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The Conservation Biology of the Sulawesi Crested Black Macaque *Macaca nigra* (Primates: Cercopithecidae): A Review of Current Knowledge and Future Research Priorities

RANDI SYAFUTRA[1,2,3]*

[1]*Doctoral Study Program of Natural Resources and Environmental Management Science, Graduate School, IPB University, Bogor 16143, West Java, Indonesia*
[2]*TERRA Indonesia, Pangkalpinang 33684, Bangka Belitung Islands, Indonesia*
[3]*Department of Natural Resources Conservation, Faculty of Engineering and Science, Universitas Muhammadiyah Bangka Belitung, Pangkalpinang 33134, Bangka Belitung Islands, Indonesia*
**Corresponding Author. Email: randi.syafutra@unmuhbabel.ac.id; https://orcid.org/0000-0001-8156-0613*

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Abstract
The endemic Sulawesi Crested Black Macaque *Macaca nigra* Desmarest, 1822 is restricted to northeastern Indonesia and is classified as Critically Endangered (CR) due to habitat fragmentation, agricultural expansion, and bushmeat hunting. This review synthesizes recent literature on the species' genetics, ecology, health, and conservation through a structured search of major academic databases. The evidence indicates that *M. nigra* is an adaptable frugivore capable of adjusting its diet and activity patterns in response to habitat disturbance and climatic variation, although these behavioral shifts may incur ecological and physiological costs. The review also incorporates findings from introduced populations in the North Moluccas and ex situ conservation programs, providing a broader perspective on the species' conservation status. Recent surveys suggest population stabilization in well-protected areas, likely supported by long-term research and community engagement, while introduced populations may serve as valuable genetic reservoirs. Continued conservation will require multidisciplinary research, effective law enforcement, and community-based education to reduce human–wildlife conflict. Key research priorities include the genetic viability of introduced populations, the consequences of dietary plasticity, zoonotic disease dynamics, climate change impacts, and the long-term success of translocation programs.

Keywords: Critically Endangered, endemic, *Macaca nigra*, primate conservation, research priorities.

Introduction

The Indonesian archipelago, specifically the Wallacea transition zone, functions as a center of biodiversity and species endemism (Riley 2010; Kementerian PPN 2025). Separated from the Sunda Shelf to the west and the Sahul Shelf to the east, the island of Sulawesi hosts an adaptive radiation of the primate genus *Macaca* (Groves 2005; Setiawan *et al.* 2023, 2024). Of the extant macaque species worldwide, seven are endemic to Sulawesi and its adjacent satellite islands, representing an evolutionary divergence in morphology, behavioral ecology, and social organization (Duboscq & Micheletta 2023; Atmoko *et al.* 2024; Syafutra 2024).

Among these endemic primates, the Sulawesi Crested Black Macaque *Macaca nigra* Desmarest, 1822 occupies a defined ecological niche in the northeastern region (Lee *et al.* 2020). Distinguished anatomically by its black pelage, pronounced cranial crest, pink ischial callosities, and a short tail measuring approximately 20 millimeters, the species exhibits sexual dimorphism and physiological adaptations suited to equatorial rainforests (Beausejour *et al.* 2021). Historically, *M. nigra* populations were distributed across the northeastern tip of Sulawesi, living in environments characterized by dense forests, year-round fruiting, and the absence of large apex predators (O'Brien & Kinnaird 1997).

Modern anthropogenic pressures, primarily driven by habitat fragmentation, illegal logging, and a culturally entrenched bushmeat trade, have led to a documented demographic decline (Lee 1999). Demographic projections and historical survey comparisons indicate that the wild population has declined by more than 80% over the last three generations, a span of approximately 33 years. This decline prompted the International Union for Conservation of Nature (IUCN) to formally classify the species as Critically Endangered (CR) under criterion A2cd, version 3.1 (Lee *et al.* 2020).

Understanding the biological and ecological mechanisms that govern this species is essential for effective management. While previous reviews have outlined general conservation needs, significant recent advances in genomic sequencing, climate-related phenological monitoring, and physiological health assessments warrant an updated synthesis. Therefore, a new review is needed to integrate these emerging disciplines with traditional ecological data. The specific objective of this review is to synthesize existing literature across these disciplines, construct a comprehensive biological profile of the species, and explicitly identify current research gaps to guide future conservation efforts.

Methods

This study employs a narrative review methodology to synthesize contemporary scientific literature regarding the conservation biology of *M. nigra*. To ensure a comprehensive review, a structured literature search was conducted across multiple academic databases, including Google Scholar, Scopus, Web of Science, and PubMed. The literature search utilized the following Boolean search string to retrieve relevant articles: ("Macaca nigra" OR "Sulawesi crested black macaque") AND (conservation OR genetics OR ecology OR physiology OR "human and wildlife conflict").

The inclusion criteria prioritized peer-reviewed research articles, long-term field studies, government conservation reports, and physiological assessments published primarily within the last two decades, to capture the most relevant and updated data. Studies focusing solely on unrelated macaque species or lacking direct relevance to the conservation biology of *M. nigra* were excluded. Based on these criteria, the literature selection process yielded a diverse array of sources, encompassing genomic analyses, behavioral observations, disease ecology studies, and conservation policy documents. Table 1 summarizes the primary review material integrated into this study, categorizing the literature by thematic area, study focus, publication year, and reference.

Table 1. Summary of the synthesized review material.

Thematic area	Key findings	Reference
Evolutionary genetics	Genetic bottlenecks and species-specific markers	Yan *et al.* 2025
Translocated populations	Introduced genetic reservoirs in the North Moluccas	Neugebauer *et al.* 2025
Foraging ecology	Dietary plasticity in primary vs degraded habitats	Katili & Saroyo 2011
Ranging behavior	Impacts of climate variation on travel distances	Joly *et al.* 2023
Population demographics	Longitudinal density trends in protected core areas	Kyes *et al.* 2013
Animal welfare	Ex situ activity budgets and allogrooming behavior	Octavia *et al.* 2017
Physiological health	Amyloidosis and zoonotic gastrointestinal parasites	Chong *et al.* 2022
Human and Wildlife Conflict	Ecotourism impacts on physiological stress markers	Bertrand *et al.* 2023
Conservation interventions	Efficacy of integrated formal school curricula	Chanvin *et al.* 2023

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Results and Discussion

Evolutionary genetics and translocated populations

The evolutionary trajectory of the Sulawesi macaques models speciation and introgressive gene flow. Whole-genome sequencing and Pairwise Sequentially Markovian Coalescent (PSMC) models reveal that macaque lineages underwent a genetic bottleneck approximately 5 million years ago. This period coincided with climatic shifts and fluctuating sea levels that facilitated the initial colonization of the Sulawesi landmass. Following this bottleneck event, the ancestral populations underwent allopatric and parapatric speciation. Despite displaying variability in body morphology and coat color, the overall genetic variation among the modern Sulawesi macaque species remains relatively low. Advanced exome sequencing of these populations has successfully identified approximately 550 divergent genes across pairwise species comparisons. Specifically, the Tyrosinase gene, which controls the rate-limiting step in melanin biosynthesis, exhibits marked genetic variation between *M. nigra* and neighboring species. Missense mutations in this gene have been directly linked to the phenotypic expression of the species' unique dark coat colors. These genetic divergences act as local environmental adaptations and provide hundreds of fixed single-nucleotide polymorphisms that function as species-specific genetic markers for monitoring populations at risk of hybridization (Yan *et al.* 2025).

While native populations in North Sulawesi face documented declines, a geographically isolated population of *M. nigra* inhabits the North Moluccas archipelago. Ethnohistorical surveys and genomic evaluations have confirmed that this is an introduced, human-mediated population. Recent comprehensive interviews and historical tracing indicate that the macaques have likely inhabited the North Moluccas for approximately 500 years. The distribution extends across the islands of Bacan,

Kasiruta, and southern Halmahera, while surveys have found no evidence of their presence on neighboring Mandioli. Unburdened by the cultural hunting practices that affect native Sulawesi populations, these Moluccan macaques live in high-density forests and serve as an unintended genetic reservoir. However, the conservation implications of these findings warrant further exploration. While these populations could potentially contribute to future recovery efforts, perhaps through carefully managed reintroductions, a specific research gap exists regarding the genomic viability of this introduced population. There is a lack of longitudinal data evaluating potential inbreeding depression or the risks associated with long-term genetic isolation in this group, presenting a requirement for future genetic monitoring programs (Neugebauer *et al.* 2025).

Habitat utilization and foraging ecology

The survival of *M. nigra* is tethered to the structural complexity and phenological rhythms of its rainforest habitats. As adaptable frugivores, their foraging strategies demonstrate plasticity, modulated by the spatial distribution of resources, seasonal climatic variations, and the degree of anthropogenic habitat degradation. In intact primary rainforest ecosystems, the diet is primarily composed of ripe fruits. The diet relies heavily on the Moraceae and Anacardiaceae plant families, with keystone species such as the New Guinea walnut and various *Ficus* species dictating the daily ranging patterns of macaque troops (O'Brien & Kinnaird 1997).

A comparative analysis of two wild groups illustrates this foraging plasticity and metabolic compensation. Table 2 outlines the comparative dietary composition based on differing habitat qualities. Group Rambo I, residing in the primary forest, maintains a highly frugivorous diet, acquiring 54.4% of its nutrition from fruits and utilizing the upper canopy. In contrast, Group Rambo II, residing in degraded secondary forest and shrubland lacking large fruiting trees, shifts its foraging to lower strata and alters its dietary profile. Fruit consumption drops to 44.6%, while the consumption of invertebrates surges to 41.4%, compared to just 22.2% in the primary forest group. This dietary substitution highlights a mechanism for adaptation, as the macaques expend greater effort foraging for protein-rich insects to meet their nutritional requirements when easily accessible fruits are scarce (Katili & Saroyo 2011).

Table 2. Comparative dietary composition of *M. nigra* groups based on habitat quality (Katili & Saroyo 2011).

Dietary component	Group Rambo I (primary forest)	Group Rambo II (secondary forest)
Fruit	54.4%	44.6%
Invertebrates	22.2%	41.4%
Leaves	20%	11.9%
Fungi and other	3.4%	2.1%

While dietary plasticity is often interpreted as evidence of adaptability, such changes may also involve ecological costs. A research gap exists regarding the biological consequences of these dietary shifts. Future studies must investigate how increased energy expenditure during invertebrate foraging and reliance on lower quality food sources influence reproductive success, overall body condition, and long-term population viability in degraded habitats.

Environmental influences on ranging behavior

The temporal abundance of critical food sources is sensitive to climatic variables. Long-term phenological monitoring conducted in the Tangkoko forest between January 2012 and July 2020 has revealed trends linked to climate variation. Over this eight-year period, researchers tracking 498 individual trees observed an overall decrease in fruit abundance, concurrent with an increase in the annual mean maximum temperature. These climatic shifts influence macaques' ranging behavior. Monthly temperature has emerged as a primary predictor of home range size. As temperatures rise, macaques increase their daily travel distances, likely in pursuit of scarce resources. This expansion is pronounced in disturbed or previously burned forest areas, which lack the thermal buffering provided by an intact upper canopy. Consequently, a research gap remains regarding predictive spatial modeling in the context of climate change. Given the growing importance of climate vulnerability, future studies are needed to examine how projected regional climate change will affect habitat suitability and adaptive capacity, and whether the species can sustain these behavioral modifications over time (Joly *et al.* 2023).

Despite historical population declines across the geographic range, long-term line transect surveys conducted over 12 years at the Tangkoko Nature Reserve suggest that the population is beginning to stabilize and recover modestly in core areas. While early surveys indicated sharp declines, data show the mean population density increased from 39.8 individuals/km2 during the 1999 to 2002 period to 51.4 individuals/km2 between 2005 and 2011, eventually reaching an estimated 61.5 individuals/km2 in 2011. One primary explanation for this apparent recovery is the increasing and sustained presence of training, research, and community outreach programs within the reserve, which help reduce illegal activities such as hunting while increasing local awareness (Kyes *et al.* 2013). However, given the reliance on data from over a decade ago, there is a critical need for updated population assessments to verify if this trend of stabilization has continued in recent years.

Ex situ behavioral management and physiological health

When the ecological pressures of the wild are removed through captivity or rehabilitation, the behavioral plasticity of *M. nigra* becomes evident, with implications for ex situ conservation and animal welfare. Observations of captive individuals housed at the Schmutzer Primate Center reveal an inversion of the natural activity budget. In provisioned zoo environments, the necessity to forage is eliminated, and resting becomes the dominant daily activity. When housed in semi-wild, enriched habituation enclosures that simulate natural spatial dynamics, the macaques redirect this surplus energy into social interactions. In these environments, social behavior is the most frequent activity, accounting for 36.6% of the day, with allogrooming at 23.5%. This focus on grooming reinforces social bonds and mitigates the psychological stress of confinement. Comprehensive welfare assessments using the Five Freedoms framework indicate that when enrichment and social structures are provided, captive populations can achieve high welfare scores, underscoring the importance of behavioral management in conservation programs (Octavia *et al.* 2017).

The physiological resilience and health of *M. nigra* can also be assessed through the prevalence of internal conditions and parasitic infections. Research on habituated groups indicates a diversity of endoparasites, with 15 distinct taxa recorded, presenting a zoonotic risk given the increasing overlap with human activities. Beyond infectious diseases, captive geriatric individuals have been documented suffering from systemic and cardiac AA amyloidosis. This condition, associated with chronic inflammation, is characterized by the extracellular deposition of amyloid fibrils in organs such as the liver, spleen, and heart, which can ultimately lead to congestive heart failure in older demographics. Within this context, a specific research gap exists regarding zoonotic epidemiological dynamics. There is a requirement for longitudinal studies that quantify the bidirectional transmission rates of these gastrointestinal parasites between human settlements and macaque populations in high-conflict agricultural zones (Chong *et al.* 2022).

Conservation interventions and conflict mitigation

The narrative of *M. nigra* is tied to the modern conservation crisis. Unlike many endangered taxa, whose decline is primarily driven by habitat loss, the species' historical decline is largely due to human exploitation. The macaques are hunted and trapped to supply the illicit bushmeat markets of North Sulawesi, where their meat is prized, particularly during major religious holidays and cultural festivals. Well-developed road systems, such as the Trans Sulawesi Highway, have opened access for hunters and facilitated the transport of wild meat to local markets in Minahasa. Furthermore, international trafficking poses an additional threat, with recent confiscations revealing the active smuggling of live macaques from Indonesia to wildlife facilities and the pet trade in the Philippines. While corporate and governmental interventions detail the rehabilitation of confiscated individuals, there is limited synthesized data evaluating the long-term survival, social integration, and reproductive success of these translocated individuals after release into the wild, creating a clear research gap in assessing translocation success rates (Gomez *et al.* 2022).

Compounding this exploitation is the human-macaque conflict at the agricultural interface. As illegal logging degrades the primary forest canopy, macaques are forced to forage in human-dominated landscapes, raiding cash crops such as coconut, maize, and papaya. Spatial modeling of these conflicts reveals that high-probability conflict zones are concentrated near village borders and in areas with high ecotourism intensity. The constant presence of humans in these ecotourism zones can also impact the macaques physiologically. Studies have shown that fecal glucocorticoid metabolite levels, a proxy for acute physiological stress, increase in female macaques when large numbers of tourists are present directly within their groups (Bertrand *et al.* 2023).

Halting the decline of this species requires multidisciplinary interventions. Leading these efforts is the Selamatkan Yaki program, a comprehensive conservation initiative operating under a formalized Species Action Plan. The program approaches the crisis holistically, focusing on strict law-enforcement partnerships to dismantle smuggling networks, capacity-building for protected-area management through SMART patrols, and positive land stewardship to enhance genetic flow. Additionally, the program addresses the cultural roots of the crisis through widespread environmental pride campaigns and by collaborating directly with local religious leaders to discourage the consumption of macaque meat on moral and ecological grounds. Operating in tandem with the Tangkoko Conservation Education program is the Tangkoko Conservation Education program, which has integrated rainforest ecology into the official school curriculum of the Bitung district. Longitudinal evaluations using pre- and post-program questionnaires show that children exposed to this curriculum exhibit enhanced ecological knowledge and adjusted behavioral attitudes toward macaques (Chanvin *et al.* 2023).

The complex intersection of *M. nigra* and human society was brought to international attention through a publicized copyright dispute. In 2011, a wild *M. nigra* appropriated equipment belonging to a British wildlife photographer and captured several self-portraits. The ensuing legal battle tested the limits of intellectual property frameworks. The United States Court of Appeals ultimately dismissed the suit, confirming that animal-created works are ineligible for copyright protection because animals cannot be considered authors. However, the widespread dissemination of the images inadvertently acted as an awareness campaign, highlighting the cognitive traits and endangered status of the species, thereby funneling attention toward local preservation efforts (Guadamuz 2016).

Conclusion

Macaca nigra exhibits considerable ecological adaptability by adjusting its diet and activity patterns in response to habitat disturbance, but this plasticity is insufficient to offset ongoing threats from habitat fragmentation, bushmeat hunting, agricultural conflict, and wildlife trade, which have driven the species to a Critically Endangered status. Long-term conservation requires integrated ecological monitoring, effective law enforcement, and community-based interventions to reduce human–wildlife conflict. Future research should prioritize the genetic viability and reintroduction potential of translocated populations, the long-term effects of dietary plasticity on fitness and reproduction, climate-driven habitat suitability, zoonotic disease dynamics, and the effectiveness of translocation programs to support evidence-based conservation strategies.

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References

Atmoko, T., Kuswanda, W., Hasanah, R., Maulana, V.S., Notosoediro, P.N., Ario, A., Wijayanto, H., Artama, W.T., Farida, M.N., Gallantiswara, P.C.D., Andrian, K.N., Mariya, S., Sulistiawati, E., Putri, Z.U., Ruskhanidar, Abimanyu, T.L., Dharma, A.P., Syafutra, R., Saroyo, Papu, A., Hidayatik, N. & Wirdateti, W. 2024. *Membingkai Satwa Primata Indonesia dalam Tiga Pilar: Biologi, Konservasi, Biomedis.* Penerbit BRIN, Jakarta Pusat, 259 pp.

Bertrand, D.A., Berman, C.M., Heistermann, M., Agil, M., Sutiah, U. & Engelhardt, A. 2023. Effects of tourist and researcher presence on fecal glucocorticoid metabolite levels in wild, habituated Sulawesi crested macaques (*Macaca nigra*). *Animals* 13(18): 2842. DOI: https://doi.org/10.3390/ani13182842

Beausejour, S., Rylands, A.B. & Mittermier, R.A. 2021. *All Asian Primates*. Re:wild, Austin, 536 pp.

Chanvin, M., Lamarque, F., Diko, N., Agil, M., Micheletta, J. & Widdig, A. 2023. Ten years of positive impact of a conservation education program on children's knowledge and behaviour toward crested macaques (*Macaca nigra*) in the Greater Tangkoko Area, North Sulawesi, Indonesia. *International Journal of Primatology* 44(4): 743–763. DOI: https://doi.org/10.1007/s10764-023-00356-9

Chong, S.M., Heng, Y., Ahmad, A.A. & Hsu, C.D. 2022. Systemic and cardiac amyloidosis in captive Celebes crested macaques (*Macaca nigra*). *Journal of Comparative Pathology* 199: 12–16. DOI: https://doi.org/10.1016/j.jcpa.2022.09.005

Duboscq, J. & Micheletta, J. 2023. *Macaca nigra* in the spotlight: Accounting for diversity in behavior, ecology, and conservation in primates. *International Journal of Primatology* 44(5): 1026–1041.

DOI: https://doi.org/10.1007/s10764-023-00386-3
Gomez, L., Sy, E.Y. & Shepherd, C.R. 2022. Evidence of illegal trade of the critically endangered black crested macaque *Macaca nigra* from Indonesia to the Philippines. *Asian Primates Journal* 10(1): 24–32.
Groves, C.P. 2005. Order Primates. *In*: Wilson, D.E.& Reeder, D.M. (Eds.), *Mammal Species of the World: A Taxonomic and Geographic Reference* (3rd Ed.). Johns Hopkins University Press, Baltimore, pp. 111–184.
Guadamuz, A. 2016. The monkey selfie: Copyright lessons for originality in photographs and internet jurisdiction. *Internet Policy Review* 5(1): 1–12. DOI: https://doi.org/10.14763/2016.1.398
Joly, M., Tamengge, M., Pfeiffer, J.-B., Price, M., Agil, M. & Engelhardt, A. 2023. Climate, temporal abundance of key food sources and home ranges of crested macaques (*Macaca nigra*) in Sulawesi, Indonesia: A longitudinal phenological study. *International Journal of Primatology* 44(4): 670–695. DOI: https://doi.org/10.1007/s10764-023-00377-4
Katili, D. & Saroyo, S. 2011. Comparison of daily activities of two groups of Sulawesi crested black macaques (*Macaca nigra*) in Tangkoko-Batuangus Nature Reserve, North Sulawesi. *Jurnal Ilmiah Sains* 15(1): 161. DOI: https://doi.org/10.35799/jis.11.2.2011.201
Kementerian PPN. 2025. *Status Keanekaragaman Hayati Ekoregion Sulawesi*. Kementerian Perencanaan Pembangunan Nasional/Badan Perencanaan Pembangunan Nasional, Jakarta, 20 pp.
Kyes, R.C., Iskandar, E., Onibala, J., Paputungan, U., Laatung, S. & Huettmann, F. 2013. Long-term population survey of the Sulawesi black macaques (*Macaca nigra*) at Tangkoko Nature Reserve, North Sulawesi, Indonesia. *American Journal of Primatology* 75(1): 88–94. DOI: https://doi.org/10.1002/ajp.22088
Lee, R. 1999. Impact of subsistence hunting in North Sulawesi, Indonesia and conservation options. In: Robinson, J.G. & Bennett, E.L. (Eds). *Hunting for Sustainability in Tropical Forests*. Columbia University Press, New York, 1000 pp.
Lee, R., Riley, E., Sangermano, F., Cannon, C. & Shekelle, M. 2020. *Macaca nigra*. The IUCN Red List of Threatened Species 2020: e.T12556A17950422. https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T12556A17950422.en. Accessed on 29 June 2026.
Neugebauer, E., Lestari, S.D., Kaletuang, I.R., Perwitasari-Farajallah, D. & Widdig, A. 2025. Distribution and human-mediated establishment of crested macaque (*Macaca nigra*) populations in the North Moluccas, Indonesia. *International Journal of Primatology* 46(2): 419–435. DOI: https://doi.org/10.1007/s10764-024-00473-z
O'Brien, T.G. & Kinnaird, M.F. 1997. Behavior, diet, and movements of the Sulawesi crested black macaque (*Macaca nigra*). *International Journal of Primatology* 18(3): 321–351. DOI: https://doi.org/10.1023/A:1026330332061
Octavia, D., Komala, R. & Supiyani, A. 2017. Studi perilaku harian dan kesejahteraan monyet hitam Sulawesi (Macaca nigra Desmarest, 1822) di Pusat Primata Schmutzer. *Bioma: Jurnal Biologi Indonesia* 13(1): 8–22. DOI: https://doi.org/10.21009/Bioma13(1).2 [Indonesian]
Riley, E. 2010. The endemic seven: four decades of research on the Sulawesi macaques. *Evolutionary Anthropology* 19(22-36). DOI: https://doi.org/10.1002/evan.20246
Setiawan, A., Iqbal, M., Pormansyah., Indriati, W., Pragustiandi, P., Melto Sevli, M., Pratiwi, P.R., Handayani, R. & Yustian, I. 2024. A wide survey to assess population of Long-Tailed Macaque *Macaca fascicularis* (Primates: Cercopithecidae) in lowland region of South Sumatra. *Conserva* 2(1): 22-31. DOI: https://doi.org/10.35438/conserva.v2i1.204
Setiawan, A., Iqbal, M., Setiawan, D., Pormansyah., Saputra, R.F., Indriati, W., Sulistyadi, E., Maharadatunkamsi. & Yustian, I. 2023. Estimate population of Long-Tailed Macaque *Macaca fascicularis* (Primates: Cercopithecidae) in Calik River, South Sumatra. *Conserva* 1(1): 23-33. DOI: https://doi.org/10.35438/conserva.v1i1.185
Syafutra, R. 2024. *Buku Ajar: Dasar-Dasar Konservasi*. Get Press Indonesia, Padang, 172 pp.
Yan, X., Arakawa, N., Widayati, K.A., Purba, L.H.P.S., Fahri, F., Suryobroto, B., Terai, Y. & Imai, H. 2025. Exome analysis reveals species divergence in TYR and identifies species genetic markers in five endemic *Macaca* species on Sulawesi Island. *BMC Ecology and Evolution* 25(1): 66. DOI: https://doi.org/10.1186/s12862-025-02407-6