Impact of Group Size and Habitat Disturbance on Parasitic Infection in Free-ranging Proboscis Monkeys

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Abstract

Group-living primates experience the benefits and costs associated with sociality, including an elevated risk of parasite transmission. However, the relative influence of group type (i.e., social structure), group size, and habitat disturbance on parasitic infection remains unclear, particularly in Southeast Asian primates. In this study, the abundance of intestinal parasites in proboscis monkeys (*Nasalis larvatus*) inhabiting a riverine forest along the Menanggul River, Sabah, Malaysian Borneo, was investigated. Fecal samples (n = 160) were collected from one-male–multifemale and all-male groups in areas with varying levels of anthropogenic disturbance, with efforts made to ensure that each sample originated from a different individual. In addition, the effects of group type, group size, and sampling location on parasite abundance were evaluated using fecal egg counts and Bayesian models. Three dominant parasite species groups (*Trichuris* sp., *Strongyloides fuelleborni*, and *Oesophagostomum aculeatum*) with an overall infection prevalence of 81.25% were identified. Results showed that group type did not significantly affect parasite abundance. However, group size showed a positive correlation with the abundance of *Trichuris* sp. and a negative correlation with *S. fuelleborni* and *O. aculeatum*. In addition, our models revealed that the infection loads of *Trichuris* sp. decreased with the increase of distance from the river mouth (less disturbed upstream areas), whereas *O. aculeatum* exhibited higher infection loads with greater distance, indicating a lower prevalence in more disturbed downstream areas. Thus, parasite abundance in proboscis monkeys may be shaped by social and environmental factors, with taxa-specific responses to these variables.

Introduction

Highly social animals such as primates exhibit complex group dynamics that influence their health, behavior, and interactions with pathogens (Kappeler et al., 2015). Although group-living promotes social support and cooperative behaviors that can mitigate some health risks (Silk, 2007), it also imposes costs, including an increased potential for pathogen transmission and heightened susceptibility to disease caused by social stress (Altizer et al., 2003). Thus, the relationship between sociality and disease risk is complicated, as factors such as group structure, contact patterns, and social hierarchies play key roles in determining infection dynamics (Nunn et al., 2015). Notably, in primates, the relationship between parasites and host social structures is bidirectional, with social factors such as group size and composition influencing parasite transmission. Consequently, infection prevalence and intensity can affect social interaction and group dynamics (Vitone et al., 2004; Nunn, 2012; Rushmore et al., 2017).

Apart from social dynamics, anthropogenic environmental changes, such as deforestation and provisioning, can also influence parasite transmission by altering host movement patterns, population densities, and contact rates (Gillespie and Chapman, 2006; Becker et al., 2018). These ecological modifications can create conditions that either facilitate or hinder parasite spread, depending on the nature and extent of human-induced disturbances. Therefore, understanding the mechanism by which environmental, social, and ecological factors contribute to parasitic infections in social animals is crucial for developing effective conservation and management strategies (Chapman et al., 2005; Gillespie and Chapman, 2006).

On the contrary, research on parasitic infection and sociality in wild primates has yielded inconsistent findings, while the effects of anthropogenic environmental changes on parasitic infections in primates have been relatively consistent (Gillespie and Chapman, 2006). The relationship between parasite load and group size is complex, as it depends on

various factors, such as host susceptibility and environmental conditions (e.g. Chapman et al., 2009; Klaus et al., 2018). Although larger groups might increase the likelihood of infection because of higher social interactions, group mobility and seasonal changes may reduce the risk of parasite transmission (e.g., increased precipitation during the rainy season washing away feces and parasites), thereby complicating the host–parasite dynamics (Nguyen et al., 2015; Radespiel et al., 2015; Knauf and Jones-Engel, 2020).

Although knowledge of parasitism in wild primates is expanding, it remains limited, particularly in Southeast Asia (Hopkins and Nunn, 2007; Cooper and Nunn, 2013). In Borneo, which is a highly biodiverse island in Southeast Asia, numerous endemic species are experiencing population declines (Wilcove et al., 2013), and the large arboreal proboscis monkey (*Nasalis larvatus*) inhabiting mangroves, peat swamps, and riverine forests is no exception to this trend (Lhota et al., 2019; Bernard et al., 2025). Several studies have provided insights into primate–parasite interactions in Sabah, including the proboscis monkey. This primate has unique parasite associations (Hasegawa et al., 2020) and infection dynamics that reflect its specialized ecological adaptations (Klaus et al., 2017) and interactions with sympatric primates (Frias et al., 2019; Frias et al., 2021). Previous studies have reported a high prevalence of helminth eggs in fecal samples, identifying five major parasite groups, with co-infections being common (Salgado-Lynn, 2010; Klaus et al., 2017; Frias et al., 2021). In addition, parasite species richness has been reported to be significantly higher in semi-wild populations than in wild ones. This increase likely results from the high levels of human disturbance, which can alter the mechanism by which parasites are transmitted. By contrast, group type and group size have been reported not to significantly affect parasite richness (Klaus et al., 2018). Despite the increasing knowledge of parasitic infections in proboscis monkeys, the fine-scale variation in infection patterns—across individuals or groups inhabiting distinct microhabitats and experiencing different levels of anthropogenic disturbance—remains unclear.

In this study, the abundance of intestinal parasites in proboscis monkeys was investigated, with particular emphasis on the effects of group type, group size, and habitat disturbance. Fecal samples collected over a 1-year period were analyzed to identify the parasites present and to examine the mechanism by which group size and social structure (i.e., group type: one-male–multifemale or all-male groups) influence parasite loads in a forest subjected to varying degrees of anthropogenic disturbance. Considering that proboscis monkeys exhibit seasonal variation in foraging behavior, ranging patterns, and intergroup spacing at our study site (Matsuda et al., 2009a; Matsuda et al., 2009b; Matsuda et al., 2010a), a year-round sampling approach may provide a comprehensive assessment of parasite dynamics. Thus, extended sampling could reveal a positive correlation between group size and parasitic infection, which is contrary to previous findings (Klaus et al., 2018). In addition, the study forest along the tributary river exhibits varying degrees of anthropogenic disturbance between the upstream and downstream areas in terms of plant diversity (Jose et al., 2024). The impact of habitat disturbance on parasite abundance can be assessed by comparing the fecal samples collected from individuals across these areas. Given that research in our study area has documented alterations in the gut microbiota of proboscis monkeys living in disturbed versus undisturbed areas (Jose et al., 2024), we hypothesize that parasite abundance would also differ between these environments because of human-induced disturbances.

Methods

Study site and subjects

This study was conducted in a riverine forest along the Menanggul River, a tributary of the Kinabatangan River, in Sabah, Malaysian Borneo (118°30′ E, 5°30′ N). The study site has a mean daily temperature range of 24°C–30°C and an annual average precipitation of 2474 mm (Matsuda et al., 2019). The river exhibits daily water-level fluctuations of approximately 1 m,

while seasonal inundation results in an average increase exceeding 3 m (Matsuda et al., 2010b). The study area spans 4 km along the Menanggul River and supports a minimum population of 200 proboscis monkeys, forming a multilevel society composed of one-male–multifemale groups and all-male groups, which frequently assemble in the riverside (Matsuda et al., 2024). The riparian zone primarily consists of secondary forest in the southern portion, while much of the northern portion has been converted to oil palm plantations, except for a narrow, protected riparian strip. Accordingly, in this tributary, forests extending upstream from the river mouth have a higher plant diversity (Jose et al., 2024). The proboscis monkeys in the study area are well habituated to the human presence, as the Menanggul River has been a major tourist attraction for over a decade, and it serves as a frequent route for boats and observers.

Sample collection

Between June 2015 and April 2016, boat surveys were conducted in the late afternoon on approximately 2–3 days per week to locate the proboscis monkeys as they typically return to the riverside trees for sleeping (Matsuda et al., 2011) and to record their group composition, along with the GPS coordinates of their sleeping locations at the riverside trees. In the early morning, before the monkeys awakened, these sleeping locations were revisited. Considering that proboscis monkeys often defecate just before moving into the forest, the area was carefully searched around their sleeping sites for fresh feces after the monkeys had departed from their sleeping trees. Multiple one-male–multifemale groups often remained close to one another along the river, making it challenging to determine to which group the feces found on the ground belonged. Therefore, we inferred the group associated with the feces based on the location of the feces and the group observed during the survey from the previous day. Only fecal samples presumed to originate from adult individuals were included, based on fecal size, which allows for differentiation between adults and immature individuals despite the

challenges in distinguishing feces from neighboring groups (Matsuda et al., 2014). Consequently, between June 2015 and April 2016, a total of 160 fecal samples were collected genetically distinct individuals (Matsuda et al., 2024). At least nine groups were identified in the study area, although the number of groups these fecal samples were collected from remains unclear, as group identification was not complete at the time the samples were collected (Matsuda et al., 2024). The fecal samples were preserved in tubes with 70% ethanol.

Parasite detection and identification

A modified protocol was used for concentrating parasite eggs using formalin-ethyl acetate sedimentation, and fecal samples were analyzed using the sequential sedimentation–flotation method (Frias et al., 2021). The final pellet was resuspended in saline, and 1 mL of aliquot was transferred into a vial and placed on a magnetic stirrer to ensure thorough homogenization during analysis. In estimating the number of eggs per gram of feces (EPG) in each sample, an aliquot was collected from the homogeneous suspension and placed in a McMaster counting chamber for examination at 100× magnification. EPG was calculated on the basis of the average of five replicate counts of parasite eggs observed within the chamber's grid, using the known weight of fecal sediment in a 0.15 mL volume. After quantifying the eggs, each sample was centrifuged again; the supernatant was discarded, and the concentrated pellet was resuspended in Sheather's solution with a specific gravity of 1.27. Two slides were examined to reduce the likelihood of overlooking less abundant helminth eggs. Parasite identification was performed using standard identification keys (Modrý et al., 2018).

Parasite prevalence and abundance

The prevalence of a given parasite was calculated as the percentage of hosts infected by that parasite, while parasite abundance was calculated as the number of individuals of a given parasite in a given sample, using the EPG as a proxy measure.

Factors influencing parasite abundance

A Bayesian model was developed using the "brms" package (Bürkner, 2018) to evaluate the mechanism by which group type (one-male–multifemale or all-male groups), group size, and fecal sampling locations, represented as the geographical distance from the river mouth to upstream, affect parasite abundance. In our analysis, parasite abundance was used as a dependent variable, rounded to the nearest integer. Group type was incorporated as a group-level effect, whereas group size and the distance of the sampling location to the river mouth were included as continuous variables. All models were controlled for host group identity. Distinct groups were not identified throughout the study period; thus, samples were assigned to the same group based on their spatial and temporal proximity along the river. This approach was guided by observations, that is, the mean distance between consecutive sleeping sites for each group was approximately 350 m in the study area (Matsuda et al., 2024). In addition, changes in food availability over time can influence spatial patterns along the river (Matsuda et al., 2010a). Consequently, two samples collected within 350 meters of each other and during the same month were classified as originating from the same group. Groups with fewer than three observations were excluded from the analysis.

Weakly informative priors were assigned to population-level effects, following a Student's t-distribution. The posterior distributions of the model parameters were estimated using Markov chain Monte Carlo methods. For this purpose, four chains were constructed, each consisting of 2000 steps, with 1000-step warm-up periods. Consequently, a total of 4000 steps were retained to estimate the posterior distributions. The independent continuous variables were scaled to aid model fitting and coefficient interpretation. Chain convergence

was assessed visually, and the potential scale reduction factor (Rhat) values were examined to ensure they were less than or equal to 1 for all parameters (Bürkner, 2018). This modeling process was repeated for the three parasites identified within the host population.

Results

Parasite prevalence and abundance

Parasites were detected in 130 out of the 160 analyzed samples, resulting in an overall parasite prevalence of 81.25%. The eggs of *Trichuris* sp. (78.12%, n = 125), *Strongyloides fuelleborni* (10.62%, n = 17), *Oesophagostomum aculeatum* (5%, n = 8), *Enterobius* (*Colobenterobius*) *serratus* (1.25%, n = 2), and Spirurida sp. (0.63%, n = 1) were identified. The mean abundance of the top three prevalent parasites was recorded at 168.2 EPG (range: 0–984), 9.41 EPG (range: 0–650), and 2.83 EPG (range: 0–109), respectively.

Factors influencing parasite abundance

A total of 124 samples were included in the models. The type of host group did not have a statistically significant effect on parasite abundance for any of the parasite groups (Fig. 1A). However, the size of the host group emerged as an important predictor of parasite abundance, with varying effects observed for specific parasite groups. The abundance of *Trichuris* sp. was positively correlated with group size, whereas that of *S. fuelleborni* and *O. aculeatum* was negatively correlated with group size (Fig. 1B). In addition, our models indicated that the distance from the river mouth to upstream locations markedly influenced the parasite abundance for *Trichuris* sp. and *O. aculeatum*. In particular, as the distance from the river increased, the abundance of *Trichuris* sp. decreased, whereas *O. aculeatum* exhibited an opposite trend, with higher counts linked to greater distances from the river mouth (Fig. 1C). A summary of the results from the models is provided in Table 1.

Discussion

In this study, the relationship among social structure (i.e., group type: one-male–multifemale and all-male groups), the degree of anthropogenic habitat disturbances within a 4-km stretch along the river, and parasite load in free-ranging proboscis monkeys was examined. A high prevalence of intestinal parasites was observed (81.25%), which is consistent with the previous prevalences recorded for proboscis monkeys along the Kinabatangan River in Sabah [i.e., 96.6% in Salgado-Lynn (2010), 92.3% in Klaus et al. (2017), and 80.2% in Frias et al. (2021)] and in Bako National Park in Sarawak [i.e., 95.4% in Adrus et al. (2019)]. The predominant parasite groups in this study included *Trichuris* sp., *Strongyloides fuelleborni*, and *Oesophagostomum aculeatum*, which have also been identified as dominant in other fecal analyses of proboscis monkeys, in wild and captive settings (Table 2), reinforcing a consistent pattern of parasitic infections across different populations. Nonetheless, given the substantial differences in proboscis monkey diets between riverine and mangrove forests (Matsuda et al., 2019), investigating the mechanism by which such habitat-linked dietary variation may contribute to individual- or population-level differences in parasitic infections across their range is necessary. Habitat type not only determines available food resources but also varies in forest height and ground use frequency (Feilen and Marshall, 2014, 2020; Atmoko et al., 2021), which may influence parasite transmission dynamics. Thus, whether similar trends of parasites are observed for proboscis monkeys on the island of Borneo with different habitat types should be examined in the future.

However, a notable link was not found between parasite abundance and group type (i.e., one-male–multifemale and all-male groups) in proboscis monkeys in this study, which is consistent with previous findings (Klaus et al., 2018), indicating that sex differences may have a limited influence on parasitic infection. This interpretation is further supported by a study conducted at the same site that examined the gut microbial composition from fecal samples and found no significant sex-based differences (Jose et al., 2024). Given that gut

microbiota, such as intestinal parasites, would be transmitted through direct or indirect social contact and shared use of space and food resources, the absence of sex-specific patterns in both types of organisms indicates that behavioral and spatial overlap between males and females minimizes sex-related divergence in microbial and parasite exposure.

Contrary to the finding of Klaus et al. (2018), our study revealed that group size might be a potential factor influencing parasite abundance for particular parasite species, that is, *Trichuris* sp. This finding supports the hypothesis that larger groups may exhibit higher infection rates probably because of increased contact rates and overlapping space use among individuals (Snaith et al., 2008; Rifkin et al., 2012; Kappeler et al., 2015). Although the exact mechanism remains unclear, a comparable trend was observed in the gut microbial diversity in the same population. A larger group size was associated with greater alpha diversity (Jose et al., 2024), indicating that higher host density may enhance intestinal parasites and microbial exposure. This association may reflect the increased direct interactions among individuals and result from enhanced environmental contamination in frequently reused areas. Given that all the parasites identified in this study could be transmitted via fecal–oral routes, the accumulation of feces in shared sleeping or foraging sites could be a key factor driving infection. Limited territoriality and habitual reuse of sleeping trees by proboscis monkeys—often shared across one-male–multifemale and all-male groups in multilevel societies—likely facilitates such transmission (Matsuda et al., 2024). Furthermore, the differences in habitat structure and spatial dynamics among the study sites may explain the contrasting results Klaus et al. (2018). They focused on groups inhabiting the main channel of the Kinabatangan River, where the river's width (>200 m) limits cross-group movement and shared space use. By contrast, our study site along narrow tributaries (15–20 m wide) may allow more frequent crossings and higher spatial overlap among groups (Matsuda et al., 2008; Matsuda et al., 2010a), thereby promoting indirect transmission through contaminated environments.

On the contrary, *S. fuelleborni* and *O. aculeatum* were negatively correlated with group size because of their differing ecological tolerances. *S. fuelleborni*, which is a parasitic nematode, may be more influenced by habitat disturbance or seasonal changes, with larger groups potentially reducing parasite exposure through increased host mobility and spatial separation from contaminated areas (Gillespie and Chapman, 2006; Radespiel et al., 2015). Similarly, *O. aculeatum* may require more stable environmental substrates for its fragile eggs, and pristine upstream habitats may provide better conditions for egg survival. By contrast, larger groups in disturbed downstream areas could hinder transmission (Kappeler et al., 2015). These findings indicate that host social dynamics and environmental factors must be considered, as species-specific responses shape infection patterns (Rifkin et al., 2012; Nguyen et al., 2015).

Our findings revealed a more complex relationship between parasite abundance and habitat disturbance than initially anticipated. Contrary to expectations that anthropogenic habitat disturbance would universally elevate parasite loads (Gillespie and Chapman, 2006), we observed that the impact of disturbance varied across different parasite taxa. In particular, the abundance of *Trichuris* sp. decreased with the increase of distance from the river mouth, indicating that higher parasite loads occur in downstream areas with more intense human activity and tourism. Conversely, *O. aculeatum* displayed the opposite trend, with greater abundance in less disturbed upstream forests. These contrasting patterns indicate that different parasite species may respond to habitat disturbance through distinct ecological mechanisms. Considering the elevated *Trichuris* abundance in downstream areas, more disturbed habitats may not be attributable to the increased host density or spatial overlap, as proboscis monkeys in these areas do not necessarily aggregate at higher densities compared with the upstream areas. Aggregation likely occurs in upstream areas, where the river width is narrower, providing a safer environment for proboscis monkeys because of their ability to escape terrestrial predators, such as clouded leopards, by jumping to the opposite bank

(Matsuda et al., 2010a). Given its greater safety from predators, this environment likely facilitates aggregation in upstream areas, making them a more favorable location for proboscis monkey groups to congregate. This interpretation is consistent with the species' highly resilient egg morphology, which supports environmental persistence even under degraded conditions (Gillespie and Chapman, 2006; Snaith et al., 2008). By contrast, the fragile eggs of *O. aculeatum* may require relatively intact environmental substrates, such as undisturbed soil, to ensure survival and successful transmission, as the eggs of many parasites are dependent on specific environmental conditions for persistence, including substrate type and humidity (Radespiel et al., 2015). Accordingly, the relatively pristine conditions in upstream sites likely provide a favorable microenvironment for their development.

Interestingly, these spatial patterns in parasite abundance are contrary to prior findings from the same population, which identified clear site-based differences in gut microbial composition, with lower microbial diversity in the downstream areas (Jose et al., 2024). Although gut microbiota and intestinal parasites share common transmission pathways, namely, social contact and environmental exposure, their ecological sensitivities appear to diverge. In general, gut microbiota are more responsive to dietary shifts and subtle ecological changes (e.g., Amato et al., 2013; Hayakawa et al., 2018; Lee et al., 2019; Barelli et al., 2020), whereas parasite abundance in our study is influenced by a combination of host social dynamics (e.g., group size and space use) and species-specific environmental tolerances. This distinction emphasizes the importance of adopting a taxon-specific approach when interpreting host–environment–parasite relationships and indicates that parasites and microbiota can influence the ecological and health dynamics of primates (Rifkin et al., 2012; Nguyen et al., 2015).

Understanding the interplay among social organization, habitat characteristics, and parasitic infection in wild primates deepens our ecological insights and informs broader questions in evolutionary biology and conservation. The findings of this study underscore the

complex, context-dependent nature of host–parasite dynamics, highlighting the mechanism by which intrinsic factors such as group size and behavior can mediate exposure risks even in the face of external environmental change. At present, given the escalating habitat disturbance, such nuanced understanding is crucial for predicting disease risks in wildlife populations and designing conservation strategies that account for social and ecological variability. Integrative approaches that consider behavioral ecology alongside environmental gradients may also be essential for safeguarding the health and persistence of socially complex yet increasingly vulnerable species such as the proboscis monkey.

Finally, the zoonotic potential of the helminths identified in this study, future research should assess cross-species transmission risks, especially in ecotourism corridors like our study site, where frequent contact occurs among humans, livestock, and wild primates. *Trichuris* sp. may include *T. trichiura*, a known human pathogen capable of infecting non-human primates (Rivero et al., 2020), while *S. fuelleborni* and *O. aculeatum* have been reported in both human and non-human hosts in Southeast Asia (Yalcindag et al., 2021; Chan et al., 2023). The presence of these helminths in areas accessible to humans highlights the need to understand their transmission dynamics and public health implications in the context of increasing anthropogenic pressure (Gillespie and Chapman, 2006).

Declarations

Ethics approval

The animal study was reviewed and approved by the Sabah Biodiversity Centre and the Sabah Wildlife Department [JKM/MBS.1000-2/2 JLD.3 (120)].

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Author contributions

MNF: conceptualization, writing—original draft, methodology; LF: conceptualization, writing—review and editing, methodology, visualization, formal analysis, investigation; EZ: conceptualization, methodology; PL: resources, writing—review and editing; JT: resources, writing—review and editing; HB: resources, writing—review and editing; VK: resources, writing—review and editing; IM: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft. All authors (except deceased EZ) gave final approval for publication and agreed to be held accountable for the work performed therein.

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References

Adrus, M., Zainuddin, R., Ahmad Khairi, N.H., Ahamad, M., Abdullah, M.T., 2019. Helminth parasites occurrence in wild proboscis monkeys (*Nasalis larvatus*), endemic primates to Borneo Island. J Med Primatol 48, 357-363. doi: 10.1111/jmp.12437

Altizer, S., Nunn, C.L., Thrall, P.H., Gittleman, J.L., Antonovics, J., Cunningham, A.A., Dobson, A.P., Ezenwa, V., Jones, K.E., Pedersen, A.B., Poss, M., Pulliam, J.R.C., 2003. Social Organization and Parasite Risk in Mammals: Integrating Theory and Empirical

Studies. Annual Review of Ecology, Evolution, and Systematics 34, 517-547. doi: 10.1146/annurev.ecolsys.34.030102.151725

Amato, K.R., Yeoman, C.J., Kent, A., Righini, N., Carbonero, F., Estrada, A., Gaskins, H.R., Stumpf, R.M., Yildirim, S., Torralba, M., Gillis, M., Wilson, B.A., Nelson, K.E., White, B.A., Leigh, S.R., 2013. Habitat degradation impacts black howler monkey (*Alouatta pigra*) gastrointestinal microbiomes. ISME J. 7, 1344-1353. doi: 10.1038/ismej.2013.16

Atmoko, T., Mardiastuti, A., Bismark, M., Prasetyo, L.B., Iskandar, E., 2021. Land cover and Proboscis monkey habitats in Berau Delta, East Kalimantan. IOP Conference Series: Earth and Environmental Science 739. doi: 10.1088/1755-1315/739/1/012062

Barelli, C., Albanese, D., Stumpf, R.M., Asangba, A., Donati, C., Rovero, F., Hauffe, H.C., 2020. The gut microbiota communities of wild arboreal and ground-feeding tropical primates are affected differently by habitat disturbance. mSystems 5. doi: 10.1128/mSystems.00061-20

Becker, D.J., Streicker, D.G., Altizer, S., 2018. Using host species traits to understand the consequences of resource provisioning for host-parasite interactions. J Anim Ecol 87, 511-525. doi: 10.1111/1365-2656.12765

Bernard, H., Mohammad-Shom, S., Kulanthavelu, M., Sha, J.C.M., Malim, T.P., Abram, N.K., Matsuda, I., 2025. Monitoring the population and distribution of the proboscis monkey (*Nasalis larvatus*) in the Klias Peninsula, Sabah, Borneo, Malaysia: insights from an 18-year study. Primates. doi: 10.1007/s10329-025-01183-7

Bürkner, P.-C., 2018. Advanced Bayesian Multilevel Modeling with the R Package brms. The R Journal 10, 395-411. doi:

Chan, A.H.E., Kusolsuk, T., Watthanakulpanich, D., Pakdee, W., Doanh, P.N., Yasin, A.M., Dekumyoy, P., Thaenkham, U., 2023. Prevalence of *Strongyloides* in Southeast Asia: a systematic review and meta-analysis with implications for public health and sustainable control strategies. Infect Dis Poverty 12, 83. doi: 10.1186/s40249-023-01138-4

Chapman, A.C., Rothman, J.M., Hodder, S.A.M., 2009. Can parasite infections be a selective force influencing primate group size? A test with red colobus, in: Huffman, M.A., Chapman, C.A. (Eds.), Primate Parasite Ecology: The Dynamics and Study of Host-Parasite Relationships. Cambridge University Press, Cambridge, pp. 423-440.

Chapman, C.A., Gillespie, T.R., Goldberg, T.L., 2005. Primates and the Ecology of their Infectious Diseases: How will Anthropogenic Change Affect Host-Parasite Interactions? Evolutionary Anthropology: Issues, News, and Reviews 14, 134-144. doi: 10.1002/evan.20068

Cooper, N., Nunn, C.L., 2013. Identifying future zoonotic disease threats: Where are the gaps in our understanding of primate infectious diseases? Evol Med Public Health 2013, 27-36. doi: 10.1093/emph/eot001

Feilen, K.L., Marshall, A.J., 2014. Sleeping site selection by proboscis monkeys (*Nasalis larvatus*) in West Kalimantan, Indonesia. Am J Primatol 76, 1127-1139. doi: 10.1002/ajp.22298

Feilen, K.L., Marshall, A.J., 2020. Responses to spatial and temporal variation in food availability on the feeding ecology of proboscis monkeys (*Nasalis larvatus*) in West Kalimantan, Indonesia. Folia Primatol (Basel), 1-18. doi: 10.1159/000504362

Frias, L., Hasegawa, H., Chua, T.H., Sipangkui, S., Stark, D.J., Salgado-Lynn, M., Goossens, B., Keuk, K., Okamoto, M., MacIntosh, A.J.J., 2021. Parasite community structure in sympatric Bornean primates. International Journal for Parasitology. doi: 10.1016/j.ijpara.2021.03.003

Frias, L., Stark, D.J., Salgado Lynn, M., Nathan, S., Goossens, B., Okamoto, M., MacIntosh, A.J.J., 2019. Molecular characterization of nodule worm in a community of Bornean primates. Ecology and Evolution. doi: 10.1002/ece3.5022

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. doi: 10.1111/j.1523-1739.2006.00290.x

Hasegawa, H., Frias, L., Peter, S., Hasan, N.H., Stark, D.J., Lynn, M.S., Sipangkui, S., Goossens, B., Matsuura, K., Okamoto, M., Macintosh, A.J.J., 2020. First description of male worms of *Enterobius* (*Colobenterobius*) *serratus* (Nematoda: Oxyuridae), the pinworm parasite of proboscis monkeys. Zootaxa 4722, 287-294. doi: 10.11646/zootaxa.4722.3.6

Hayakawa, T., Nathan, S., Stark, D.J., Saldivar, D.A.R., Sipangkui, R., Goossens, B., Tuuga, A., Clauss, M., Sawada, A., Fukuda, S., Imai, H., Matsuda, I., 2018. First report of

foregut microbial community in proboscis monkeys: are diverse forests a reservoir for diverse microbiomes? Environmental Microbiology Reports 10, 655-662. doi: 10.1111/1758-2229.12677

Hopkins, M.E., Nunn, C.L., 2007. A global gap analysis of infectious agents in wild primates. Diversity and Distributions 13, 561-572. doi: 10.1111/j.1472-4642.2007.00364.x

Jose, L., Lee, W., Hanya, G., Tuuga, A., Goossens, B., Tangah, J., Matsuda, I., Kumar, V.S., 2024. Gut microbial community in proboscis monkeys (*Nasalis larvatus*): implications for effects of geographical and social factors. Royal Society Open Science 11. doi: 10.1098/rsos.231756

Kappeler, P.M., Cremer, S., Nunn, C.L., 2015. Sociality and health: impacts of sociality on disease susceptibility and transmission in animal and human societies. Philos Trans R Soc Lond B Biol Sci 370. doi: 10.1098/rstb.2014.0116

Klaus, A., Strube, C., Roper, K.M., Radespiel, U., Schaarschmidt, F., Nathan, S., Goossens, B., Zimmermann, E., 2018. Fecal parasite risk in the endangered proboscis monkey is higher in an anthropogenically managed forest environment compared to a riparian rain forest in Sabah, Borneo. PLoS One 13, e0195584. doi: 10.1371/journal.pone.0195584

Klaus, A., Zimmermann, E., Röper, K.M., Radespiel, U., Nathan, S., Goossens, B., Strube, C., 2017. Co-infection patterns of intestinal parasites in arboreal primates (proboscis monkeys, Nasalis larvatus) in Borneo. International Journal for Parasitology: Parasites and Wildlife. doi: 10.1016/j.ijppaw.2017.09.005

Knauf, S., Jones-Engel, L., 2020. Neglected Diseases in Monkeys: From the Monkey-Human Interface to One Health. Springer Cham, Switzerland AG.

Lee, W., Hayakawa, T., Kiyono, M., Yamabata, N., Hanya, G., 2019. Gut microbiota composition of Japanese macaques associates with extent of human encroachment. Am J Primatol 81, e23072. doi: 10.1002/ajp.23072

Lhota, S., Sha, J.C.M., Bernard, H., Matsuda, I., 2019. Proboscis monkey conservation: beyond the science, in: Behie, A.M., Teichroeb, J.A., Malone, N.M. (Eds.), Primate Research and Conservation in the Anthropocene. Cambridge University Press, Cambridge pp. 182-196.

Matsuda, I., Kubo, T., Tuuga, A., Higashi, S., 2010a. A Bayesian analysis of the temporal change of local density of proboscis monkeys: implications for environmental effects on a multilevel society. American Journal of Physical Anthropology 142, 235-245. doi: 10.1002/ajpa.21218

Matsuda, I., Murai, T., Grueter, C.C., Tuuga, A., Goossens, B., Bernard, H., Yahya, N.K., Orozco-terWengel, P., Salgado-Lynn, M., 2024. The multilevel society of proboscis monkeys with a possible patrilineal basis. Behavioral Ecology and Sociobiology 78. doi: 10.1007/s00265-023-03419-2

Matsuda, I., Nakabayashi, M., Otani, Y., Yap, S.W., Tuuga, A., Wong, A., Bernard, H., Wich, S.A., Kubo, T., 2019. Comparison of plant diversity and phenology of riverine and mangrove forests with those of the dryland forest in Sabah, Borneo, Malaysia, in: Nowak, K., Barnett, A.A., Matsuda, I. (Eds.), Primates in Flooded Habitats: Ecology and Conservation. Cambridge University Press, Cambridge, pp. 15-28.

Matsuda, I., Tuuga, A., Akiyama, Y., Higashi, S., 2008. Selection of river crossing location and sleeping site by proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. American Journal of Primatology 70, 1097-1101. doi: 10.1002/ajp.20604

Matsuda, I., Tuuga, A., Bernard, H., 2011. Riverine refuging by proboscis monkeys (*Nasalis larvatus*) and sympatric primates: Implications for adaptive benefits of the riverine habitat. Mammalian Biology 76, 165-171. doi: 10.1016/j.mambio.2010.03.005

Matsuda, I., Tuuga, A., Hashimoto, C., Bernard, H., Yamagiwa, J., Fritz, J., Tsubokawa, K., Yayota, M., Murai, T., Iwata, Y., Clauss, M., 2014. Faecal particle size in free-ranging primates supports a 'rumination' strategy in the proboscis monkey (*Nasalis larvatus*). Oecologia 174, 1127-1137. doi: 10.1007/s00442-013-2863-9

Matsuda, I., Tuuga, A., Higashi, S., 2009a. The feeding ecology and activity budget of proboscis monkeys. American Journal of Primatology 71, 478-492. doi: 10.1002/ajp.20677

Matsuda, I., Tuuga, A., Higashi, S., 2009b. Ranging behavior of proboscis monkeys in a riverine forest with special reference to ranging in inland forest. International Journal of Primatology 30, 313-325. doi: 10.1007/s10764-009-9344-3

Matsuda, I., Tuuga, A., Higashi, S., 2010b. Effects of water level on sleeping-site selection and inter-group association in proboscis monkeys: why do they sleep alone inland on flooded days? Ecological Research 25, 475-482. doi: 10.1007/s11284-009-0677-3

Modrý, D., Pafcŏ, B., Petrzĕlková, K.J., Hasegawa, H., 2018. Parasites of Apes: an Atlas of Coproscopic Diagnostics. Chimaira, Frankfurt.

Nguyen, N., Fashing, P.J., Boyd, D.A., Barry, T.S., Burke, R.J., Goodale, C.B., Jones, S.C., Kerby, J.T., Kellogg, B.S., Lee, L.M., Miller, C.M., Nurmi, N.O., Ramsay, M.S., Reynolds, J.D., Stewart, K.M., Turner, T.J., Venkataraman, V.V., Knauf, Y., Roos, C., Knauf, S., 2015. Fitness impacts of tapeworm parasitism on wild gelada monkeys at Guassa, Ethiopia. Am J Primatol 77, 579-594. doi: 10.1002/ajp.22379

Nunn, C.L., 2012. Primate disease ecology in comparative and theoretical perspective. Am J Primatol 74, 497-509. doi: 10.1002/ajp.21986

Nunn, C.L., Jordan, F., McCabe, C.M., Verdolin, J.L., Fewell, J.H., 2015. Infectious disease and group size: more than just a numbers game. Philos Trans R Soc Lond B Biol Sci 370. doi: 10.1098/rstb.2014.0111

Radespiel, U., Schaber, K., Kessler, S.E., Schaarschmidt, F., Strube, C., 2015. Variations in the excretion patterns of helminth eggs in two sympatric mouse lemur species (*Microcebus murinus* and *M. ravelobensis*) in northwestern Madagascar. Parasitol Res 114, 941-954. doi: 10.1007/s00436-014-4259-0

Rahman, F.G., Nurliani, A., Rezeki, A., Rusmiati, R., 2023. Identification of intestine parasite worms eggs in feces proboscis monkey (*Nasalis larvatus*). Proceeding of International Conference on Biology Education, Natural Science, and Technology 1, 541-549. doi:

Ramadhani, M., Nurhidayah, N., Kurniawati, D.A., Purmadi, M., Rafiq, F.A., Kusumaningtyas, E., Endrawati, D., Hidayatik, N., Prastiya, R.A., Mariya, S.S., Mufasirin, Hastutiek, P., 2024. Gastrointestinal helminths of captive proboscis monkey (*Nasalis larvatus*) in Surabaya zoo, Indonesia. J Med Primatol 53, e12719. doi: 10.1111/jmp.12719

Rifkin, J.L., Nunn, C.L., Garamszegi, L.Z., 2012. Do animals living in larger groups experience greater parasitism? A meta-analysis. Am Nat 180, 70-82. doi: 10.1086/666081

Rivero, J., Cutillas, C., Callejon, R., 2020. *Trichuris trichiura* (Linnaeus, 1771) From Human and Non-human Primates: Morphology, Biometry, Host Specificity, Molecular Characterization, and Phylogeny. Front Vet Sci 7, 626120. doi: 10.3389/fvets.2020.626120

Rushmore, J., Bisanzio, D., Gillespie, T.R., 2017. Making New Connections: Insights from Primate-Parasite Networks. Trends Parasitol 33, 547-560. doi: 10.1016/j.pt.2017.01.013

Salgado-Lynn, M., 2010. Primate viability in a fragmented landscape: genetic diversity and parasite burden o f long-tailed macaques and proboscis monkeys in the Lower Kinabatangan Floodplain, Sabah, Malaysia. Cardiff University, Cardiff.

Silk, J.B., 2007. The adaptive value of sociality in mammalian groups. Philos Trans R Soc Lond B Biol Sci 362, 539-559. doi: 10.1098/rstb.2006.1994

Snaith, T.V., Chapman, C.A., Rothman, J.M., Wasserman, M.D., 2008. Bigger groups have fewer parasites and similar cortisol levels: a multi-group analysis in red colobus monkeys. Am J Primatol 70, 1072-1080. doi: 10.1002/ajp.20601

Vitone, N.D., Altizer, S., Nunn, C.L., 2004. Body size, diet and sociality influence the species richness of parasitic worms in anthropoid primates. Evolutionary Ecology Research 6, 183-199. doi:

Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B., Koh, L.P., 2013. Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. Trends Ecol Evol 28, 531-540. doi: 10.1016/j.tree.2013.04.005

Yalcindag, E., Stuart, P., Hasegawa, H., Streit, A., Dolezalova, J., Morrogh-Bernard, H., Cheyne, S.M., Nurcahyo, W., Foitova, I., 2021. Genetic characterization of nodular worm infections in Asian Apes. Sci Rep 11, 7226. doi: 10.1038/s41598-021-86518-2

Table and figure legends

Table 1. Summary of the fitted models.

Table 2. Comparison between the parasite species detected and parasite prevalence (%) in fecal samples of proboscis monkeys in each study.

Fig. 1. Posterior distributions of the differences in parasite abundance for *Trichuris* sp. (top), *S. fuelleborni* (middle), and *O. aculeatum* (bottom) in relation to host group type (A). The green shaded areas represent the posterior distributions, with the black dot indicating the median estimate and the black horizontal line shown in boldface representing the 99% credible interval. The vertical dashed line at zero represents no difference in infection rates among the groups. The predicted probability of abundance for the same parasite groups in relation to host group size (B) and sampling location represented by the distance from the river mouth (C). Credible intervals are set at 89%.

Table 1. Summary of fitted models

	Parameter	Est.	Est. error	95% CI (Lower)	95% CI (Upper)	Rhat	Bulk ESS	Tail ESS
Trichuris sp.	*Random Effects*							
	sd (Intercept)	0.92	0.22	0.6	1.44	1	1600	2336
	Fixed Effects							
	Intercept	4.32	0.51	3.29	5.32	1	3515	4008
	group type	0.81	0.55	-0.27	1.93	1	3151	3511
	group size (scaled)	0.16	0.01	0.14	0.19	1	6937	4494
	distance to river (scaled)	-0.7	0.14	-0.97	-0.44	1	2949	3362
S. fuelleborni	*Random Effects*							
	sd (Intercept)	5.74	1.67	3.37	9.71	1	2691	3424
	Fixed Effects							
	Intercept	-1.68	3.25	-8.21	4.77	1	3101	3670
	group type	-1.09	3.7	-8.69	5.88	1	2916	3602
	group size (scaled)	-1.62	0.12	-1.86	-1.38	1	9301	5682
	distance to river (scaled)	1.03	0.71	-0.35	2.44	1	5057	4881
O. aculeatum	*Random Effects*							
	sd (Intercept)	10.54	3.96	5	20.28	1	2116	3425
	Fixed Effects							
	Intercept	-5.12	6.63	-18.87	7.67	1	3150	3920
	group type	-0.47	7.58	-16.08	14.32	1	2693	3620
	group size (scaled)	-1.48	0.19	-1.87	-1.11	1	7942	5445
	distance to river (scaled)	3.46	1.4	0.71	6.27	1	3953	4708

576 **Table 2.** Comparison of the parasite species detected and parasite prevalence (%) in fecal samples of proboscis monkeys in each study

Study site	Bekantan Rescue Center Sahabat Bekantan Foundation	Surabaya Zoo	Labuk Bay Proboscis Monkey Sanctuary	Bako National Park	Lower Kinabatangan (Lot. 1-7 areas)	Lower Kinabatangan (Lot. 6 area)	Lower Kinabatangan (Lot. 1-4 areas)	Lower Kinabatangan (Lot. 4 area)
Forest type	N/A	N/A	Mangrove	Mangrove	Riverine forest	Riverine forest	Riverine forest	Riverine forest
Living-condition	Captive	Captive	Semi-free ranging	Free-ranging	Free-ranging	Free-ranging	Free-ranging	Free-ranging
No. of individuals	3	< 27	< 195	Unknown	Unknown	< ca. 200	Unknown	160
No. of samples	60	20	90	65	91	652	146	160
Parasite species								
Anatrichosoma spp.			2.8			1.4	2.1	
Ascaris sp.		5.0		30.8			67.1	
Ascaris lumbricoides			2.2			8.6		
Dipylidium-like morphs							9.6	
Diphyllobotrium sp.				1.5				
Enterobius (Colobenterobius) serratus					1.25			1.25

Enterobius spp. (genus within Oxyurida)						5.5		
Fasciola sp.				1.5				
Hymenolepis sp.				3.1				
Hymenolepis nana		5.0						
Oesophagostomum sp.	5.0		31.4	33.8		22.8		
Oesophagostomum aculeatum								5.0
Physaloptera sp.				3.1				
Schistosoma sp.				1.5				
Spirurida sp.					2.1			
Strongyloides spp.		5.0	65.6	21.5	20.8	32.7	5.5	
Strongyloides fuelleborni								10.6
Strongyloides stercoralis				4.6				
Taenia sp.							28.8	
Trichostrongylus spp.	10.0		36.0	9.2		48.5		
Trichuris spp.		85.0	21.8–47.1	35.4	80.2	82.1	91.8	78.1

Trichuris trichiura	15.0			44.6				
Strongylida			43.3		29.6	3.1		
Spirurida sp.					0.63			0.63
strongylid			4.6				45.2	
oxyurid							4.1	
Ref.	Rahman et al. (2023)	Ramadhani et al. (2024)	Klaus et al. (2017); Klaus et al. (2018)	Adrus et al. 2019	Frias et al. (2021)	Klaus et al. (2017); Klaus et al. (2018)	Salgado-Lynn (2010)	This study

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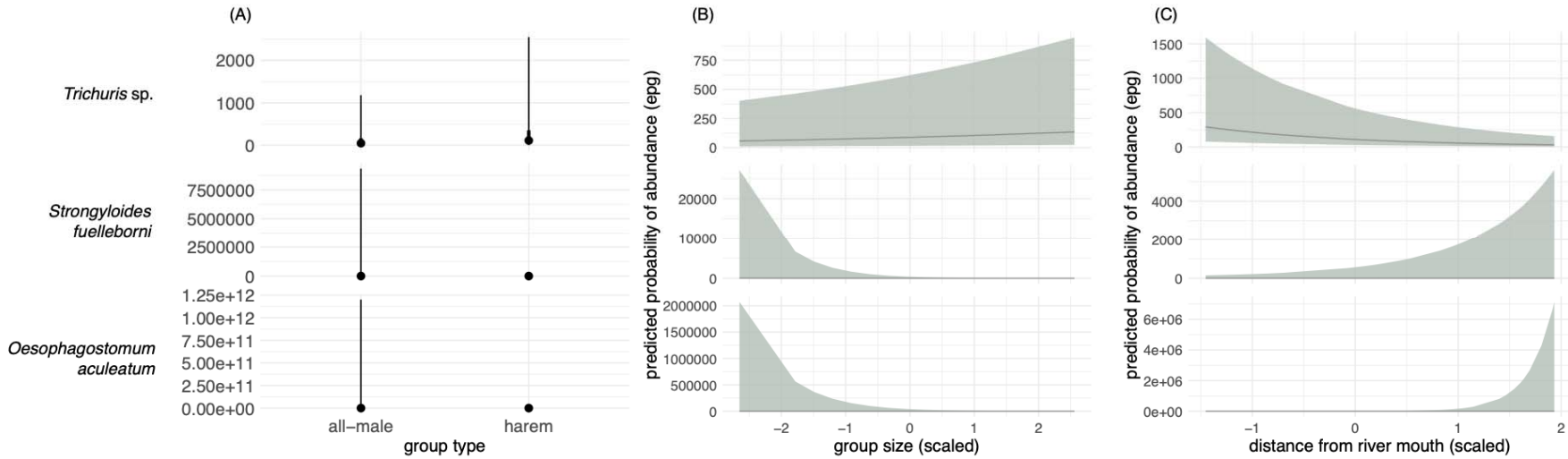

Fig. 1. Posterior distributions of the differences in parasite abundance for *Trichuris* sp. (top), *S. fuelleborni* (middle), and *O. aculeatum* (bottom) in relation to host group type (A). The green shaded areas represent the posterior distributions, with the black dot indicating the median estimate and the black bold horizontal line representing the 99% credible interval. The vertical dashed line at zero represents no difference in infection rates between groups. Predicted probability of abundance for *the same parasite groups* in relation to host group size (B) and sampling location represented by the distance from the river mouth (C). Credible intervals are set at 89%.