

Haplotype analysis of long-tailed macaques in TNB Bukit Selambau, Peninsular Malaysia, leads to inferences of fission-fusion social structure

Siti Nur Aliah Mohd-Isa¹, Nor Amna Abu-Hassan¹, Nur Azimah Osman^{1,2}, Mohamad Khairulmunir¹, Aisah Md-Shukor³, Ayuni Samsul-Bahri³, Shukor Md-Nor¹, Kayal Vizi Karuppannan⁴, Muhammad Abu Bakar Abdul-Latiff⁵, Abd Rahman Mohd-Ridwan⁶, Badrul Munir Md-Zain^{1*}

¹Department of Biological Sciences and Biotechnology, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, 43600, Bangi, Selangor, Malaysia

²School of Biology, Faculty of Applied Sciences, Universiti Teknologi Mara (UiTM) Negeri Sembilan, Kula Pilah Campus, 72000, Kuala Pilah, Negeri Sembilan, Malaysia

³TNB Research Sdn. Bhd. No. 1, Kawasan Institusi Penyelidikan, Jln Ayer Hitam, 43000, Kajang, Selangor, Malaysia

⁴Department of Wildlife and National Parks (DWNP) KM10, Jalan Cheras, 56100, Kuala Lumpur, Malaysia

⁵Faculty of Applied Sciences and Technology, Universiti Tun Hussein Onn Malaysia (Pagoh Campus), 84000, Muar, Johor, Malaysia

⁶Centre for Pre-University Studies, Universiti Malaysia Sarawak, 94300, Kota Samarahan, Sarawak, Malaysia

*Email: abgbadd@ukm.edu.my

Received: 18 May 2023// Revised: 28 June 2023 / Accepted: 15 July 2023/ Published online: 01 Aug 2023. Ministry of Sciences, Research, and Technology, Arak University, Iran.

How to cite: Mohd-Isa S.N.A., Abu-Hassan N.A., Osman N.A., Khairulmunir M., Md-Shukor A., Samsul-Bahri A., Md-Nor S., Karuppannan K.V., Abdul-Latiff M.A.B., Mohd-Ridwan A.R., Md-Zain B.M. (2023). Haplotype analysis of long-tailed macaques in TNB Bukit Selambau, Peninsular Malaysia, leads to inferences of fission-fusion social structure, *Journal of Wildlife and Biodiversity*, 7(4), 159-170. DOI: <https://doi.org/10.5281/zenodo.8225124>

Abstract

Long-tailed macaques have been roaming near Tenaga National Berhad Bukit Selambau Solar (TBSS) causing human-macaque conflicts. This study reveals the social organization and genetic variation of these macaques. Macaques' groups were determined via direct observation and closed-circuit television. Genomic DNA from 29 fecal samples were extracted and proceeded with amplification of the D-loop region of mitochondrial DNA. There are four main groups of primates at TBSS. Some members of the Kuil group and the Pekan group shared haplotype 1, forming a fission-fusion society. This finding can be used for TNB in mitigation plans involving human-macaque conflict.

Keywords: *Macaca fascicularis*, pest, nuisance, phylogeny, Mitochondrial DNA

Introduction

A long-tailed macaque (*Macaca fascicularis*) is considered to be one of the most successful primate species because of its widespread distribution (Abegg & Thierry, 2002). In Malaysia, the long-tailed macaque is locally known as *kera* and is highly adaptable to anthropogenic environmental changes (Osman et al., 2022). It is the most prevalent macaque species in Malaysia and has a wide distribution across Peninsular Malaysia and Borneo (Md-Zain et al., 2022). Long-tailed macaques have recently been classified as endangered in the International Union for Conservation of Nature Red List (Hansen et al., 2022) due to their population declines over time. Human activities are believed to be the primary cause of this decline and subsequent species extinctions (Estrada et al., 2017).

Macaques that live near human interface may cause property damage in rural, urban, and semi-urban areas (Hambali et al., 2012, 2014). Conflict at the human–macaque interface area arises as long-tailed macaques are frequently seen intruding on TNB Bukit Selambau Solar Station (TBSS), causing much damage to TNB properties such as lamp posts and closed-circuit television (CCTV) cameras. This site can be easily accessed by macaques because it is surrounded by oil palm plantations. To determine the human–macaque conflict status, the basic ecological data of long-tailed macaques such as group size, gender, and age structure should be obtained. We also need to determine the genetic structure of the existing long-tailed macaque group to see how they are related to each other.

The noninvasive molecular approach has made significant progress in primate genetics research. DNA can be extracted from feces, hairs, feathers, skin, or saliva without the subject being captured, restrained, or even observed (Abdul-Latiff et al., 2019). The development of molecular techniques, such as polymerase chain reaction (PCR) has allowed primatologists to investigate and study primate systematic and social structure in greater depth (Md-Zain et al., 2010a). Several genes of interest have been amplified using the mitochondrial genome for species identification, phylogenetic, and population genetics studies (Abdul-Latiff et al., 2019; Md-Zain et al., 2018). This study aims to determine the social organization and genetic structure among long-tailed macaque groups in TNB Bukit Selambau Solar Station, Peninsular Malaysia. The D-loop region was selected as a locus candidate based on its suitability in the genetic analysis at the population level (Abdul-Latiff et al., 2014; Abdul-Latiff & Md-Zain, 2021; Aifat et al., 2020) and closely related taxa (Abdul-Latiff et al., 2019). The D-loop region is also known as a suitable candidate locus for studying the complex social structure in primates (Fredsted et al., 2004). Genetic information is important for operational activities and managing human–macaque conflict at

agriculture and TNB premises. The findings will lead to portraying long-tailed macaque dispersal status among available groups roaming in TBSS, which creates conflict with the TNB premise.

Materials and methods

Group surveys and genetic sampling

The study site was located at TBSS, Kedah (Figure 1). The group structure was identified via direct observation and CCTV. The observations were made from October 2021 to December 2022. Group identifications were performed by special marks on the individual's face, roaming area, and any physical disabilities. Fecal genetic sampling was conducted at the group roaming areas.

DNA extraction and amplification

Noninvasive molecular genetics methods are best for extracting DNA from biological samples (e.g., fecal, urine, and follicles) (Abdul-Latiff et al., 2017). The 29 fecal samples were collected in sterile 50 ml tubes and fixed in 99% ethanol for long-term storage. The samples were labeled and stored at -20°C . DNA was extracted from 0.5 to 1.0 g of fecal samples using the innuPREP Stool DNA Kit (Analytik Jena) following the manufacturer's protocol. The mtDNA D-loop region was chosen as a locus candidate to amplify DNA through PCR using a Mastercycler Nexus (Eppendorf North America, Inc.). The PCR amplification of the D-loop gene was conducted using one set of primers, forward 5'-ACAGTCCTAGTATTAACCTGC-3' and reverse 5'-CAAGGGGTGTTTAGTGAAGT-3' (Abdul-Latif et al., 2017). We used Red Taq Mix (Bioline) to conduct the PCR using the following steps: 95°C initial denaturation for 3 min, followed by 30 cycles of denaturation at 95°C for 1 min, 59°C annealing for 15 s, and 72°C extension for 10 min. The PCR products were examined through the electrophoresis process using 1.5% agarose gel in

1× TAE buffer. PCR products will be sent to Apical Scientific Sdn Bhd, Malaysia, for sequencing purposes.

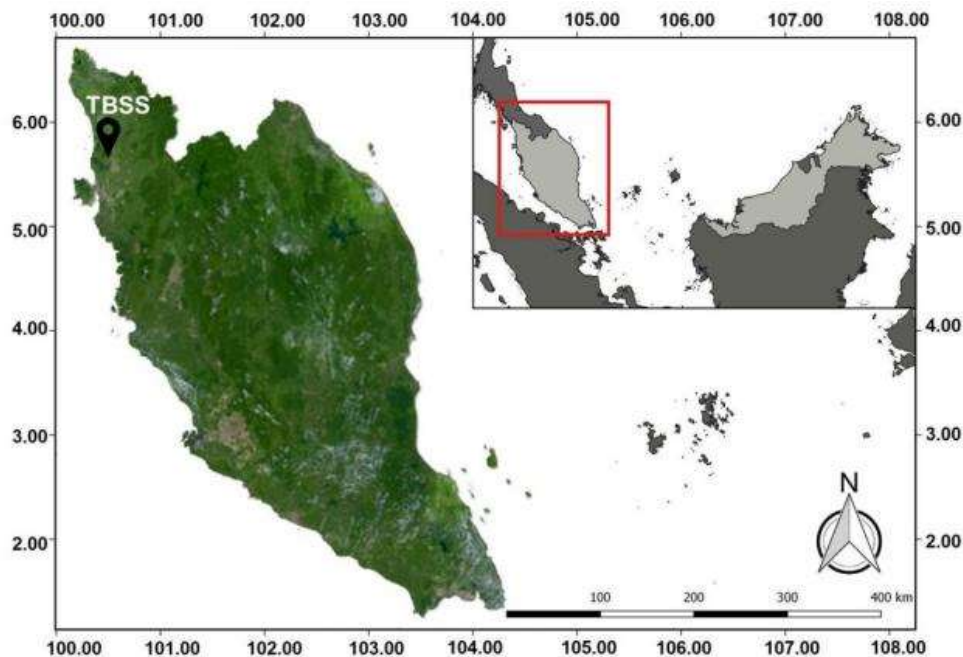


Figure 1. Map of study site of TNB Bukit Selambau Solar Station

Sequence alignment and phylogenetic analyses

Bioedit Sequence Alignment Editor was used to edit the obtained raw sequences and blasted through GenBank BLASTn for sequence similarity search analysis (Abdul-Latiff et al., 2019; Aifat et al., 2016). Additional *M. fascicularis* sequences from Abdul-Latif et al. (2014) were also used for comparison with the current samples. The *Macaca nemestrina* was employed as an outgroup for the analysis. The sequences were then aligned using MEGA7 ClustalW multiple alignments (Kumar et al., 2016). To obtain a graphical representation of the variation of the D-loop gene, the neighbor-joining (NJ) tree and minimum spanning networks (MSNs) of haplotype were constructed using the median-joining method in the Network 10.0.0 software (Fluxus Technology).

Results and discussion

Social organization

During more than 1 year study period, three groups of long-tailed macaques were observed ranging in the adjacent or within the TBSS compound. The largest number of individuals discovered by direct observation was about 100 individuals for the Suria group, 104 individuals for the Kuil group, and 84 in the Pekan group (Table 1, Figure 2). These findings showed that group members in TBSS were quite high when compared to those in previous studies (Md-Zain et al., 2010b; Zamri & Md-Zain, 2022; Zhao et al., 2021).

Gender and age groupings were successfully identified for each group in TBSS, although these aspects are challenging to measure. The adult category was found to be the highest members in TBSS (Table 1). Members of the group were classified by age primarily based on physical traits (Taufet-Rosdi & Md-Zain 2023; Zamri & Md-Zain, 2022). The male adult was found to be larger in size, with a tail that was longer and thicker. Female adults have longer nipples, and facial hair is always present. The color of the female adult body hair is gray and faded. The juvenile was noted to be slimmer, and gender can sometimes be elusive. Infants under 3 months old have naked, pale, unpigmented face skin, and a blackish dorsal pelage. Age range roughly from 1 to 4 years for juveniles, at least 5 years for male adults, and at least 4 years for female adults (Fittinghoff, 1978).

Table 1. Long-tailed macaque social organization at TNB Bukit Selambau Solar Station (TBSS)

Date	Group	Individu	Male	Female	Adult	Juvenile	Baby
18/10/2021	Kuil	7	0	0	3	1	3
13/11/2021	Pekan	44	11	2	19	21	4
15/12/2021	Kuil	~40	7	7	12	12	4
19/01/2022	Pekan	~40-50	10	7	10	7	5
28/02/2022	Kuil	54	9	8	16	17	4
17/03/2022	Suria	~100	8	9	0	6	2
13/04/2022	Pekan	~50	5	2	25	7	0
06/05/2022	Pekan	~40-50	4	3	10	4	1
2/06/2022	Kuil	~50-60	6	8	21	20	1
20/07/2022	Kuil	~80-90	3	7	49	23	6
16/08/2022	Pekan	~50-60	6	2	11	3	0
25/09/2022	Kuil	~70-80	1	9	46	18	7
20/10/2022	Pekan	~40-50	3	6	13	6	6
7/11/2022	Pekan	30	4	2	12	19	5
30/12/2022	Kuil	~80-90	9	12	5	40	3



Figure 2. Long-tailed macaque of group: 1) Kuil, 2) Pekan, 3) Suria and 4) Dusky Langur

From Oct 2021 to January 2022, the Kuil group was seen roaming in the TBSS compound, at Zone 1 Pole 1–3 and Zone 4 Pole 34–35. For the Pekan group, macaques were frequently seen at Zone 1 Pole 5–8 and Zone 2 Pole 9–11. For the Suria group, macaques were initially seen roaming at Zone 4 Pole 30–31. Three rows of oil palm were cleared on January 22–31, 2022. Instead of roaming in the TBSS area, the Kuil group was seen roaming at the temple’s area and Chinese cemetery, whereas the Pekan group was seen roaming at the junction of Taman Cempaka Indah. The members of the Suria group have shifted their roaming to the Leader Solar and Solar Pack area. After the electric fence was installed in the TBSS compound in July 2022, most of the macaques transferred to a nearby site. The Kuil group was observed spending the majority of its time at the oil palm plantation near the temple and Chinese cemetery, whereas the Pekan group relocated at the junction of Taman Cempaka Indah and was rarely seen at the local’s rubber estate. Ruppert et al. (2018) reported that pig-tailed macaques use oil palm fields near forests as a crucial part of their home range. However, for the members of the Suria group, no observation was made after March 2022 as they had wandered outside the study site. As such, macaques that dwell in or near human interface areas consumed anthropogenic foods, spend less time eating wild fruits and flowers, and have a greater home range (Sha & Hanya, 2013). According to Cheney and Seyfarth (1987), the primate group with the most females is likely to have a larger home range to reduce competition. Forested habitats were less frequently used and had larger mean total home ranges

(Mohammad & Wong, 2019). Interestingly, dusky langurs (the fourth group) were seen three times near the Chinese cemetery, overlapping with the Kuil group. The exact group members were difficult to determine as they move and disappeared quickly. The dusky langur group was estimated to have 10 individuals. They were observed interacting with long-tailed macaques by sharing space and traveling together. These mixed-species associations may have occurred for space- and food availability-related reasons, besides primate densities being high in a certain area (Md-Zain et al., 2021).

Genetic structure

A total of 29 genetic samples of *M. fascicularis* were successfully amplified to generate DNA sequences of the D-loop region. Out of the total sample, 28 haplotypes were produced. The MSN tree was developed based on the haplotype information gathered to represent the relationships among three macaque groups in TBSS compared with previous data of Abdul-Latiff et al. (2014). The results showed that unique haplotypes of TBSS long-tailed macaques have been discovered that distinguish them from other states in Peninsular Malaysia (Figure 3, Table 2). The haplotype distribution pattern based on MSN analysis was consistent with NJ phylogenetic tree topology (NJ is not shown).

Many members of the Kuil group and the Pekan group shared haplotype 1, implying that these group's members were genetically related. This was not surprising considering that some macaque species have a fission–fusion social structure that allows individuals to switch groups (Ménard & Vallet, 1993). The possibility of genetic exchange between the Kuil group and the Pekan group has arisen in November 2022, when the clearing of oil palm plantations have been taken place that involve both groups roaming areas. Their respective roaming areas were close to one another and thus will potentially overlap in future roaming areas. The Suria group did not share haplotype with the Kuil and Pekan groups, as the roaming area between these groups is nearly 2 km, except for one individual. Thus, there is little probability of gene flow occurring as its roaming areas did not coincide with those of the nearby groups. A comparison of two populations of fat-tailed dwarf lemur (*Cheirogaleus medius*) living about 3 km apart revealed no evidence for spatial clustering of same-sex individuals with identical mitochondrial haplotypes within each of the two subpopulations but significant clustering between them (Kappeler, 2008).

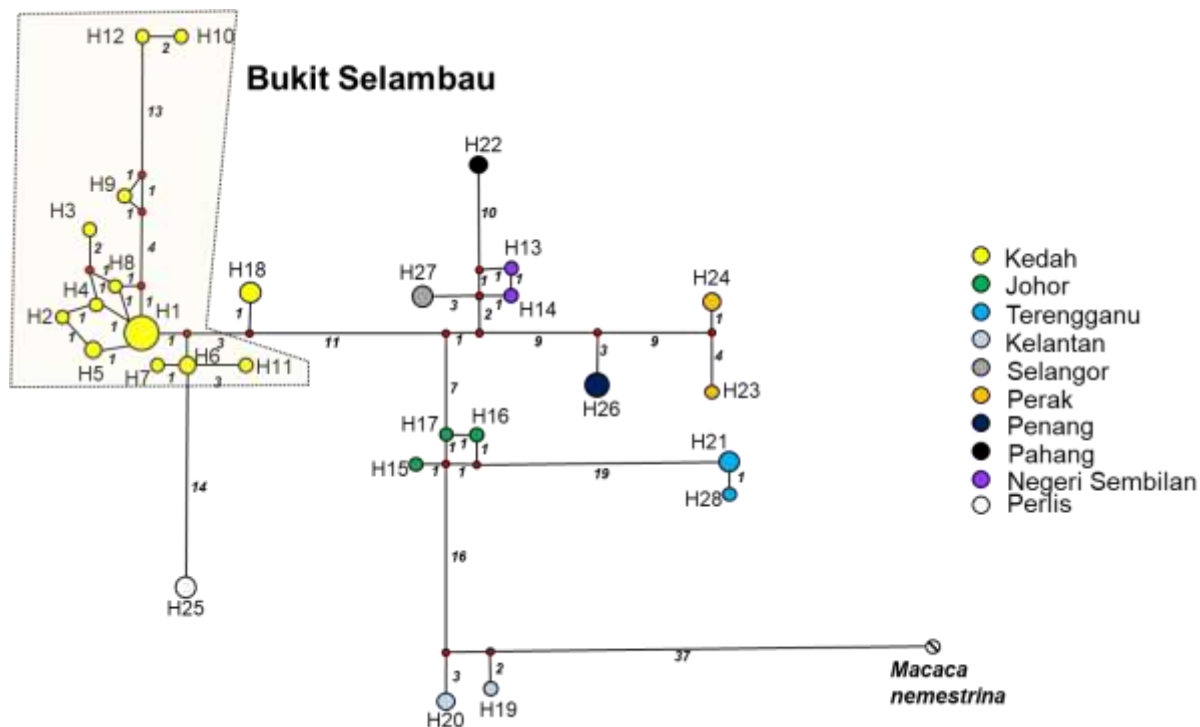


Figure 3. Minimum-spanning network (MSN) of the D-loop sequence illustrating the relationships of the long-tailed macaques, *M. fascicularis*, in 10 states. Each circle represents a haplotype, and the diameter is scaled to the haplotype frequency (Table 2)

Table 2. Distribution of long-tailed macaque mtDNA haplotypes in TBSS

Haplotype	Group and Sample Code
1	Kuil: FK821, FK824, FK825, FK808, FK819, FK811 Pekan: FK831 FK832 FK833 FK834 FK836 FK837 FK847 FK848 Suria: FK 877
2	Kuil: FK820
3	Kuil: FK822
4	Kuil: FK826
5	Kuil: FK807 Pekan FK828
6	Suria: FK857 Kuil: FK864
7	Suria: FK858
8	Kuil: FK827
9	Pekan: FK829
10	Suria: FK879
11	Suria: FK880
12	Suria: FK881

MSN tree indicated that there was no sharing of haplotype between TBSS and Abdul-Latiff et al. (2014) samples. This finding showed that long-tailed macaques of TBSS are permanent residents. There were no relocated populations of macaques from other states to TBSS areas. The Gunung Jerai is the nearest study site of Abdul-Latiff et al. (2014) samples and is situated in the same state, Kedah; hence no sharing haplotype was observed between these localities. Moreover, the network analysis revealed a closer spatial connection between these groups in Peninsular Malaysia. The Bukit Selambau population was found to be more strongly connected to those in the northern populations as there were fewer mutational steps between the populations compared to other Malay Peninsular populations.

As this study has been conducted for more than 1 year, the three TBSS long-tailed macaque groups were found to be sensitive to human presence. These macaques were also regarded as being just partially habituated since they would escape when they encountered humans. Since long-tailed macaques spend most of their daily hours traveling from one site to another in search of food sources, macaques may have not entirely adapted to human presence (Mohammad & Wong, 2019). As TNB management is planning to enlarge the solar panel area, this would also have an impact on TBSS's long-tailed macaque social organization and genetic structure in the future.

Conclusion

There are four groups of primates detected consisting of three groups of macaques and one group of mixed dusky langur and long-tailed macaques. The total number of long-tailed macaques detected in TBSS was approximately 200–300. The Kuil group was frequently observed to roam in the temple's area, whereas the Pekan group was at the junction of Taman Cempaka Indah; the Suria group was at the edge of the TBSS zone 4 area. Adult long-tailed macaques are still the dominant age structure followed by juveniles and infants. Haplotype analysis indicated that there was a genetic exchange between individuals of the Pekan group and the Kuil group, whereas there was no genetic exchange between the Suria and Pekan/Kuil groups. These fundamental data are vital for TNB as these can be applied to mitigation planning that involves human–macaque conflicts. Future studies should be conducted on the behavioral ecology aspect to determine specific human–macaque conflicts. It is also interesting to know the dietary diversity of TBSS long-tailed macaques as revealed by DNA metabarcoding of the next-generation sequencing approach.

Acknowledgments

We thank the Department of Wildlife and National Park (DWNP) Peninsular Malaysia especially YBhg. Dato' Abdul Kadir bin Abu Hashim, Director General of the DWNP for providing research permit: JPHL&TN(IP):100- 34/1.24Jld16(14). The authors are deeply indebted to Universiti Kebangsaan Malaysia, TNB Research Sdn. Bhd., TNB Bukit Selambau Second Large-Scale Solar (LSS) Plant for providing necessary facilities and assistance during field observation especially Muhammad Nazry Chik, Mohd Fadzli Hamidon, Haliff Anas Anuar, Muhammad Aizat, Muhamad Nornasriq Hakimi, Syafiq Syarqawi, Mohd Hanif, and Mohd Aqil Anwar. The authors appreciate the supports from TNB Research Sdn. Bhd., for funding the present work through the Grant ST-2021-017 registered at Universiti Kebangsaan Malaysia.

References

- Abdul-Latiff, M. A. B., Ruslin, F., Faiq, H., Hairul, M. S., Rovie-Ryan, J. J., Abdul-Patah, P., Yaakop, S., & Md-Zain, B. M. (2014). Continental monophyly and molecular divergence of Peninsular Malaysia's *Macaca fascicularis fascicularis*. *BioMed Research International*, 2014, 897682. <https://doi.org/10.1155/2014/897682>
- Abdul-Latiff, M. A. B., Aifat, N. R., Yaakop, S., & Md-Zain, B. M. (2017). A noninvasive molecular approach: Exploiting species-locus-specific PCR primers in defeating numts and DNA cross-contamination of Cercopithecidae. *Journal of Animal and Plant Sciences*, 27(3), 1015-1023.
- Abdul-Latiff, M. A. B., Baharuddin, H., Abdul-Patah, P., & Md-Zain, B. M. (2019). Is Malaysia's banded langur, *Presbytis femoralis femoralis*, actually *Presbytis neglectus neglectus*? Taxonomic revision with new insights on the radiation history of the *Presbytis* species group in Southeast Asia. *Primates*, 60(3), 63-79. <https://doi.org/10.1007/s10329-018-0699-y>
- Abdul-Latiff, M. A. B., & Md-Zain, B. M. (2021). Taxonomy, evolutionary and dispersal events of pig-tailed macaque, *Macaca nemestrina* (Linnaeus,1766) in Southeast Asia with description of a new subspecies, *Macaca nemestrina perakensis* in Malaysia. *Zoological Studies*, 60(50), 1-23. <https://doi.org/10.6620/ZS.2021.60-50>
- Abegg, C., & Thierry, B. (2002). Macaque evolution and dispersal in insular south-east Asia. *Biological Journal of the Linnean Society*, 75(4), 555-576. <https://doi.org/10.1046/j.1095-8312.2002.00045.x>
- Aifat, N. R., Abdul-Latiff, M. A. B., Roos, C., & Md-Zain, B. M. (2020). Taxonomic revision and evolutionary phylogeography of dusky langur (*Trachypithecus obscurus*) in Peninsular Malaysia. *Zoological Studies*, 59, 64. <https://doi.org/10.6620/ZS.2020.59-64>
- Aifat, N. R., Yaakop, S., & Md-Zain, B. M. (2016). Optimization of partial Cyt *b* gene sequence from selected ancient *Presbytis* museum skin specimens. *Malaysian Applied Biology*, 45(1), 93-96.
- Cheney, D. L., & Seyfarth, R. M. (1987). The influence of intergroup competition on the survival and reproduction of female vervet monkeys. *Behavioral Ecology and Sociobiology*, 21(6), 375-386. <https://doi.org/10.1007/BF00299932>
- Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di-Fiore, A., Nekar, K. A. I., Nijman, V., Heymann, E. W., Lambert, J. E., & Rovero, F. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, 3(1), e1600946. <https://doi.org/10.1126/sciadv.1600946>
- Fittinghoff, N. A. Jr. (1979). *Macaca fascicularis of Eastern Borneo: Ecology, demography, social behavior, and social organization in relation to a refuging habitus* [Doctoral dissertation, University of California, Davis]. Hathi Trust Digital Library. <https://babel.hathitrust.org/cgi/pt?id=uc1.x14110&view=1up&seq=2>
- Fredsted, T., Pertoldi, C., Olesen, J. M., Eberle, M., & Rappeler, P. M. (2004). Microgeographic heterogeneity in spatial distribution and mtDNA variability of gray mouse lemurs (*Microcebus*

- murinus*, Primates: Cheirogaleidae). *Behavioral Ecology and Sociobiology*, 56(4), 393-403. <https://doi.org/10.1007/s00265-004-0790-9>
- Hambali, K., Ismail, A., Zulkifli, S. Z., Md-Zain, B. M., & Amir, A. (2012). Human-macaque conflict and pest behaviour of long-tailed macaques (*Macaca fascicularis*) in Kuala Selangor Nature Park. *Tropical Natural History*, 12(4), 189-205.
- Hambali, K., Ismail, A., Md-Zain, B. M., Zulkifli, S., & Amir, A. (2014). Ranging behavior of long-tailed macaques (*Macaca fascicularis*) at the entrance of Kuala Selangor Nature Park. *Malaysian Applied Biology*, 43(2), 129-142. <http://dx.doi.org/10.7593/abm/3.2.58>
- Hansen, M. F., Ang, A., Trinh, T. T. H., Sy, E., Paramasivam, S., Ahmed, T., Dimalibot, J., Jones-Engel, L., Ruppert, N., Griffioen, C., Lwin, N., Phiapalath, P., Gray, R., Kite, S., Doak, N., Nijman, V., Fuentes, A., & Gumert, M. D. (2022). *Macaca fascicularis* (amended version of 2022 assessment). The IUCN Red List of Threatened Species 2022. <https://dx.doi.org/10.2305/IUCN.UK.2022-2.RLTS.T12551A221666136>
- Kappeler, P.M. (2008). Genetic and ecological determinants of primate social systems. In J. Korb, & J. Heinze (Eds.), *Ecology of social evolution*. (pp. 225-243). Springer. https://doi.org/10.1007/978-3-540-75957-7_11
- Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis (version 7.0) for bigger datasets. *Molecular Biology and Evolution*, 33(7), 1870-1874. <https://doi.org/10.1093/molbev/msw054>
- Md-Zain, B. M., Abdul-Latiff, M. A. B., Mohd-Ridwan, A. R., & Najmuddin, M. F. (2022). *Primat Semenanjung Malaysia*. Jabatan Perhilitan Semenanjung Malaysia.
- Md-Zain, B. M., Lee, S. J., Lakim, M., Ampeng, A., & Mahani, M. C. (2010a). Phylogenetic position of *Tarsius bancanus* based on partial Cytochrome b DNA sequences. *Journal of Biological Sciences*, 10(4), 348-354. <https://doi.org/10.4238/vol9-4gmr942>
- Md-Zain, B. M., Sha'ari, N. A., Mohd-Zaki, M., Ruslin, F., Idris, N. I., Kadderi, M. D., & Idris, W. M.R. (2010b). A comprehensive population survey and daily activity budget on long-tailed macaques of Universiti Kebangsaan Malaysia. *Journal of Biological Sciences*, 10(7), 608-615. <https://doi.org/10.3923/jbs.2010.608.615>
- Md-Zain, B. M., Abid-Kamal, S. N. A., Aifat, N. R., Abdul-Latiff, M. A. B., Mohd-Hashim, A., Ampeng, A., Yaakop, S., & Samat, A. (2018). Molecular identification of shark fins in Malaysian Borneo's local markets. *Biodiversitas*, 19(3), 1035-1043. <https://doi.org/10.13057/biodiv/d190336>
- Md-Zain, B. M., Mohd-Ridwan, A. R., Muhd-Sahimi, H. N., Abdul-Latiff, M. A. B., & Chan, E. (2021). Mixed-species association among Malaysian primates during the COVID-19 outbreak in Genting Highlands, Peninsular Malaysia. *Journal of Sustainability Science and Management*, 16(1), 1-10. <https://doi.org/10.46754/jssm.2021.01.001>
- Ménard, N., & Vallet, D. (1993). Dynamics of fission in a wild Barbary macaque group (*Macaca sylvanus*). *International Journal of Primatology*, 14(3), 479-500. <https://doi.org/10.1007/BF02192778>
- Mohammad, M., & Wong, A. (2019). The daily activity budgets of long-tailed macaque (*Macaca fascicularis*) at Padang Teratak Wildlife Sanctuary, Beaufort, Sabah, Malaysia. *Journal of Tropical Biology and Conservation*, 16, 165-183 <https://doi.org/10.51200/jtbc.v16i0.2037>
- Osman, N. A., Abdul-Latiff, M. A. B., Mohd-Ridwan, A. R., Yaakop, S., Karuppanan, K. V., & Md-Zain, B. M. (2022). Metabarcoding data analysis revealed the plant dietary variation of long-tailed macaque *Macaca fascicularis* (Cercopithecidae, Cercopithecinae) living in disturbed habitats in Peninsular Malaysia. *Biodiversity Data Journal*, 10(3), e89617. <https://doi.org/10.3897/BDJ.10.e89617>
- Ruppert, N., Holzner, A., See, K. W., Gisbrecht, A., & Beck, A. (2018). Activity budgets and habitat use of wild Southern pig-tailed macaques (*Macaca nemestrina*) in oil palm plantation and forest. *International Journal of Primatology*, 39(2), 237-251. <https://doi.org/10.1007/s10764-018-0032-z>
- Sha, J. C. M., & Hanya, G. (2013). Diet, activity, habitat use, and ranging of two neighboring groups of food-enhanced long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, 75(6), 581-592. <https://doi.org/10.1002/ajp.22137>
- Taufet-Rosdi N. E. A., & Md-Zain B. M. (2023). Human-long-tailed macaque interactions and ecotourism potential in the Gunung Keriang Recreational Park, Kedah, Peninsular Malaysia. *Journal of Animal and Plant Sciences* 33(4), 1021-1033. <https://doi.org/10.36899/JAPS.2023.4.0695>
- Zamri, M., & Md-Zain, B. M. (2022). Long-tailed macaques of the Batu Caves, Peninsular Malaysia: population estimate, nuisance behaviours, and human perception. *Journal of Animal and Plant*

Sciences, 32(4), 1150-1158. <http://doi.org/10.36899/JAPS.2022.4.0520>

Zhao, Y. Y., Matsuda, I., Wong, A., & Bernard, H. (2021). The distribution and abundance of long-tailed macaques in the main campus of Universiti Malaysia Sabah and its vicinity. *Journal of Tropical Biology and Conservation*, 18, 185-202. <https://doi.org/10.51200/jtbc.v18i.3453>