

Following the trail of the elusive proboscis monkey in Borneo

Ikki Matsuda^{1,2,3,4} 

¹Chubu University Academy of Emerging Sciences, Kasugai-shi, Japan

²Chubu Institute for Advanced Studies, Chubu University, Kasugai-shi, Japan

³Wildlife Research Center of Kyoto University, Kyoto, Japan

⁴Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, Kota Kinabalu, Malaysia

Correspondence

Ikki Matsuda, Chubu University Academy of Emerging Sciences, 1200, Matsumoto-cho, Kasugai-shi, 6 Aichi 487-8501, Japan.
Email: ikki-matsuda@isc.chubu.ac.jp

Funding information

Inamori Foundation; Japan Science and Technology Agency Core Research for Evolutional Science and Technology 17941861, Grant/Award Number: JPMJCR17A4; Japan Society for the Promotion of Science KAKENHI, Grant/Award Numbers: 21770261, 24657170, 26711027, 15K14605, 19KK0191; National Geographic Society, Grant/Award Number: 9254-13; Primate Origins of Human Evolution and Human Evolution Project of Primate Research Institute of Kyoto University; Wildlife Reserves Singapore Conservation Fund, Grant/Award Number: Exp14/10; Sumitomo Foundation, Grant/Award Number: 130164; Chubu University Grant (S), Grant/Award Number: 22-04S

Abstract

For decades, knowledge about the endangered proboscis monkey was gleaned from limited information about their behavior from boat surveys conducted along riverbanks, where the monkeys rest during the early morning and late afternoon. This was due to the dense and swampy habitats they live in, which made them nearly impossible to track once they moved into inland forests. By conducting full-day continuous observations on foot in riverine forests in Sabah, Borneo, Malaysia, alongside my colleagues, we produced pioneering research about this species. Conducted over a period of more than 15 years since 2005, our studies have resulted in the comprehensive collection of information about the proboscis monkey with regards to its feeding and ranging behaviors as well as novel findings about its fascinating digestive strategy of rumination and the unique functionality of its “odd-nose.”

KEYWORDS

Borneo, folivore, foregut-fermenters, primates, primatology

1. INTRODUCTION

Primate research is primarily the study of fossil and existing nonhuman primates to understand human evolution. Japanese primatology emerged shortly after World War II; at present, based on intensive long-term behavioral observations, Japan is one of the world's leading countries in

this field of study (Nakamura, 2009). The majority of Japanese long-term field research projects for nonhuman primates (primates from here on) that are active and ongoing are concentrated in Africa, where great apes, such as chimpanzees, bonobos, and gorillas live (Kappeler & Watts, 2012). The Japanese macaque research projects are an exception to this (Nakagawa et al., 2010). Conversely, in

Ikki Matsuda is the recipient of the 20th Miyadi Award of the Ecological Society of Japan.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Author. *Ecological Research* published by John Wiley & Sons Australia, Ltd on behalf of The Ecological Society of Japan.

Southeast Asia, despite the high diversity of primates, long-term primate research projects by Japanese researchers exceeding 10 years are scarce, and our knowledge of the primates that inhabit the region is still restricted.

In 2005, I began a long-term primate research project in the Lower Kinabatangan, Sabah, Borneo, Malaysia, which continues to this day with the help of local government agencies, universities, and NGOs. In addition to conducting research at an established long-term research site, setting up a new research site entails numerous challenges since all preparations must begin from the ground up. This opens a whole new range of possibilities in field research. I have focused on the proboscis monkey (*Nasalis larvatus*), a species that is endemic to Borneo whose ecology has remained a mystery because of its preference for dense forests along the coast and riverside, where the ground is muddy, and thus access and observations are difficult. As a result, early research on the proboscis monkey was primarily based on short-term studies from boat-based surveys focused on the basic understanding of their social organization and habitat use (Grueter et al., 2022). In the late 1980s, longer-term studies (<5 years) pioneered by Carey P. Yeager, Elizabeth L. Bennett, and Ramesh Boonratana were conducted in Kalimantan, Sarawak, and Sabah, respectively (Bennett & Sebastian, 1988; Boonratana, 2000; Yeager, 1989). These studies helped to elevate the proboscis monkey from an interesting but little-understood “weird big-nose” monkey into a flagship species for conservation. Unfortunately, these studies did not continue.

In the 2000s, a growing number of researchers began to focus their attention on this one-of-a-kind monkey, and academic studies were conducted to obtain a better knowledge of the species. I am one of those researchers. Despite the limitations, the long-term observations I have made over more than 15 years have revealed much information about the ecology of the proboscis monkey. In particular, the discovery of the first primate behavior of regurgitation and remastication, that is, “rumination strategy,” in the proboscis monkey (Matsuda et al., 2011) attracted international attention. To elucidate why such a rumination strategy only occurred in this species, I looked into several factors, including foraging behavior, anatomical characteristics of their digestive system, bacterial flora, and mastication efficiency (Hayakawa et al., 2018; Matsuda et al., 2014; Matsuda et al., 2022; Matsuda, Espinosa-Gómez, et al., 2019).

The proboscis monkey's social structure is also unique. In the proboscis monkey, the basic minimum reproductive unit is a one-male (or harem) group consisting of one adult male, several adult females, and immatures, which aggregates to form a further, higher-level society, the multilevel society (Murai, 2004; Yeager, 1991). The degree of aggregation varies depending on local conditions, such as

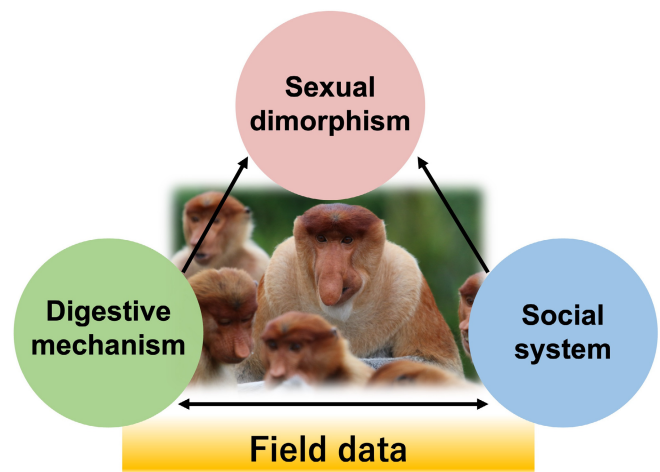


FIGURE 1 Emerging collaborations and diverse research topics achieved while investigating the ecology of the proboscis monkey. As the arrows indicate, each of the research topics, which appear to be independent, are indeed interrelated, and in the process of elucidating them, further interesting topics emerge [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/1440-1703.12343)]

food availability and predation threats (Matsuda, Kubo, et al., 2010; Matsuda, Tuuga, & Higashi, 2010). The evolution of the proboscis monkey's complex societies, which are also common to humans but do not occur in great apes, cannot be explained by phylogenetic history, thus, providing important insight into the origins and evolutionary history of human societies and cultures (Grueter, 2022; Grueter et al., 2012). Our research into their ecology and social structure has been key to understanding the distinctive large body and nose size of male proboscis monkeys (Koda et al., 2018; Matsuda et al., 2020). Thus, my ultimate study goal is to answer the enigma of the ecological, social, and morphological specialization of the proboscis monkey, and to elucidate the common mechanisms underlying the evolution of sexual dimorphism in a wide range of primates, including humans (Figure 1).

2. MAIN FINDINGS

2.1. Ecological study of digestive mechanisms

Over 3500 h of observation based on full day follows (including observations from all hours of the day) revealed previously unknown data about proboscis monkey foraging behavior (Matsuda et al., 2009a; Matsuda et al., 2009b). As a result of adaptation to a folivore diet, the proboscis monkey evolved the foregut fermentation digestive system with four (“quadripartite”) chambers in the forestomach (Hoshino et al., 2021; Matsuda et al., 2022; Matsuda, Chapman, & Clauss, 2019) along with a long digesta retention

time, that is, approximately 40 h (Matsuda et al., 2015) and is the only primate that exhibits regurgitation and remastication (Matsuda et al., 2011). To elucidate the functional significance of regurgitation and remastication, we extended our research to other primate species and other mammalian taxa. In terrestrial herbivores, chewing is the primary factor determining digesta particle size, and the digestive processes themselves have little effect on changes in the particle size of digesta (reviewed in Fritz et al., 2009). Thus, analysis of fecal particle size is a simple and noninvasive, but valuable, approach for assessing chewing efficiency in the proboscis monkey. By comparing the fecal particle sizes of over 200 mammalian species, we demonstrated that the fecal particle size in the proboscis monkey was finer than in other primates and similar to that of foregut-fermenting mammals with a rumination strategy. This led us to conclude that, like other ruminants, regurgitation and remastication are critical components of the digestive strategy of the proboscis monkey (Matsuda et al., 2014). However, according to our findings, primates have a lower chewing efficiency and a smaller particle size reduction of consumed foods than other mammalian species (Dunbar & Bose, 1991; Fritz et al., 2009; Matsuda et al., 2014).

To better understand the digestive mechanisms of the proboscis monkey, we looked at the species patterns of solute excretion and different-sized particle passage markers in captivity. We expected that similar to functional ruminants (ruminants and camelids), rumination by the proboscis monkey would be facilitated by a particle sorting mechanism in the forestomach that selectively retains larger particles and subjects them to repeated mastication. This expectation was partially based on the fact that foregut-fermenting primates, including the proboscis monkey (like ruminants), have a preference for certain postures, that is, sitting posture (Matsuda et al., 2017). Ruminants typically adopt a sternal resting posture (Balch, 1955) and rarely lie on their side since the sternal resting position ensures a constant orientation of the reticulum relative to gravity, which facilitates particle sorting. Further experiments on excretion patterns revealed that, unlike many other mammalian taxa, primates, including the proboscis monkey, generally have limited digesta washing and mixing, suggesting a constraint in saliva production and hence somewhat less favorable conditions for plant material fermentation than in other mammalian herbivores (Matsuda, Espinosa-Gómez, et al., 2019; Müller et al., 2011). Thus, our findings indicated that primates are not characterized by high degrees of morphophysiological adaptations of the digestive tract compared to other mammals as suggested by Milton (1986). However, this suggests that the reason primates with less elaborate digestive physiology were able to

defend their dietary niches from other mammals is because they were able to successfully exploit various niches with their behavioral flexibility through cognitive adaptations (Matsuda & Clauss, 2022; Matsuda, Espinosa-Gómez, et al., 2019).

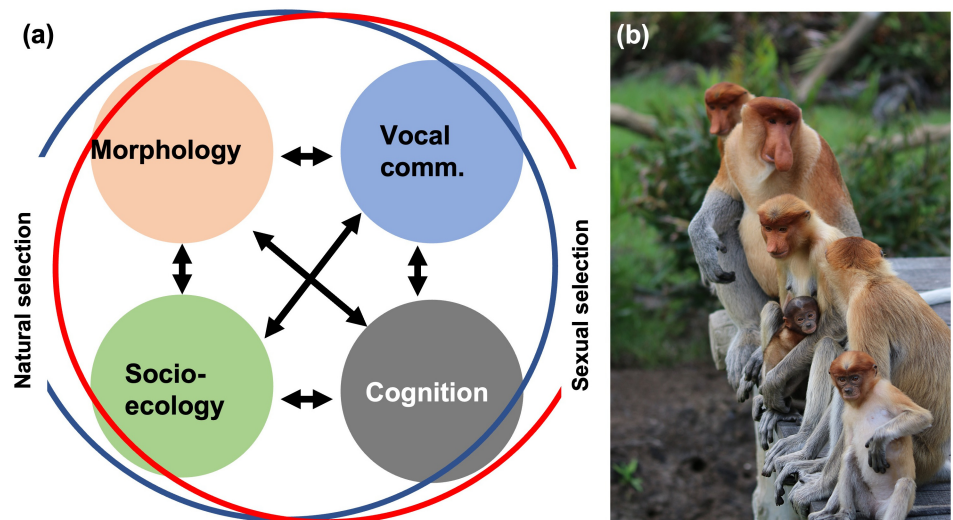
2.2. Social system

In most primates, interunit encounters typically involve avoidance or agonism due to mating and/or resource competition. However, there are a small number of primate species where social units regularly interact amiably and coordinate activities. Such social organization is referred to as multilevel (Grueter, 2022; Grueter et al., 2012). The proboscis monkey is one of these exceptional species, forming a multilevel society with multiple harem groups of the minimum reproductive unit, that is, one adult male, several adult females, and their offspring, totaling over 60 individuals (Murai, 2004; Yeager, 1990, 1991). By observing interactions between proboscis monkey groups, we quantified the influence of habitat heterogeneity, food abundance, and predation pressure on spatiotemporal changes in aggregation size among harem groups (Matsuda, Kubo, et al., 2010). Species that form multilevel societies with overlapping ranges among groups, such as proboscis monkeys, are rare. Even the great apes, which are closely related to humans, are antagonistic toward other groups, with each group living within its territory (Mitani et al., 2010). Therefore, the fact that the emergence of a human-like multilevel society is expressed in the phylogenetically distant proboscis monkey presents an important insight into the social evolution of humans. Assessing the social system of the proboscis monkey has provided insights into the evolution of human society.

2.3. Evolutionary mechanisms of sexual dimorphism

Since the proboscis monkey is not territorial, multiple harems sleep in close proximity (Matsuda et al., 2008; Matsuda, Kubo, et al., 2010; Matsuda, Tuuga, & Higashi, 2010) and females transfer between groups (Matsuda et al., 2012; Murai et al., 2007). Thus, there is the potential for both female mate-choice and competition between males for females. We found significant correlations among nose, body, and testis sizes and a clear link between nose size and the number of females in the corresponding males' harem (Koda et al., 2018). Therefore, there is evidence supporting both male-to-male competition and female choice as causal factors in the

FIGURE 2 Proposed empirical evolutionary model in which morphology, communication (vocal communication), and specific society (socio-ecology) interact to accelerate sexual dimorphism in the proboscis monkey (a); the sexual dimorphism of the proboscis monkey is characterized not only by the body mass difference between the sexes, but also by the prominently large nose of the male (b). Cognitive ability is a factor that should be investigated further [Color figure can be viewed at wileyonlinelibrary.com]



evolution of enlarged male noses. We also discovered that nasal expansion alters the resonance parameters of male vocalizations in a systematic way, implying that male quality is encoded. According to our findings, the audiovisual contributions of bigger male noses serve as advertisements for females in their mate selection. Furthermore, in a sexually competitive environment, male noses with nasalized voice sounds are likely to communicate sexual quality signals as a badge of status that exposes a male's social position widely to other rival males, potentially averting critically fatal encounters.

We also analyzed canine size, another common sexually selected male trait of the proboscis monkey. Since females transfer between groups, we expected male canines to serve as crucial weapons for mate competition or defense. Contrary to expectations, body size was negatively correlated with absolute canine size (Matsuda et al., 2020). Large male noses reduce the role of canines as weapons. In addition, longer canines are opposed by natural selection because larger canines increase the required gape opening for harvesting food, which reduces foraging efficiency (Hylander, 2013). For a species as large as the proboscis monkey (male weight: >20 kg) whose primary diet consists of fibrous leaves that require approximately 40 h of mean retention duration, this foraging cost may be harmful to survival (Matsuda et al., 2009a; Matsuda et al., 2015). As a result, the interaction between sexual and natural selection has led to the unusual evolution of a trade-off between morphological traits in the proboscis monkey. To expand our research to assess how proboscis monkeys perceive enlarged noses, and to determine how an enlarged male nose contributes ecologically to mating success in the social systems of the proboscis monkeys in the future, we propose a scenario where various factors, such as

morphology, communication, and specific social system interact to accelerate sexual dimorphism (Figure 2).

3. PERSPECTIVES ON FIELD PRIMATOLOGY IN JAPAN

Hypothesis-testing research is common in many fields, including primatology. However, to be honest, when I started my research on the proboscis monkey, I was devoted to their observation without having a specific hypothesis. The field-discovery style of research, in which one challenges an unknown research subject, used to be the forte of Japanese primatologists; however, it has become less common and tends to be discouraged. But the field-discovery method does not rule out the possibility of hypotheses. While observing animals in the field, various hypotheses about their behavior spring up, and to confirm them, we would excitedly observe the animals again and specifically record the behaviors related to the hypothesis. One research strategy is to go into the field with a well-developed hypothesis, but I believe that the unexpected discoveries and findings made in the field are the most fascinating aspects of field research.

My interest in tropical environments and my curiosity about the unknown species that inhabit them were the driving forces that prompted me to engage in the study of proboscis monkeys while still a student. One of the great advantages of field research is that it can be done simply with binoculars, a notebook and pen, and the courage to dive into an unfamiliar world. Despite the difficulty for inexperienced students to find research sites on their own, there is more to gain from it than just the research outcomes. Conducting research in a foreign nation necessitates interaction with and assistance from a diverse

group of people who speak a variety of languages and have a variety of cultural backgrounds. Through my field research on proboscis monkey, I have developed collaborative research on diverse topics and met various researchers from around the world. My field studies have given me the opportunity to form valuable relationships that have enriched my life.

Despite receiving the honor of the Miyadi Award from the Ecological Society of Japan in 2016, I am ashamed that I did not write this award-winning paper until now. The reason for writing this article 6 years later is that I was shocked by the reorganization and dismantling of the Primate Research Institute at Kyoto University. The inappropriate use of a huge amount of research funds by a group of faculty members in the Language and Intelligence Section (Gibbons, 2020) led to the abolition of not only that section but also the sections investigating ecology and social systems, which had absolutely nothing to do with the misuse of funds. Following the institute's closure, a new center has started to conduct multidisciplinary research and educational activities to better understand the evolutionary origins of human behaviors, with a focus on body and brain structures, molecular functions, brain functions, and cognitive abilities. Japanese field primatologists need to seriously reconsider the notion that field-based primate ecology and social research were not important in the study of human evolution.

Now is the time for Japanese field primatologists to highlight “breakthroughs” to overcome this critical situation. For example, one breakthrough could be the fusion of field primatology, which reveals primate ecology and society through steady observation, with new engineering technologies such as drones, sensor tags, and genome analysis.

ACKNOWLEDGMENTS

I can continue my research in this way even at present because of the help extended by many people. I can only write the names of a few of them because if I were to thank all of them by name, it would be more than the main text. I would not have had the successes of my research without my good friends and mentors, A. Nishimura, K. Izawa, S. Higashi, G. Hanya, H. Koda, M. Yayota, S. Seino, A. Tuuga, H. Bernard, J. Sha, B. Goossens, L. Isabelle, B. Md-Zain, C. van Schaik, and J. Hummel. I also thank C. Chapman and M. Clauss, in particular, for their comments on this manuscript. It is with the support of the Sabah Wildlife Department, Sabah Forestry Department, and Universiti Malaysia Sabah that field research can be carried out. Furthermore, I would like to express my gratitude to the local research assistants, Asnih, Rudy, Ahmad, Udin, and others who helped my small project to continue till date.

I would like to thank my wife, Yuko, and our children, Niko, Miko, Jo, and Koko, for their encouragement and support, not only in my research but also in my life.

CONFLICT OF INTEREST

The author declares that there is no conflict of interest.

ORCID

Ikki Matsuda  <https://orcid.org/0000-0002-0861-7801>

REFERENCES

- Balch, C. C. (1955). Sleep in ruminants. *Nature*, *175*, 940–941. <https://doi.org/10.1038/175940a0>
- Bennett, E. L., & Sebastian, A. C. (1988). Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest in Sarawak. *International Journal of Primatology*, *9*, 233–255. <https://doi.org/10.1007/bf02737402>
- Boonratana, R. (2000). Ranging behavior of proboscis monkeys (*Nasalis larvatus*) in the lower Kinabatangan, Northern Borneo. *International Journal of Primatology*, *21*, 497–518. <https://doi.org/10.1023/a:1005496004129>
- Dunbar, R. I. M., & Bose, U. (1991). Adaptation to grass-eating in gelada baboons. *Primates*, *32*, 1–7. <https://doi.org/10.1007/bf02381596>
- Fritz, J., Hummel, J., Kienzle, E., Arnold, C., Nunn, C., & Clauss, M. (2009). Comparative chewing efficiency in mammalian herbivores. *Oikos*, *118*, 1623–1632. <https://doi.org/10.1111/j.1600-0706.2009.17807.x>
- Gibbons, A. (2020). Famed primatologist fired for mismanagement of funds for chimp habitat. *Science*. <https://doi.org/10.1126/science.abf9637>
- Grueter, C. C. (2022). Causes and consequences of the formation of multilevel societies in colobines. In I. Matsuda, C. C. Grueter, & J. A. Teichroeb (Eds.), *The Colobines: Natural history, behaviour and ecological diversity* (pp. 293–311). Cambridge University Press.
- Grueter, C. C., Erb, W. M., Ulibarri, L. R., & Matsuda, I. (2022). Ecology and behaviour of odd-nosed colobines. In I. Matsuda, C. C. Grueter, & J. A. Teichroeb (Eds.), *The Colobines: Natural history, behaviour and ecological diversity* (pp. 156–185). Cambridge University Press.
- Grueter, C. C., Matsuda, I., Zhang, P., & Zinner, D. (2012). Multilevel societies in primates and other mammals: Introduction to the special issue. *International Journal of Primatology*, *33*, 993–1001. <https://doi.org/10.1007/s10764-012-9614-3>
- Hayakawa, T., Nathan, S., Stark, D. J., Saldívar, 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. <https://doi.org/10.1111/1758-2229.12677>
- Hoshino, S., Seino, S., Funahashi, T., Hoshino, T., Clauss, M., Matsuda, I., & Yayota, M. (2021). Apparent diet digestibility of captive colobines in relation to stomach types with special reference to fibre digestion. *PLoS One*, *16*, e0256548. <https://doi.org/10.1371/journal.pone.0256548>
- Hylander, W. L. (2013). Functional links between canine height and jaw gape in catarrhines with special reference to early

- hominins. *American Journal of Physical Anthropology*, 150, 247–259. <https://doi.org/10.1002/ajpa.22195>
- Kappeler PM, Watts DP (2012) Long-term field studies of primates.
- Koda, H., Murai, T., Tuuga, A., Goossens, B., Nathan, S., Stark, D. J., Ramirez, D. A. R., Sha, J. C. M., Osman, I., Sipangkui, R., Seino, S., & Matsuda, I. (2018). Nasalization by *Nasalis larvatus*: Larger noses audiovisually advertise conspecifics in proboscis monkeys. *Science Advances*, 4, eaaq0250. <https://doi.org/10.1126/sciadv.aaq0250>
- Matsuda, I., Chapman, C. A., & Clauss, M. (2019). Colobine forest-mach anatomy and diet. *Journal of Morphology*, 280, 1608–1616. <https://doi.org/10.1002/jmor.21052>
- Matsuda, I., Chapman, C. A., Shi Physilia, C. Y., Mun Sha, J. C., & Clauss, M. (2017). Primate resting postures: Constraints by foregut fermentation? *Physiological and Biochemical Zoology*, 90, 383–391. <https://doi.org/10.1086/691360>
- Matsuda, I., & Clauss, M. (2022). Morphology and physiology of colobine digestive tracts. In I. Matsuda, C. C. Grueter, & J. A. Teichroeb (Eds.), *The Colobines: Natural history, behaviour and ecological diversity* (pp. 64–77). Cambridge University Press.
- Matsuda, I., Espinosa-Gómez, F. C., Ortmann, S., Sha, J. C. M., Osman, I., Nijboer, J., Schwarm, A., Ikeda, T., & Clauss, M. (2019). Retention marker excretion suggests incomplete digesta mixing across the order primates. *Physiology & Behavior*, 208, 112558. <https://doi.org/10.1016/j.physbeh.2019.112558>
- Matsuda, I., Kubo, T., Tuuga, A., & Higashi, S. (2010). 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. <https://doi.org/10.1002/ajpa.21218>
- Matsuda, I., Murai, T., Clauss, M., Yamada, T., Tuuga, A., Bernard, H., & Higashi, S. (2011). Regurgitation and remastication in the foregut-fermenting proboscis monkey (*Nasalis larvatus*). *Biology Letters*, 7, 786–789. <https://doi.org/10.1098/rsbl.2011.0197>
- Matsuda, I., Sha, J. C., Ortmann, S., Schwarm, A., Grandl, F., Caton, J., Jens, W., Kreuzer, M., Marlana, D., Hagen, K. B., & Clauss, M. (2015). Excretion patterns of solute and different-sized particle passage markers in foregut-fermenting proboscis monkey (*Nasalis larvatus*) do not indicate an adaptation for rumination. *Physiology & Behavior*, 149, 45–52. <https://doi.org/10.1016/j.physbeh.2015.05.020>
- Matsuda, I., Stark, D. J., Saldivar, D. A. R., Tuuga, A., Nathan, S. K. S. S., Goossens, B., van Schaik, C. P., & Koda, H. (2020). Large male proboscis monkeys have larger noses but smaller canines. *Communications Biology*, 3, 522. <https://doi.org/10.1038/s42003-020-01245-0>
- Matsuda, I., Takano, T., Shintaku, Y., & Clauss, M. (2022). Gastrointestinal morphology and ontogeny of foregut-fermenting primates. *American Journal of Biological Anthropology*, 177, 735–747. <https://doi.org/10.1002/ajpa.24476>
- 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. <https://doi.org/10.1002/ajp.20604>
- Matsuda, I., Tuuga, A., Bernard, H., & Furuichi, T. (2012). Inter-individual relationships in proboscis monkeys: A preliminary comparison with other non-human primates. *Primates*, 53, 13–23. <https://doi.org/10.1007/s10329-011-0259-1>
- 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. <https://doi.org/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. <https://doi.org/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. <https://doi.org/10.1007/s10764-009-9344-3>
- Matsuda, I., Tuuga, A., & Higashi, S. (2010). 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. <https://doi.org/10.1007/s11284-009-0677-3>
- Milton, K. (1986). Digestive physiology in primates. *Physiology*, 1, 76–79.
- Mitani, J. C., Watts, D. P., & Amstler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, 20, R507–R508. <https://doi.org/10.1016/j.cub.2010.04.021>
- Müller, D. W., Caton, J., Codron, D., Schwarm, A., Lentle, R., Streich, W. J., Hummel, J., & Clauss, M. (2011). Phylogenetic constraints on digesta separation: Variation in fluid throughput in the digestive tract in mammalian herbivores. *Comparative Biochemistry and Physiology Part A, Molecular & Integrative Physiology*, 160, 207–220. <https://doi.org/10.1016/j.cbpa.2011.06.004>
- Murai, T. (2004). *Social structure and mating behavior of proboscis monkey Nasalis larvatus (Primates; Colobinae)* (p. 40). Graduate School of Environmental Earth Science, Hokkaido University.
- Murai, T., Mohamed, M., Bernard, H., Mahedi, P. A., Saburi, R., & Higashi, S. (2007). Female transfer between one-male groups of proboscis monkey (*Nasalis larvatus*). *Primates*, 48, 117–121. <https://doi.org/10.1007/s10329-006-0005-2>
- Nakagawa, N., Nakamichi, M., & Sugiura, H. (2010). *The Japanese Macaques*. Springer Japan.
- Nakamura, M. (2009). Interaction studies in Japanese primatology: Their scope, uniqueness, and the future. *Primates*, 50, 142–152. <https://doi.org/10.1007/s10329-009-0133-6>
- Yeager, C. P. (1989). Feeding ecology of the proboscis monkey (*Nasalis larvatus*). *International Journal of Primatology*, 10, 497–530. <https://doi.org/10.1007/bf02739363>
- Yeager, C. P. (1990). Proboscis monkey (*Nasalis larvatus*) social organization: Group structure. *American Journal of Primatology*, 20, 95–106. <https://doi.org/10.1002/ajp.1350200204>
- Yeager, C. P. (1991). Proboscis monkey (*Nasalis larvatus*) social organization: Intergroup patterns of association. *American Journal of Primatology*, 23, 73–86. <https://doi.org/10.1002/ajp.1350230202>

How to cite this article: Matsuda, I. (2022). Following the trail of the elusive proboscis monkey in Borneo. *Ecological Research*, 37(5), 562–567. <https://doi.org/10.1111/1440-1703.12343>