Pachyderm

FIELD NOTE OPEN ACCESS

A conceptual framework for understanding rhinoceroses' persistence and extinction in Borneo

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Submission date: 2 June 2026 | **Accepted date**: 6 July 2026

Introduction

At the end of the Pleistocene epoch, *Dicerorhinus sumatrensis* occupied much of Southeast Asia from roughly a line between Shanghai (China) and Assam (India) southwards to Sumatra and Borneo (Rookmaaker 2006; Payne 2022). This species is still commonly known as the Sumatran rhino because the type specimen came from Sumatra. The Bornean rhino (*D. s. harrissoni*) is one of three formally recognized subspecies (Groves and Kurt 1972). Fossils show that it diminished in adult body size rapidly over geological time scales, from the Late Pleistocene to the present (Cranbrook 1986). There was another similarly widespread Southeast Asian rhino species at the end of the Pleistocene, the Javan rhinoceros (*Rhinoceros sondaicus*), also with three recognized subspecies (Grubb, 2005).

The beginning of the end

In popular storytelling, *D. s. harrissoni* is on the brink of extinction due to poaching and habitat loss. We argue that the evidence does not support this conclusion. It is more accurate to say that the key factors that resulted in almost inevitable extinction can be summarized in chronological sequence as the cumulative outcome of a series of historical, ecological and anthropogenic processes. These include: (a) the Late Pleistocene to Early Holocene loss of more than half of the former Sunda land mass, as sea levels rose naturally by over 100 m between approximately 20,000 and 10,000 years ago, separating mainland Asia from what are now the islands of Sumatra, Borneo, Java and the southern Philippines; (b) a subsequent decline driven by the species–area relationship, whereby the loss of approximately half of the available habitat would be expected to reduce overall species richness by around 10%; (c) the post-Pleistocene expansion of closed-canopy dipterocarp forest across Borneo, replacing the cooler, drier and more open vegetation of the Late Pleistocene; (d) a corresponding (massive) decline in the productivity of rhino food plants; (e) a natural reduction in rhino population density; (f) the demographic risks associated with the species' long interbirth interval; (g) demand from China for rhino hides to manufacture body armour between approximately 3,500 and 2,200 years ago; (h) following the near extinction of rhinoceroses in China, increasing demand for rhino horn as an ingredient in traditional Chinese medicine because rhino horn was durable and could be transported easily, and stored over long periods without decay; (i) widespread hunting of rhinos across rural Southeast Asia from around 700 CE until the early twentieth century to supply the Chinese market, leading to a pronounced

Allee effect; and finally, (j) the failure of many twentieth-century commentators and decision makers to recognise or adequately account for these interacting historical and biological factors.

Situation from a century ago to end of the twentieth century

By the early twentieth century, all available evidence suggested that the principal challenge facing *Dicerorhinus* rhinos was their small, fragmented, and increasingly non-viable populations, and that this, rather than poaching, was the problem to address. Poaching merely accelerated the inevitable loss of the remaining clusters. Yet, each time evidence of poaching emerged, the prevailing response was to focus on stopping poaching rather than prioritizing the unification of rhinos for a managed breeding programme.

This bias still exists, perhaps reinforced by popular literature that fails to distinguish between the five extant rhino species, referring to them collectively as 'rhinos'. In fact, there are few similarities between African rhinos and *D. s. harrissoni*, other than their belonging to the same zoological family. Despite severe declines and continuing poaching pressure, populations of both African rhino species have recovered from historic lows through intensive conservation efforts. Thus, the challenge for African rhino conservation in recent decades has largely been to protect and rebuild populations still numbering in the thousands. The *Dicerorhinus* problem has been how to boost the numbers of a species that has existed at extremely low population density with infrequent births for many decades and is on a trajectory to extinction.

The first experience of the first author (JP) with *Dicerorhinus sumatrensis* was in 1977 in the proposed Endau-Rompin National Park (NP) in Peninsular Malaysia, where teams were fielded under the guidance of Nico van Strien and Rodney Flynn. The area was under closed-canopy rainforest, and surveys had to be conducted by teams measuring and recording fresh footprints. JP was concerned that he found only Malayan tapir footprints and that some surveyors might have been counting tapirs as rhinos. Flynn and Tajuddin (1983) conducted four such surveys in the same area between 1977 and 1981. In each case, they recorded the presence of about eight rhinos. They extrapolated and concluded that there were 20–25 rhinos present overall. A survey in the same area by the second author (ZZZ) in 1995 found only five rhinos, none with juveniles, (Zainuddin 1995). Similar survey efforts were undertaken to seek *Dicerorhinus* rhinos in Sumatra, Peninsular Malaysia and Sabah over the period 1995–1998 under the aegis of a Global Environment Facility Programme (GEF 1994). Similar results—very low and declining numbers, with no breeding—were obtained at all surveyed sites.

By the 1990s, the available evidence pointed increasingly towards demographic decline as a fundamental constraint on the persistence of *Dicerorhinus* populations. Too few calves had been born over the preceding century, with deaths consistently outpacing births—even in the absence of poaching. This made a unified, managed breeding programme essential to reverse the decline. Instead, a flawed consensus continued to blame low rhino numbers on poaching, leading to a passive approach of monitoring.

Post-Pleistocene large mammal extinctions in Borneo

Three main features of rhino biology drive the trajectory towards the extinction of the Bornean rhinoceros.

Large mammal ecology

Four large mammal species went extinct in Borneo in the Late Pleistocene or Holocene: Malayan tapir (*Tapirus indicus* or *Acrocodia indica*; Cranbrook and Piper 2013), Javan rhinoceros (Cranbrook and Piper 2007), tiger (*Panthera tigris*, Piper et al. 2007a) and giant pangolin (*Manis palaeojavanica*; Piper et al. 2007b). One might guess that there would be one underlying main reason to account for this, rather than different reasons for each species.

The human population density of Borneo, say 10,000 years ago, would have been both extremely low on average (less than 1 person per km^2) and unevenly scattered. The idea that humans with poisoned darts with an average 30 m visibility in forests and using wooden traps (there were no metal tools) could have wiped out tiger, tapir and Javan rhino, but failed to

wipe out Bornean rhino, elephants (*Elephas maximus*), banteng (*Bos javanicus*) and pigs (*Sus barbatus*), which are all still present, appears difficult to reconcile with the available evidence. Human hunting could surely have caused local extinctions where humans were concentrated but could not have been the sole cause of total extinctions across Borneo's 74 million hectares of land.

There is a common contributory reason why elephants, banteng and pigs have survived in Borneo, but the rhinos and tapir did not. The former live in herds that usually present a normal demographic balance, with dominant males always close to the herd and ready to mate with any receptive female. As long as food is adequate to sustain the herd, interbirth intervals can be maximized, and the risk of fertile and receptive females not being mated is low. In solitary species such as rhinos and tapirs, where young adults leave their mothers and move to a different area, if overall population density declines, the risk of potentially fertile adult individuals failing to meet and mate increases over time.

The 'Javan' rhino died out in Borneo before Chinese demand for horns reached Borneo (Cranbrook and Piper 2007), and the now extinct Bornean tapir has no horns, yet the Bornean *Dicerorhinus sumatrensis* survived until the twentieth century after a millennium of targeted hunting. Examination of the literature on all three species shows that the 'Javan' rhino (Hoogerwerf 1970) and tapir (Simpson et al. 2013) are almost entirely feeders on secondary growth plants while the Bornean rhino can tolerate—but does not favour—a diet that includes saplings of primary forest plants (Payne 2022). The superior ability of the Bornean rhino to tolerate low-quality food (leaves rich in tannins, fibre and natural secondary compounds) is likely a contributory reason for its more recent (albeit precarious) survival. It is also noteworthy that none of these species has been recorded feeding on plants of the family *Dipterocarpaceae*, the tree family that dominates most Borneo forests.

Nutrition

The underlying reason that closed canopy evergreen rainforest is sub-optimal for large mammals is down to nutrition. Only 2–3% of sunlight reaches the ground (Whitmore 1975). In high rainfall areas, soils tend to be leached and are relatively deficient in some minerals. Annual rainfall in Borneo varies greatly, but island-wide, 3,000 mm is typical (Vijith and Dodge-Wan 2021). Plant productivity inside the forest at ground level is low compared to other tropical, sub-tropical and Mediterranean biomes (Knapp et al. 2014). It is well known in many biomes that large mammals visit naturally concentrated mineral sources. The possibility, rarely stated explicitly, must be acknowledged that such concentrated sources might be essential for reproduction, if the leafy diet is deficient in elements such as sodium, phosphorus, calcium or trace elements. Dierenfeld et al. (2006) found that amounts of sodium and phosphorus in wild-harvested browse fed to captive Bornean rhinos were potentially limiting compared to equid nutrient requirements, the nearest animal for which reliable information is available. Nico van Strien (1985) noted that the food plants of rhinos in his Aceh study area contained sodium at concentrations more than ten times lower than the daily minimum recommended for horses. This issue of insufficient critical elements in basic food plants will be especially pronounced in breeding females, who need ample calcium and phosphorus.

Support for this view is provided by observations of captive *Dicerorhinus* in Malaysia. Offered a choice, all four rhinos kept in captivity at Tabin Wildlife Reserve, Sabah, between 2010–2019 selected leaves from pioneer woody plant species as food and rejected leaves from species characteristic of closed-canopy forest (Payne 2022). In addition, these rhinos were given horse pellets daily to help maintain body weight, which declined in the absence of this supplementary food. This observation implies that natural food plants may determine not only rhino health but also whether or not this rhino species can exist at all in some areas.

Additional support for the idea that nutrition might limit the ability of *Dicerorhinus* to sustain reproduction in the wild is provided by captive observations. The only published birth weights for this species are 24 kg for a birth in Peninsular Malaysia, 3.5 months after the mother living in the wild had been caught (Tajuddin et al. 1988) and 33–39 kg for three Cincinnati Zoo births (Konstant 2013). The Malaysian-born mother rhino was fed mainly leaves from the nearby forest while the Cincinnati-born mother rhino enjoyed a zoo diet. In the absence of alternative explanations, we believe the quality of food of the mothers during

pregnancy may have affected birth weight. Nico van Strien (1985) noted that in his Aceh study area, "a female Sumatran rhino normally only breeds again a considerable time after she has separated from her calf. It may be that this long interval between births is caused by poor quality of the available food."

Physiology

Although declining access to adequate daily nutrition may account in part for the observed reduction in size of *Dicerorhinus* post-Pleistocene, increasing temperatures and humidity would have exerted additional pressure towards body mass reduction, as a means to increase the surface area:body mass ratio. This is because a low surface area: mass ratio limits the skin's capacity to release heat, making large equatorial rainforest mammals prone to overheating from a large-bodied mammal into a hot environment. Bornean rhinos under the care of the authors in forest paddocks would sleep in a mud wallow for the six hottest hours of the day to help lose excess body heat as well as to help maintain good skin condition.

Research by Thomas Hildebrandt and his team on all rhino species indicates that female rhino infertility develops in tandem with a lack of pregnancies due to isolation from breeding males (Hermes et al. 2014). A review by Schaffer et al. (2020) of all female *Dicerorhinus sumatrensis* captured or born in captivity after 1984 found that 17 out of 26 adult females examined had significant reproductive pathologies.

Decision-making and conservation implications

The history of *Dicerorhinus* conservation illustrates the difficulty of responding effectively to species that decline gradually over long periods (Payne et al. 2025). Discussions, advice and decision making on *Dicerorhinus sumatrensis* from the first meeting of the IUCN SSC Asian Rhino Specialist Group in 1979 until recent years seemed largely oblivious to the biological issues outlined above. People became accustomed over time to observing many small, fragmented, reproductively compromised and declining clusters of individuals instead of a viable population. We fail to recognize the severity of the problem until too few breeding animals remain to sustain the overall population. Under such circumstances, habitat protection and anti-poaching measures, while necessary, are insufficient.

The Bornean rhinoceros provides a cautionary example of how extinction can occur despite legal protection and conservation attention when populations become too small and isolated to sustain themselves. Future conservation strategies for highly endangered rhino populations should therefore integrate ecological, demographic and reproductive considerations within a coordinated management framework (Payne 2022; Payne et al. 2025).

References

Cranbrook E. 1986. A review of fossil and prehistoric remains of rhinoceroses of Borneo. *Sabah Museum and Archives Journal* 1 (1): 50–110.

Cranbrook E, Piper P. 2007. The Javan rhinoceros *Rhinoceros sondaicus* in Borneo. *The Raffles Bulletin of Zoology* 55 (1): 217–220.

Cranbrook E, Piper P. 2013. Paleontology to policy: the Quaternary history of Southeast Asian tapirs (Tapiridae) in relation to large mammal species turnover, with a proposal for conservation of Malayan tapir by reintroduction to Borneo. *Integrated Zoology* 8(1): 95–120. doi: 10.1111/j.1749-4877.2012.00319.x

Dierenfeld ES, Kilbourn A, Karesh W, Bosi E, Andau M, Alsisto S. 2006. Intake, utilization, and composition of browses consumed by the Sumatran rhinoceros (*Dicerorhinus sumatrensis harissoni*) in captivity in Sabah, Malaysia. *Zoo Biology* 25: 417–431.

Flynn RW, Tajuddin Abdullah M. 1983. Distribution and number of Sumatran rhinoceros in the Endau Rompin region of peninsular Malaysia. *Malayan Nature Journal* 36 (4): 219–247.

GEF. 1994. Indonesia and Malaysia: conservation strategies for rhinos in Southeast Asia. Global Environment Faculty, New York.

Groves CP, Kurt F. 1972. *Dicerorhinus sumatrensis*. *Mammalian Species* 21:1–6

Grubb P. 2005. Species *Rhinoceros sondaicus*. In: Wilson, DE, Reeder DM (Eds.), *Mammal species of the world: a taxonomic and geographic reference* (3rd edn.). Johns Hopkins University Press, Baltimore. ISBN 978-0-8018-8221-0. OCLC 62265494

Hermes R, Göritz F, Saragusty J, Stoops MA,

Hildebrandt TB. 2014. Reproductive tract tumours: the scourge of woman reproduction ails Indian rhinoceroses. *PLoS ONE 9* (3): e92595. https://doi.org/10.1371/journal.pone.0092595

Hoogerwerf, A. 1970. *Udjung Kulon, the land of the last Javan rhinoceros. With local and general data on the most important faunal species and their preservation in Indonesia*. EJ. Brill, Leiden.

Knapp AK, Carroll CJ, Fahey TJ. 2014. Primary production in terrestrial ecosystems: patterns and controls in a changing world. In: Monson R. (Ed.), *Ecology and the environment*. Springer, New York. https://doi.org/10.1007/978-1-4614-7612-2_2-1

Konstant B. 2013. Everybody's favourite rhino. *The Crash* January 2013: 4–5.

Payne J. 2022. *The hairy rhinoceros. History, ecology and some lessons for management of the last Asian megafauna*. Natural History Publications (Borneo), Kota Kinabalu

Payne J, Dixon KK, Sukianto L, Zainuddin ZZ, Indrawan M, Rookmaaker KLC, Schaffer NE, Ahmad ZA, Kretzschmar P, Havmøller RW, Agil M, Yoganand K. 2025. The most endangered extant rhino species is now on the verge of extinction. *Pachyderm* 66: 214–220.

Piper PJ, Cranbrook E, Rabett RJ. 2007a. Confirmation of the presence of the tiger *Panthera tigris* (L.) in Late Pleistocene and Holocene Borneo. *Malayan Nature Journal* 59 (3): 259–267.

Piper PJ, Cranbrook E, Rabett RJ. 2007b. New Discoveries of an extinct giant pangolin (Manis cf. Palaeojavanica Dubois) at Niah Cave, Sarawak, Borneo: biogeography, palaeoecology and taxonomic relationships. *The Sarawak Museum Journal* LXIII (84): 185–197.

Rookmaaker L. 2006. Distribution and extinction of the rhinoceros in China: review of recent Chinese publications. *Pachyderm* 40 (1): 101–105. https://doi.org/10.69649/pachyderm.v40i1.1267

Schaffer NE, Agil M, Zainuddin ZZ. 2020. Ramifications of reproductive diseases on the recovery of the Sumatran rhinoceros *Dicerorhinus sumatrensis* (Mammalia: Perissodactyla: Rhinocerotidae). *Journal of Threatened Taxa* 1F2 (3): 15279–15288.

Simpson BK, Shukor MN, Magintan D. 2013. Food selection of the Malayan tapir (*Tapirus indicus*) under semi-wild conditions. *AIP Conference Proceedings* 1571, 317–324. https://doi.org/10.1063/1.4858676

Tajuddin Abdullah M, Zainuddin ZZ, Shukor MN, Noliah bt Bakar, Zainun bt. Abd. Razak. 1988. Notes on the birth of a Sumatran rhinoceros at the Malacca Zoo, Malaysia. *Journal of Wildlife and Parks (Malaysia)* 6/7: 39–42.

Van Strien NJ. 1985. *The Sumatran rhinoceros in the Gunung Leuser National Park, Sumatra, Indonesia: its distribution, ecology and conservation*. Doctoral thesis. Wageningen University, The Netherlands.

Vijith H, Dodge-Wan D. 2021. Statistical trend characteristics of rainfall in the Baram river basin (Malaysian Borneo). *Papers in Applied Geography* 7 (2): 131–160. https://doi.org/10.1080/23754931.2020.1847728

Whitmore T. 1975. *Tropical rainforests of the Far East*. Clarendon Press, Oxford.

Zainuddin ZZ. 1995. Review of Sumatran rhinoceros *Dicerorhinus sumatrensis* population in Peninsular Malaysia. *Journal of Wildlife and Parks* 14: 1–15.