free-Ranging Howler Monkey (*Alouatta palliata*) Population in Panama." *Journal of Zoology* 239, no. 1: 39–63. https://doi.org/10.1111/j.1469-7998.1996.tb05435.x.

Milton, K., and R. H. McBee. 1983. "Rates of Fermentative Digestion in the Howler Monkey, *Alouatta palliata* (Primates: Ceboidea)." *Comparative Biochemistry and Physiology Part A: Physiology* 74, no. 1: 29–31. https://doi.org/10.1016/0300-9629(83)90706-5.

Moore, J. 2002. *Parasites and the Behavior of Animals*. Oxford: Oxford University Press.

Mooring, M. S., A. A. McKenzie, and B. L. Hart. 1996. "Grooming in Impala: Role of Oral Grooming in Removal of Ticks and Effects of Ticks in Increasing Grooming Rate." *Physiology & Behavior* 59, no. 4–5: 965–971. https://doi.org/10.1016/0031-9384(95)02186-8.

Müller-Klein, N., M. Heistermann, C. Strube, et al. 2019. "Physiological and Social Consequences of Gastrointestinal Nematode Infection in a Nonhuman Primate." *Behavioral Ecology* 30, no. 2: 322–335. https://doi.org/10.1093/beheco/ary168.

Murray, M. D. 1987. "Effects of Host Grooming on Louse Populations." *Parasitology Today* 3, no. 9: 276–278. https://doi.org/10.1016/0169-4758(87)90105-0.

Nilssen, A. C. 1997. "Effect of Temperature on Pupal Development and Eclosion Dates in the Reindeer Oestrids *Hypoderma tarandi* and *Cephenemyia trompe* (Diptera: Oestridae)." *Environmental Entomology* 26, no. 2: 296–306. https://doi.org/10.1093/ee/26.2.296.

Ortíz-Zárate, R. J., A. Rangel-Negrín, A. Coyohua-Fuentes, S. Ibáñez-Bernal, J. Cristóbal-Azkarate, and P. A. D. Dias. 2024. "Bot Fly Parasitism in Mantled Howler Monkeys (*Alouatta palliata*): General Patterns and Climate Influences." *American Journal of Primatology* 86, no. 11: e23680. https://doi.org/10.1002/ajp.23680.

Pastor-Nieto, R. 2015. “Health and Welfare of Howler Monkeys in Captivity.” In *Howler Monkeys: Behavior, Ecology, and Conservation*, edited by M. M. Kowalewksi, P. A. Garber, L. Cortés-Ortiz, B. Urbani, and D. Youlatos, 313–355. New York: Springer.

Payne, J. A., P. B. Dunaway, G. D. Martin, and J. D. Story. 1965. “Effects of *Cuterebra angustifrons* on Plasma Proteins of *Peromyscus leucopus*.” *Journal of Parasitology* 51, no. 6: 1004–1008. https://doi.org/10.2307/3275894.

R Core Team. 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, accessed May 23, 2024. https://www.R-project.org/.

Ramanantsalama, R. V., A. Adrianarimisa, A. P. Raselimanana, and S. M. Goodman. 2018. “Rates of Hematophagous Ectoparasite Consumption During Grooming by an Endemic Madagascar Fruit Bat.” *Parasites & Vectors* 11, no. 330: 1–8. https://doi.org/10.1186/s13071-018-2918-1.

Rangel Negrín, A., A. Coyohua Fuentes, A. de la Torre Herrera, et al. 2021. “Female Reproductive Energetics in Mantled Howler Monkeys (*Alouatta palliata*): A Follow-Up Study.” *American Journal of Physical Anthropology* 174, no. 3: 396–406. https://doi.org/10.1002/ajpa.24222.

Robar, N., G. Burness, and D. L. Murray. 2010. “Tropics, Trophics and Taxonomy: The Determinants of Parasite-Associated Host Mortality.” *Oikos* 119, no. 8: 1273–1280. https://doi.org/10.1111/j.1600-0706.2009.18292.x.

Roberts, L. S., J. Janovy, Jr., and S. Nadler. 2013. *Gerald D. Schmidt & Larry S. Roberts´ Foundations of Parasitology* (9th ed.). New York: McGraw-Hill.

Sandeman, R. M. 1996. “Immune Rresponses to Mosquitos and Flies,” In *The Immunology of Host-Ectoparasitic Arthropod Relationship*edited by S. K. Wikel, 175–203. Oxford: Oxford University Press.

Schwanz, L. E. 2008. “Chronic Parasitic Infection Alters Reproductive Output in Deer Mice.” *Behavioral Ecology and Sociobiology* 62, no. 8: 1351–1358. https://doi.org/10.1007/s00265-008-0563-y.

Smith, D. H. 1978. “Effects of Bot Fly (Cuterebra) Parasitism on Activity Patterns of *Peromyscus maniculatus* in the Laboratory.” *Journal of Wildlife Diseases* 14, no. 1: 28–39. https://doi.org/10.7589/0090-3558-14.1.28.

Snowball, G. 1956. “The Effect of Self-Licking By Cattle on Infestations of Cattle Tick, *Boophilus microplus* (Canestrini).” *Australian Journal of Agricultural Research* 7, no. 3: 227–232. https://doi.org/10.1071/AR9560227.

Takasaki, H., and K. Hunt. 1987. “Further Medical Plant Consumption in Wild Chimpanzees?” *African Study Monographs* 8, no. 2: 125–128. https://doi.org/10.14989/68025.

Tanaka, I. 1995. “Matrilineal Distribution of Louse Egg-Handling Techniques During Grooming in Free-Ranging Japanese Macaques.” *American Journal of Physical Anthropology* 98, no. 2: 197–201. https://doi.org/10.1002/ajpa.1330980208.

Thatcher, H. R., C. T. Downs, and N. F. Koyama. 2021. “The Costs of Urban Living: Human–Wildlife Interactions Increase Parasite Risk and Self-Directed Behaviour in Urban Vervet Monkeys.” *Journal of Urban Ecology* 7, no. 1: 1–9. https://doi.org/10.1093/jue/juab031.

Zamma, K. 2002. “Leaf-Grooming By a Wild Chimpanzee in Mahale.” *Primates* 43, no. 1: 87–90. https://doi.org/10.1007/BF02629579.

Zamma, K. 2011. “Frequency of Removal Movements During Social Versus Self-Grooming Among Wild Chimpanzees.” *Primates* 52, no. 4: 323–328. https://doi.org/10.1007/s10329-011-0267-1.

Zeledón, R., Q. Otto Jiménez, and R. R. Brenes. 1957. “*Cuterebra baeri* Shannon y Greene, 1926 en el mono aullador de Costa Rica.” *Revista de biología tropical* 5, no. 2: 129–134.

Zumpt, F. 1965. *Myiasis in Man and Animals in the Old World: A Textbook for Physicians, Veterinarians, and Zoologists*. London: Butterworths.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.