A beautiful male Javan rhinoceros in its natural habitat in Ujung Kulon National Park
Krásný samec nosorožce jávského ve svém přirozeném prostředí v národním parku Ujung Kulon

Photo/Foto Tobias Nowlan

New data on the ecology and conservation of the Javan rhinoceros *Rhinoceros sondaicus* Desmarest, 1822 (Perissodactyla, Rhinocerotidae)

Nové údaje o ekologii a ochraně nosorožce jávského *Rhinoceros sondaicus* Desmarest, 1822 (Perissodactyla, Rhinocerotidae)

FRANCESCO NARDELLI[1),2)] & JAN ROBOVSKÝ[3)]

[1)] IUCN/SSC Conservation Planning Specialist Group and Asian Rhino Specialist Group, Gland, Switzerland
[2)] Save the Rhino International, London, United Kingdom
[3)] Department of Zoology, Faculty of Science, University of South Bohemia, Branišovská 1760, 370 05 České Budějovice, Czechia

Corresponding author: Francesco Nardelli (franardelli@gmail.com)

Summary

Despite investing great effort into *in situ* data collection, the Javan rhinoceros *Rhinoceros sondaicus* is still a poorly known species. Previously, this taxon was present throughout South-east Asia, from Bangladesh to Vietnam, and from Southern China to Java. Unfortunately, only about 60 *Rhinoceros sondaicus* remain today, mostly males, and all reside in the Ujung Kulon National Park, on the island of Java, Indonesia. This second largest mammal of the South-east Asian rainforest is a solitary dweller of lowland woodlands and does not climb mountains. Its upper lip is prehensile and differs from that of the grazer *Rhinoceros unicornis* in both length and adaptation, as the Javan rhinoceros is a generalist browser. A prominent distinctive feature of the Javan rhinoceros is the 'saddle' on the neck, while the female horn is nearly absent, allowing sexual distinction to be made even among young individuals. Based on data from camera traps we suspect that *Rhinoceros sondaicus* has also developed a peculiar and complex behaviour, as well as characteristic vocalization related to mud wallows. As this species is sometime wrongly classified as *Rhinoceros unicornis*, to aid in better differentiation, a distinctive behavioural trait of mothers and their calves is described in this work. A goal is also to highlight the need for a much greater effort to know and preserve the surviving individuals to ensure that this unique species will not disappear forever. Conservation is dangerously lacking constant management control and a second population establishment is not considered as a priority. The authors propose increasing the carrying capacity of the current area, as the rhinos are confined within the Ujung Kulon National Park, which has limited suitable habitat. They propose creating new clearings by falling large trees in palm-free areas, allowing saplings to grow and increasing the quantity of food available to the rhinos as well as highlighting the urgency of *ex situ* management strategies and biobanking of cell cultures for the maximizing conservation options for the survival of this valuable species.

Souhrn

Nosorožec jávský zůstává navzdory značnému úsilí nejméně známým druhem nosorožce. Dříve se tento taxon vyskytoval v celé jihovýchodní Asii, od Bangladéše po Vietnam a od jižní Číny po Jávu. Bohužel v současnosti přežívá jen cca 60 jedinců, v nevyváženém poměru pohlaví ve prospěch samců, a pouze v národním parku Ujung Kulon na západě Jávy. Tento druhý největší savec tropických deštných pralesů jihovýchodní Asie je samotářským druhem obývajícím nížinné lesy. Má citlivý horní pysk, což s dalšími znaky značí, že patří mezi býložravci k tzv. okusovačům. Dalším charakteristickým rysem nosorožce jávského je „sedlo" na krku, jakož i téměř chybějící roh u samic, což umožňuje rozlišovat pohlaví u pozorovaných jedinců, včetně mladých zvířat. Na základě dat z fotopastí tušíme, že nosorožec jávský vykazuje řadu jedinečných prvků chování, včetně vokalizace v místě vyhledávaných bahnisk. Oproti nejpříbuznějšímu nosorožci indickému jeho mláďata následují matku, což je může činit zranitelnějšími. Příspěvek se snaží poukázat na potřebu mnohem většího úsilí o poznání biologie druhu, jakož i na zachování přeživších jedinců, aby tento jedinečný druh nezmizel navždy. Z ochranářského hlediska příspěvek poukazuje na refugiální výskyt tohoto druhu v prostředí, které má omezenou nosnou kapacitu, navíc obývané území má významný podíl suboptimálního prostředí. Proto autoři navrhují zvýšit nosnou kapacitu oblasti vytvářením mýtin padajícími velkými stromy v oblastech bez palem, což by umožnilo růst stromků a zvýšilo by tak množství potravy pro nosorožce. Dále apelují na založení záložní populace kombinující principy *ex* a *in situ* ochrany, jakož i uchování buněčných kultur z každého možného jedince jako prostředek ke zvýšení šancí na udržení tohoto druhu pro další generace.

Keywords

badak Jawa, poaching, lesser one-horned rhinoceros, distribution, behaviour, refugee species, conservation, *ex situ* management

Introduction

This contribution reviews some of our knowledge about this taxon with respect to some rather neglected parameters of this species on the verge of extinction. This analysis also contains several recommendations related to its scientific documentation and conservation.

Morphology

The Javan rhinoceros measures 3–3.5 m in length, has a shoulder height of 1.2–1.7 m, and weighs between 1,200 and 1,500 kg (Groves & Leslie 2011). Its hide colour is typically gray to dusky gray, and is entirely covered by peculiar epidermal mosaic-like polygons that resemble scales (Lydekker 1907, Peacock 1933, Harper 1945). They are clearest on the limbs and can be detected even from a distance. The fold behind the occiput is situated close to the head, while another fold stretches like a hood transversely across the middle of the shoulders and extends on either side beneath the throat, almost forming a continuous circle. A second doubling, which also encircles nearly the entire body, is situated behind the shoulders. The species is further characterized by a transversal fold above each foreleg and a larger one that crosses the posterior, and descends on either side in front of the thighs. A slight depression extends forward upon the thigh on either side from the root of the tail.

The upper lip is prehensile and differs from that of its congeneric grazer *R. unicornis* in both length and adaptation, as the Javan rhinoceros is a generalist browser, mostly feeding on twigs, saplings and leaves, very little fruit as it is recorded also for the Sumatran rhinoceros (Sody 1959, Groves 1982, Nardelli 2013). The browsing status of this species was fully supported by dental microwear textures (Hullot et al. 2019), mesowear analysis (Hernesniemi et al. 2011), extended mesowear method (Taylor et al. 2013), semicircular canal orientation and head posture (Schellhorn 2018). Still, the Javan rhinoceros is probably most recognizable by the remarkable 'saddle' on its neck, which is indicative of the species (Sody 1941).

Very rare, original *Rhinoceros sondaicus annamiticus* skull with intact nasal bone, but missing the incisors and premaxillary bones. The specimen, collected in 1880, was presented to an antique shop in France by a missionary in Indochina – 'gift of R. P. Boutier'. His Mission was at that time in Hanoi, Vietnam, very close to China. It was acquired in 1997 by the Museum of Osteology in Oklahoma City, USA

Velmi vzácná lebka patřící poddruhu *Rhinoceros sondaicus annamiticus.* Lebka je v překvapivě dobrém stavu včetně neporušených nosních kostí, od dokonalosti ji dělí chybějící řezáky a řezákové kosti. Původ tohoto exempláře je datován rokem 1880 a byl darován starožitnictví ve Francii misionářem v Indočíně – ‚dar R. P. Boutier'. Jeho mise probíhala v Hanoji ve Vietnamu, tedy velmi blízko Číny. V roce 1997 jej získalo Osteologické muzeum v Oklahoma City (USA)

Photo/Foto Jay Villemarette Sr.

Although a sparse, hairy covering has been noted by some authors (Groves 1967, Cave 1969, Jan Robovský pers. obs. in *R. sondaicus inermis* – Museum für Naturkunde Berlin, 2010), there is a prevalent view that *R. sondaicus* is hairless. It was merely speculated that juveniles were covered by body hair, which would gradually disappear as they mature, leaving only ear fringes, eyelashes, and tail bristles in adults (Groves 1997). Its tail stands out distinctly from the hind quarters, so that its whole extent is exposed in a side view. They are also distinguished by the female's horn, which in *R. sondaicus* is merely a protuberance, allowing individuals' sex to be determined at a very young age (Groves 1971, Groves 1982).

Our knowledge about the morphology of this species is quite extensive in case of osteological comparisons (Groves & Leslie 2011, Asriastita 2014, Darda 2016, Schellhorn 2018, Mallet et al. 2019), but quite limited in case of soft anatomy. The brain, digestive system and reproductive systems were described by Beddard & Treves (1887), Garrod (1877), Cave & Aumonier (1963) and Laurie et al. (1983) based on two specimens, one inspected by Beddard & Treves in (1887) come from Java *R. s. sondaicus* and one inspected by Garrod (1877) originated from the Sundarbans *R. s. inermis* (Rookmaaker 1998).

Distribution and subspecies

The Sundaic, or lesser one-horned rhino, popularly known as the Javan rhinoceros *Rhinoceros sondaicus* Anselme Gaëtan Desmarest, 1822 is also referred to by Indonesian names, such as badak or baduk Jawa, warak and Abah Gede. Its distribution once extended throughout the swampy forests of southern Bangladesh and south-east West Bengal – the Sundarbans – the lowland forests of central Bangladesh, the north-eastern Indian regions, western and south Myanmar, south Thailand, Cambodia, Laos, Vietnam, Peninsula Malaysia, Sumatra, and Java (Loch 1937, Rookmaaker 1980, Grubb 2005) with some indications that it had once been present in southern China as well (Rookmaaker 2006, Antoine 2012). Basing on few fossil records, Cranbrook & Piper (2007) concluded that this species also occupied Borneo during the late Pleistocene-early Holocene, its possible later survival is however excluded (Rookmaaker 1977). While over the years remnants of *R. sondaicus* have been collected on multiple occasions in the north-eastern regions of India and the Sundarbans (Rookmaaker 1980, 1997, 2002), all rhinoceros reports from Bhutan refer to greater one-horned rhinoceroses *Rhinoceros unicornis* Linnaeus, 1758 (Rookmaaker 2016).

Javan rhinoceros distribution map. Modified image from https://badak.or.id/research-and-education/javan-rhino/
Mapa výskytu nosorožce jávského. Upravený obrázek https://badak.or.id/research-and-education/javan-rhino/

Unfortunately, of the three *R. sondaicus* subspecies – *R. sondaicus sondaicus*, *R. sondaicus inermis*, and *R. sondaicus annamiticus* – (Grubb 2005, Groves & Grubb 2011), only *R. sondaicus sondaicus* barely survives today on the Ujung Kulon peninsula, at the western tip of Java island, where this rhinoceros has reached its peak population density (Nardelli 1988, 2016), while it was once distributed across Malaysia and Sumatra, and most of Java. On the other hand, *R. sondaicus inermis* Lesson, 1838 was previously distributed across the Sundarbans and central Bangladesh, northern West Bengal, north-east India and western Myanmar, while *R. sondaicus annamiticus* Heude, 1892 used to be found in south Myanmar, south Thailand, Cambodia, Laos, Vietnam and southern China, but are both currently extinct.

Zin-Maung-Maung-Thein et al. (2006) found *R. sondaicus* fossils in Myanmar and concluded that the species most likely originated in the early Pleistocene in the Irrawaddy plain, and that it is the most primitive of the genus *Rhinoceros*. This discovery suggests that this species originated in continental Asia, and that it possibly migrated into Sundaland during the early Pleistocene and later ages.
The first phylogeographic assessment of Javan rhinos estimated the timing of divergence between *R. s. sondaicus* and *R. s. annamiticus* around 2 Myr to 300,000 years ago (Fernando et al. 2006). The only subsequent study (Margaryan et al. 2020) supported the separation of both these Javan rhino subspecies, and additionally identified the distinctiveness of North Bengal specimen with an estimated time of divergence around 540,000 years ago. All three recognized subspecies of Javan rhinoceros are supported by genetic evidence; the priority is to obtain nuclear or genomic data across the former distribution of the Javan rhino (Moodley & Robovský, in press.).

Considering the uniqueness of the Javan rhino, it is worth to mention that the time of divergence between *R. unicornis* and *R. sondaicus* is estimated at 4,3 Myr based on whole genomes (Liu et al. 2021). The subspecies *R. s. annamiticus* survived in Vietnam until 2010 (Brook et al. 2011, Brook et al. 2012). Based on the footprint diameter, its skull size is estimated to be 75–80% of *R. s. sondaicus* (Polet et al. 1999, Groves 1967, Groves & Guérin 1980), indicating that it was probably the smallest of the three subspecies. *R. s. inermis* maybe is the least known, although possibly not the rarest. As noted by Rookmaaker (1997: 38):

…every ship of the Dutch, French and British East India Companies trying to reach their stations along the Ganges had to pass the Sundarbans. One could suggest (but not prove) that when in those early days people mentioned rhinos in India or Bengal, they might have referred to the Javan species rather than "the Great Indian rhino", *Rhinoceros unicornis*…

According to Spartaco Gippoliti (pers. comm. 2023), it is likely that *R. sondaicus* was in the past often misclassified as *R. unicornis*. Marine transport and the opening of the Suez Canal in 1869 facilitated the transfer of goods across vast distances, making it easier for zoos and museums to acquire specimens from distant locations.

One of the last *Rhinoceros sondaicus annamiticus* in Cat Tien National Park in Vietnam. Although the 2009–2010 field survey (Brook et al. 2012) did not conclusively pointed to the extirpation of the Javan rhinoceros from Vietnam, the results of the surveys strongly indicated the extinction of this taxon
Jeden z posledních jedinců *Rhinoceros sondaicus annamiticus* ve vietnamském národním parku Cát Tiên. Přestože terénní výzkum (Brook et al. 2012) provedený v letech 2009–2010 jednoznačně neprokázal vymření tohoto taxonu ve Vietnamu, je to více než pravděpodobné

Photo/Foto ©WWF Vietnam

Thus, during the late 19th and early 20th century, as ships from India and Bangladesh navigated to the harbour of Trieste, (at that time part of the Austro-Hungarian Empire), they would also take additional cargo for animal dealers like Carl Hagenbeck who had a major live animals' depot at that port (Hagenbeck 1912: 148). At the time, it was probably also more practical to collect rhinos from the Sundarbans in close proximity to the Bay of Bengal, due to which very few greater one-horned rhinoceros specimens would have been brought alive to Indian ports as this species was present only in northern parts of the Indian subcontinent. This hypothesis is confirmed by the fact that, in Naples (Italy), a skeleton of a supposed greater one-horned rhinoceros, certainly died there, and the University Zoological Museum has recently 're-classified' it as a Javan rhinoceros (Improta & De Francesco 2022). A systematic census of the Museums *Rhinoceros* specimens would be certainly worthwhile (Robovský & Rookmaaker 2022).

The skeleton of Javan rhinoceros at the Zoological Museum of the University Federico II of Naples (Italy). The horn was stolen but replaced with an excessively long replica
Kostra nosorožce jávského v Zoologickém muzeu Univerzity Fridricha II. v Neapoli (Itálie). Roh byl po krádeži nahrazen, ovšem příliš dlouhou replikou

Photo Zoological Museum of Naples /Foto Zoologické museum v Neapoli

Behaviour

Given the rarity of Javan rhinoceros and no breeding in captivity (Rookmaaker 1998), current knowledge on this species' reproductive biology and social behaviour is limited. This issue is further compounded by the lack of live specimens living in controlled environments, making direct observations challenging. Owing to the cryptic nature and shyness of *R. sondaicus*, very little is known about its reproductive behaviour (Groves & Leslie 2011) and current data is mostly based on early accounts pertaining to few individuals (Hoogerwerf 1970, Ammann 1986). According to Gokkon (2020), 74 animals still exist, and all live in isolation; studying this species is difficult (Dinerstein 2011). In 2019, based on camera trap identification, the Javan rhinoceros population in Ujung Kulon National Park (UKNP) comprised 28 adult males (41.2%), 23 adult females (33.8%), 8 young males (11.8%), and 9 subadult females (13.2%) (Putra et al. 2020). According to Putro (2023), 76 rhinoceroses plus 3 calves were present in 2022. A recent report is challenging those figures (see below the section Conservation).

According to some records, Javan rhinoceros was highly prevalent in the country in the 18th century (Groves 1967) and its hunting was endorsed by the Javan government (Ramono et al. 1993). However, even during the T'ang Dynasty (618–906 AD), rhinoceros horn exports were an important source of income for Java, which likely contributed to the demise of this species (Nardelli 1988).

Nardelli (2016) recently opined that the Javan rhinoceros is not a gregarious species, and that this species is not a mountain dweller, claims made by several researchers (Horsfield 1824, Sody 1941, Hoogerwerf 1970, Ellis & Talukdar 2020, Britnell et al. 2021).

As previously noted, given that females are more sociable, their territories overlap considerably, but males tend to protect their territories from other males and these may overlap at the periphery only. This behaviour is like that of *Dicerorhinus sumatrensis*, but counters that noted for *R. unicornis*, an herbivore occupant of semi-open grasslands. A typical male territory may extend from 12 to 21 km^2 while a female's covers 4 to 13 km^2 only (Ammann 1986).

Therefore, much of what we know today about this species derives from the work of whom studied tracks (e.g., footprints, urine squirting and dung), which could reveal very little about its actual reproductive behaviour (Horsfield 1824, Sody 1941, Hoogerwerf 1970, Ammann 1986). Nonetheless, Ammann's (1986) observations of several cows and their calves suggest that they form permanent associations. The author further speculated that female calves would remain with their mothers, while associations between males and females would be severed after 4–5 days, a time span possibly corresponding to the duration of the female's oestrus.

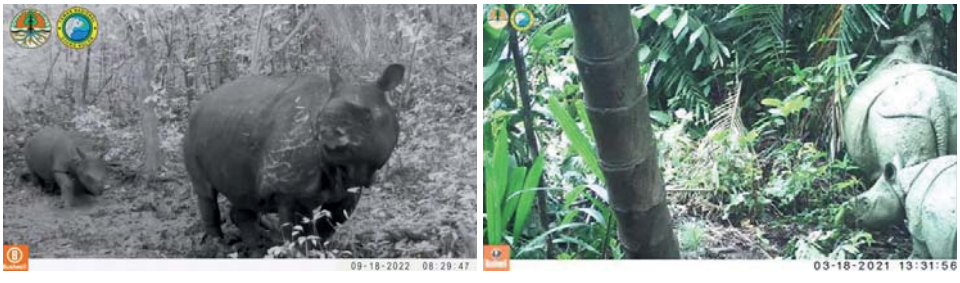
These findings were recently substantiated by Wilson (2021) who, among some first time observations, established that both male and female Javan rhinoceroses prefer solitary existence. According to this author's extensive thesis, social behaviour is mostly restricted to wallowing sites, which serve as shared habitats used for thermoregulatory purposes and provide opportunities for communicating, meeting, and interacting with other rhinos. As a result, *R. sondaicus* tend to vocalize three times more frequently (and use different calling sounds) in and around wallows than in forest habitats. Although female Javan rhinoceroses with calves have been found to form social bonds with other females and their offspring, such social interaction does not typically extend to adult males, unless females are sexually receptive. For this reason, male Javan rhinoceroses regularly visit wallowing sites. According to Wilson (2021), females are noticeably more vigilant when approaching wallows and clearings, and may even turn away if males are already present.

Javan rhino's mud wallow
Bahniště využívané nosorožcem jávským

Photo/Foto International Rhino Foundation

Wilson's (2021) analysis of the rhino vocal calls from camera trap videos taken at and near wallows reveal presence of seven vocalization descriptors with accompanying sonograms. Wilson (2021) was also able to determine that both sexes exhibit a flehmen response after drinking wallow water or when tasting or ingesting soil or mud, which the author attributed to the instinctive need to determine the sex, as well as reproductive and dominance status of other wallow users. As wallows frequented by rhinos are usually well concealed by vegetation, as they are formed in depressions of 6–7 m × 3–5 m dimensions in which rainwater can pool, mothers can monitor them from a relative safety before entering with their calves.

Javan calves tend to walk behind the mother (Nardelli 2017). This behaviour, however, has also been observed in Sumatran and black rhino calves (Joubert & Eloff 1971; Benda et al. 2020, Van Strien 1986). On the other hand, white and greater one-horned rhinoceros calves walk in front of the female (Owen-Smith 1973, 1975, Laurie 1978, 1982), making them less likely to be victims of lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*) as explained by Hitchins (1986), and tigers (*Panthera tigris*) (Dinerstein 2003). These observations should lead to the conclusion that the calves of rhinoceros browsers walk behind their mother (allowing the mother to clear the rough vegetation and expose edible leaves and sprouts), while grazers' offspring walk in front (which obscures calves from predators' view in open terrain).



Javan rhinoceros females with calves following them, more evident from the video available at https://www.facebook.com/watch/?v=529657705848991

Fotografie dokumentující, že nosorožec jávský patří k těm druhům nosorožců, u kterých mládě následuje samici, což je ještě více patrné z videa dostupného na https://www.facebook.com/watch/?v=529657705848991

Photo Ministry of Forestry and Environment and Ujung Kulon National Park – Republic of Indonesia
Foto Ministerstva lesnictví a životního prostředí a Národní park Ujung Kulon – Indonéská republika

A further protection is afforded by vocalizations between mothers and calves that are barely audible, as this species calves are occasionally preyed upon by the Javan leopard *Panthera pardus melas* or the pack-hunting Javan dhole *Cuon alpinus sumatrensis* (Wilson 2021). It is also believed that Javan tiger *Panthera tigris sondaica* may have previously predated on young Javan rhinoceroses and might have caused a considerable reduction in the population.

As Javan rhinoceros requires a considerable amount of food, population densities should be reduced to more productive levels (Wilson 2021). However, this can be difficult to achieve. The greater one-horned rhino female's age at first breeding is estimated at 7–7.5 years, suggesting that the same is possibly true for the Javan rhino (Dinerstein 2003). Owing to their small population, this means that only a few Javan females may be reproductively active simultaneously. On the other hand, its longevity may help with the population recovery. Nonetheless, these suppositions can only be confirmed or refuted through further research (Wilson 2021).

Similarly, it is presently unknown if the Javan rhinoceros is a spontaneous ovulator as in the greater one-horned, the black and the white, or its ovulation is induced (stimulated) by copulation as in the Sumatran rhinos (Roth et al. 2001).

The length of pregnancy is also unknown and is at present estimated at 16 months, given that mating has rarely been observed, making the timing of conception difficult. Dinerstein (2003) considers that greater one-horned rhinoceroses could produce a calf every 2.5 years, in the wild.

When ready for mating, males and females engage in easily recognizable courtship behaviour, whereby males would make repeated 'short-pant' calls, to which females respond with repeated

'moo-bray' calls. Upon coming closer, males would rub their chosen female under the neck with their horn. If receptive, female would respond by opening her mouth and rubbing against the male with her back (Wilson 2021). According to Wilson (2021), both males and females copulate with several partners (polygynous).

As was shown in the preceding discussions, comparisons between *R. sondaicus* and *R. unicornis* may lead to wrong conclusions, as these taxa have differing ecology. Therefore, when formulating conservation strategies, it is essential to note that the Javan rhinoceros needs vast, contiguous lowland rainforest to repopulate, and such habitats are presently only available in a small number of areas in Sumatra. Asian rhinoceroses as one of last remnants of megafauna would be also very important for ecological restorations (Louys et al. 2014).

It is also essential to consider the fact that political and logistic issues are likely to impede translocation of some rhinos to optimal and well managed *ex situ* breeding centers (Nardelli 2016). Thus, unless these challenges are overcome, the Javan rhinoceros is, in all probability, doomed to extinction.

Diet, habitat and ecological role

The Javan rhinoceros is the second largest mammal of the south-east Asian rainforest and is highly dependent on lowland forests, as their density protects these sensitive animals from sunlight and ensures a stable water supply, while trees produce ample saplings and leaves, which are its main food source. This species is a generalist browser (just occasionally it was found around crop fields), but unlike the once-sympatric Sumatran rhinoceros *Dicerorhinus sumatrensis* (Fischer 1814) – also a browser and a rainforest inhabitant – fitted with 'grip-shaped hoofs', it cannot climb up and down hills.

Rhinoceros sondaicus feeds primarily on twigs and leaves, consuming about 80–100 kg on a daily basis, (e.g. the Sumatran rhinoceros eats 60–70 kg. and weighs 700–900 kg), which can be already challenging to acquire for a single animal (pers. obs.).

The Javan rhinoceros currently occupies lowland evergreen secondary forests in Java, and it occupied marginal habitat in Vietnam (Groves & Leslie 2011). But considering its former known historical and prehistoric distribution (Groves 1967, Groves & Leslie 2011), it occupied likely greater variety of habitats in respect of regionally typical vegetations and lowland/mountain climates (Morley 2018). Combining vegetation map of South-East Asia (Morley 2018) with localities of the Javan rhino (Groves 1967), it occupied rain forests, seasonal evergreen, semi-evergreen and moist deciduous forests.

The Javan rhinoceros seems to meet criteria for a refugee species (Kerley et al. 2012), like: a much wider distribution in the past, current presence in a very restricted geographic range in very low numbers, and living in a location with some portion of suboptimal quality (Griffiths 1993).

Comparison of rhinoceros foot - left: Sumatran rhinoceros; right: Javan rhinoceros - a unique mounted part
Srovnání distálních částí končetin nosorožců - vlevo nosorožec sumaterský; vpravo nosorožec jávský - ve formě dermoplastického preparátu

Left photo/Foto vlevo Mark Carwardine/naturepl.com
Right photo/Foto vpravo David Ayre

Conservation

At present, the number of Javan rhino *Rhinoceros sondaicus* individuals is stagnating – if not declining – owing probably to inadequate habitat and population management measures, poaching and inbreeding, as well as limited reproduction capacity for the extremely low number of breeding females. In particular, as human population continues to increase, failure to address these issues will further undermine the value of current management practices, thereby putting an already fragile rhino population to even greater risk of extinction. Therefore, the existing protection and conservation strategies need to be revised, with a primary focus on the prevention of poaching, which continues to be driven by high demand for rhino horn in Asia.

To overcome these challenges, the carrying capacity of the existing protection area needs to be increased as well. For example, *Rhinoceros sondaicus* is confined within the 120,000 ha Ujung Kulon National Park (UKNP) perimeters, but according to Griffiths (1993), only 30,000 ha of the UKNP area are considered suitable for rhinos, divided in three major enclaves (Manurung et al. 2023). Moreover, 60% of this habitat (18,000 ha) is at the optimal level, while the remaining 40% (12,000 ha) is of sub-optimal quality (Griffiths 1993) mostly due to palm forests of invasive *Arenga obtusifolia*, *Calamus* sp. and *Pandanus* sp. Given that this appraisal includes the Gunung Payung area, where no rhinos are found, it is evident that, without improvements, Javan rhino subsistence cannot be guaranteed within the UKNP, on a long term basis.

It is a question whether some supplementary feed could help to improve the health, survival and reproduction of this last population of the Javan rhinoceros – i.e. new clearings can be created by falling several large trees, well apart, in palm free areas, so saplings can grow to increase the quantity of food available to the rhinos. The space in the canopy left by a fallen tall tree, allows more light to reach the forest floor as well as creates room for other vegetation to take root and flourish. If a tree falling takes others down with it, helps the re-growth around it even more. This new protocol could be implemented immediately, at very low cost.

Fallen tree with about two years old re-growth of saplings
Padlý strom obklopený asi dvouletými stromky v růstu

Photo/Foto Amphoe Muang Phatthalung

Rhinoceros sondaicus female feeding on saplings close to a fallen tree. Arenga palms (*Arenga obtusifolia*) now dominate the rainforest in many areas of the park, and reduce available rhino foraging, by limiting the growth of rhino food plants
Samice nosorožce jávského krmící se na stromcích v blízkosti padlého stromu. Palma arenga (*Arenga obtusifolia*) nyní dominuje v mnoha pralesních oblastech parku a omezuje růst rostlin, kterými se nosorožci živí

Photo Ministry of Forestry and Environment and Ujung Kulon National Park – Republic of Indonesia/
Foto Ministerstva lesnictví a životního prostředí a Národní park Ujung Kulon – Indonéská republika

Further issue arises from inadequate protection from poaching, as the Rhino Protection Units (RPUs) and the Park's Guards entrusted with physical security control (Haryono et al. 2015) do not have the power to patrol such a large area. Camera traps were installed throughout the park for inspection and count rhinos, evidently these can only identify security breaches, rather than preventing unauthorized access. Still, owing to the extent of professional poaching, which has proliferated in recent years, any figures published in official reports can quickly change. There is evidence that these criminals have moved from Sumatra into the UKNP (Manurung et al. 2023). For example, a male rhino was killed in 2018, and when the carcass was recovered, a bullet hole was found in its skull, while, in an unspecified year, cameras captured an injured rhino with two holes on its back.

Therefore, firm commitment by all stakeholders is crucial to guarantee that the UKNP can operate at a stable maximum carrying capacity, which is estimated at 50–60 individuals (Ammann 1986, Nardelli 1986, Santiapillai 1990, Fernando et al. 2006, Haryono et al. 2016). Although this figure was established in the 1980s, it is in accordance with the most recent assessment by Manurung et al. (2023).

Further evidence pointing to the urgency of stakeholders action can be found in the report published by a local NGO – Auriga Nusantara – in April 2023, indicating that the number of the surviving Javan rhinos has been grossly overestimated by the Indonesian government agencies (Manurung et al. 2023). Specifically, although these agencies claim that 76 rhinos reside within the UKNP (Putro 2023), at least 15 have recently not been captured by the 220 cameras set throughout the park.

Therefore, only about 60 individuals presently occupy UKNP (Manurung et al. 2023), and given that only 23 were females (Haryono et al. 2015) there is a possibility that just around a dozen of the latter may be successfully breeding today, the population has no capacity to increase.

Although combating any poaching activities remains the most pressing issue, the Javan rhinoceros genetic diversity is also in a critical state. The genetic research conducted by Fernando & Melnick (2003) and Fernando et al. (2006) indicates that the *Rhinoceros sondaicus* population is nearly homozy-

gous, with only two allele variations and two female parent lineages (haplotype), whereby only 14% of the total population carries haplotype 2. Recent observations of the Javan rhino's morphological characteristics also indicate that 13 individuals are affected by birth defects, which were attributed to inbreeding depression (Putro 2023).

Thus, future efforts aimed at Javan rhino conservation in Ujung Kulon must focus on protecting their safety, improving the quality of their habitat and enhancing their genetic viability, as failure to address these issues will lead to population stasis or decline. Even though some researchers and stakeholders are of view that having the entire Javan rhino population restricted to a peninsula would facilitate their greater protection, lack of habitat diversity also increases the risk of environmental hazards and disease outbreaks. Therefore, to limit the impact of any genetic mutations (Stephens & Sutherland 1999) and prevent rapid disease spread, Javan rhino should be provided with alternative sites (Wilson 2021).

As proposed by some authors (Ammann 1986, Nardelli 1986, 2016, Santiapillai & Suprahman 1986, Seal & Foose 1989, Haryono et al. 2016), a managed population should be established at an alternate location. Although Leader-Williams (1993) cautioned that population increase rates tend to be lower for rhinos in captivity compared to well-protected wild populations, this is presently the only viable option. An *ex situ* breeding program as a part of a broader conservation initiative will greatly contribute to the Javan rhino recovery and once sufficient progress has been made, other options may be considered, such as pair wise reintroductions in optimal habitats. Specifically, such measures have been successfully applied to the greater one-horned rhino *Rhinoceros unicornis*, resulting in a marked increase in the species' meta-population as a result of improved breeding rates and the establishment of new populations in different locations nevertheless, because *unicornis* ecology is dissimilar from the *sondaicus* one, the same achievement cannot be taken for granted.

When considering the alternatives outlined above, the recommendations provided in the Auriga Nusantara report (Manurung et al. 2023: 28) should serve as valuable guidance:

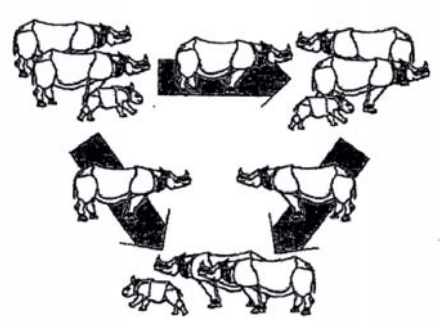
1. There should be an overall improvement in the protection of the Javan rhino and Ujung Kulon National Park;
2. The National Park Office and/or Ministry of Environment and Forestry should calculate the Javan rhino population in accordance with academic standards (and using various parallel methods);
3. Conduct a thorough evaluation of the Ujung Kulon National Park Office, looking at its institutional, budgetary and programmatic arrangements;
4. Implement a Javan rhino second population or second habitat programme in earnest;
5. Encourage and open up space for research into Javan rhinos.

Implementing the aforementioned measures, effective means of expanding the limits of Javan rhino distribution must be found to prevent an inevitable genetic collapse in the future. Moreover, if no suitable territory large enough to serve as a quality habitat for a greater number of the Javan rhinoceros can be found in Java, Sumatra should be considered as an alternative. The main factors to consider when selecting a new site for settling *Rhinoceros sondaicus* are safety from disease and poaching, and the carrying capacity of at least 50. This is deemed the lowest number of individuals that can ensure population growth (Haryono et al. 2016).

As outlined, an emergency *ex situ* action plan is urgently needed to save the Javan rhinoceros from extinction. This can only be achieved with genuine interest and commitment from all stakeholders, especially those with political decision-making power – and unbiased opinions – as their support is essential for enhancing the current management capacity. At present, however, the focus seems to be on retaining all Javan rhinos on Java and addressing the most immediate concerns related to poaching. This short-sighted perspective fails to account for the risks imposed by lack of genetic

diversity caused by interbreeding within the same area, which can only be overcome by establishing a second population, at least. Thus, strong leadership by the national government is critical to offer this highly threatened species a chance to survive and potentially thrive in the future.

As pointed out by Maguire et al. (1987), *ex situ* breeding is not always optimal substitute for providing endangered species with adequate habitat in the wild. Nonetheless, it is fundamental to secure the survival of breeding colonies. In the case of the Javan rhino, as about 60 individuals reside in a tiny enclave without any opportunities for natural expansion, an *ex situ* strategy is the safest viable option (Nardelli 1986, Seal & Foose 1989). While every measure should be taken to sustain the *Rhinoceros sondaicus* in the UKNP at the maximum density, the dangers outlined above will still be present unless a secondary site is established (Wilson 2021).



Managed migration among sub-populations to sustain gene flow in a meta-population
Řízená migrace mezi subpopulacemi pro udržení toku genů v metapopulaci

Diagram/Schéma Tom Foose

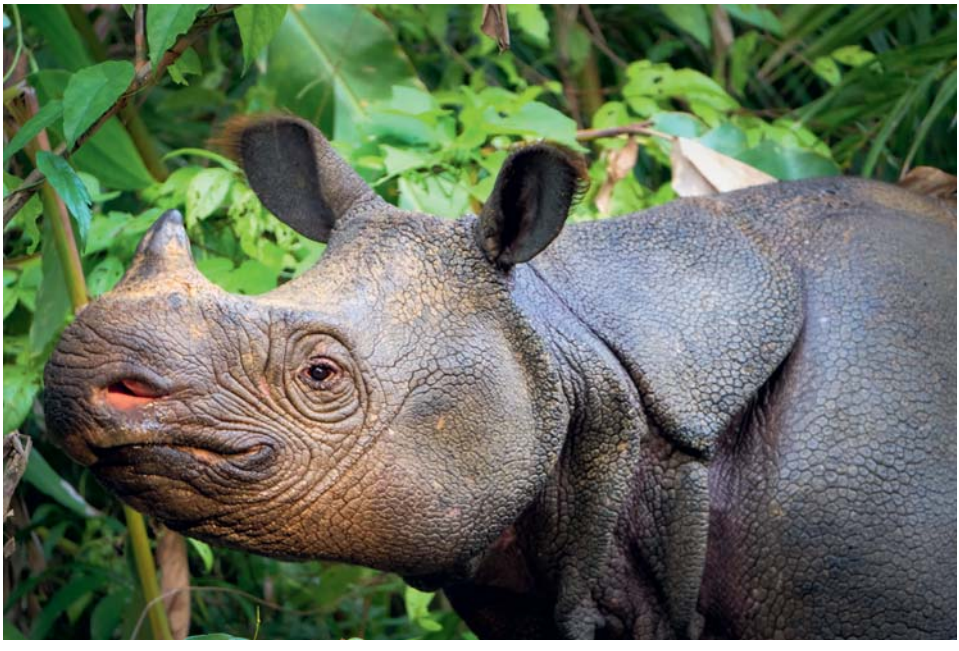
These arguments are supported by the recent Auriga Nusantara study (Manurung et al. 2023, Gokkon 2023), the findings of which confirm that maintaining the *status quo* is counterproductive. Further evidence substantiating their validity can be found in Malaysia, Sabah and Indonesia, where several Sumatran rhino populations have become extinct in the last three decades. The situation is rapidly declining, and more advanced field technologies demonstrate that wild populations are at a crisis point and are in need of major interventions.

Sumatran rhinoceros *Dicerorhinus sumatrensis*, feeding on leaves
Nosorožec sumaterský při okusování listoví

Photo/Foto Alain Compost

Conversely, the *ex situ* population of Sumatran rhino, in a single facility, is flourishing to such an extent that the establishment of a new Sumatran Rhino Sanctuary (SRS) in a secure location, distinct from the original, has become necessary. The final target of an *ex situ* managed plan is a wild population produced by the *ex situ* bred rhinos to be released into the surrounding forest. However, thus far, no areas for future releases have been located, as the aim is also to avoid competition for resources with Sumatran rhinos, elephants or predation by tigers, in Sumatra.

It is also worth noting that artificial reproductive technology (ART), such as artificial insemination (AI), is already sufficiently advanced, but it is presently only feasible in well managed facilities. Nonetheless, in the event that the Javan rhino population declines rapidly due to diseases, old age or other factors, ART involving stem cells and biotechnology will be essential. According to Hildebrandt et al. (2021), AI has already produced viable offspring in more than 50 wildlife species, including two rhinoceros. The biobanking of cell cultures are very perspective conservation options, the preservation of them should be therefore highly recommended as in case of the Sumatran rhinoceros (Brandt et al. 2018).



Javan rhinoceros head close-up image. Clearly visible is the outstanding skin, entirely covered by peculiar epidermal mosaic-like polygons that resemble scales and the prehensile upper lip. The anterior surface of the horn possesses a groove that it is typical for the whole genus (Groves 1971)
Detail hlavy nosorožce jávského. Jasně viditelný je polygonální vzor kůže a chápavý horní pysk. Na přední hraně rohu můžeme pozorovat rýhu, která je typická pro celý rod (Groves 1971)

Photo/Foto Tobias Nowlan

The problematic sex ratio

Ample body of research indicates that the risk of extinction increases significantly when the population is below certain threshold, due to Allee effects (Stephens & Sutherland 1999) and stochasticity (Courchamp et al. 1999). Moreover, as the population size declines, so does the genetic pool, increasing the probability of propagation of genetic defects as well as accumulation of deleterious mutations due to random drift and inbreeding (Seal & Foose 1989, Allendorf & Luikard 2007).

While individual fitness level can be improved by manipulating the sex ratio, such interventions require specialized facilities that can only be realized *ex situ*. Thus far, some success has been achieved, with other taxa, through non-invasive methods such as those aimed at modifying sex-determining ecological or social factors. Nonetheless, invasive methods – including hormone treatment of embryos or sperm sexing prior to using assisted reproductive technologies (ART) – are more prevalent in practice as they tend to yield more reliable outcomes (Wedekind 2012).

According to Haryono et al. (2015), at 35 males and 23 females, the male/female ratio in the Javan rhino population was 1:0.76 in 2012, declining to 1:0.66 in 2013. The same observation of much rarer females was made already by Hoogerwerf (1970). Sex ratio bias and extinction risk are very important conservation issues in isolated populations (Clout et al. 2002, Grayson et al. 2014, Barrientos 2015) and should be assessed seriously in the case of the Javan rhino.

However, as more recent data is not available, it is difficult to extrapolate this downward trend to form reliable projections. This issue is further compounded by the fact that, despite recommendations, female Javan rhinos have not been monitored constantly and individually (Nardelli 2016) even with 220 camera traps deployed at random locations to determine the total number – the figure most at heart to the laymen.

As the number of females determines the potential population increase for any species, having considerably more male Javan rhinos is a major demographic problem. It also increases the competition for mates and frustration of reproductive partners, resulting in sexual conflict that can have detrimental results in case of severe injuries and psychological subordination.

Therefore, sex ratio manipulation may be required for increasing the reproduction rate in this near-extinct species. It is also worth noting that wild African rhinoceros *in situ* are able to adapt the sex of their offspring, thus naturally limiting breeding competition and maintaining a healthy gender balance (Berkeley 2011). These preliminary findings may suggest that a similar gender control mechanism could be possible for Javan rhinos, provided that they are given state of the art *ex situ* facilities, where these compensatory responses can be initiated. In sum, as males continue to dominate in the Javan rhino *in situ* population, genetic deterioration is inevitable, confirming the urgency of *ex situ* management strategies for the survival of this most valuable species.

Another issue in reproduction biology of captive rhinos is the optimization of breeding conditions, like transfers of males, the size of breeding groups etc. (Scott et al. 2023). In case of potential captive breeding of this species, the exchanges of males and their separate holding should be precisely assessed based on the known biology of this species and experiences with other rhino species under captivity conditions.

Perspectives in understanding the biology of the Javan rhino

Summarizing our review, we recommend these topics to document biological parameters of the Javan rhino:

1. Catalogues of preserved collection specimens and biobanking specimens of the Javan rhinoceros should be recommended with respect to morphological and genetic investigations; the only currently available lists of collection specimens of the Javan rhino were published in the 1930s (Barbour and Allen 1932, Loch 1937);

2. Since the anatomical parameters of the Javan rhino are limited by samples size and only to some organ systems, it would be worth to measure all available specimens in future, as to preserve as many body parts as possible in case of dead individuals. Studying the morphological and anatomical characteristics of the Javan rhino provides insights into its physical adaptations, such as its unique skin folds. The sexual dimorphism with possibly larger females in this species (reviewed by Groves 1982) is an issue that requires a verification based on larger sample size. Detailed examination of its skeletal system, reproductive organs, and other anatomical features helps in understanding its physiological capabilities and reproductive biology;

3. Biobanking of cell cultures for every available live specimens of the Javan rhino is of the great conservation value as explained in Brandt et al. 2018 in case of the Sumatran rhino, Saragusty et al. 2016 and Korody et al. 2021 in case of the Northern white rhinoceros;

4. Since the Javan rhino is the last rhino species without the known karyotype (Houck et al. 1994, Trifonov et al. 2012), the cell culture could be used for the detailed inspection of chromosomal parameters;

5. In spite of some current advances in documentation of sound repertoire in the Javan rhino (Wilson 2021), the infrasound has not been recorded; it should be clarified whether the Javan rhino is the only rhino species without infrasound or not (von Muggenthaler et al. 1993);

6. Since the isotope evidence could indicate some diet and habitat shifts, and the refugee species characters of some species (Kaczensky et al. 2017, Suraprasit et al. 2020; Isarankura Na Ayudhya et al. 2022), the isotope evidence from historic and current populations is of great importance for our understanding of original habitat and diet preferences of this species;

7. Genetic research plays a crucial role in understanding the Javan rhino's population dynamics, genetic diversity, and relatedness to other rhinoceros species. Analysing more Javan rhino's genomes can provide valuable information about its evolutionary history, potential genetic vulnerabilities, and factors contributing to its decline;

8. Investigating the behaviour and ecology of the Javan rhino helps in understanding its habitat requirements, feeding habits, social structure, and mating behaviour. Studying its movements, activity patterns, and preferred habitat types can aid in identifying critical conservation areas and designing effective management strategies;
9. The reproductive biology of the Javan rhino is of utmost importance in its conservation. Research on mating systems, breeding success, gestation period, and the factors influencing reproduction can guide efforts to enhance the species' breeding success, both in captivity and in the wild;
10. Monitoring the health status of Javan rhinos is crucial to identify and mitigate potential threats, such as diseases or parasites. Investigating their immune system, susceptibility to specific pathogens, and health risks associated with habitat degradation or human interactions can inform conservation strategies, including disease prevention and management;
11. Understanding the Javan rhino's habitat requirements, including preferred vegetation types, water sources, and landscape connectivity, is essential for effective conservation planning. Studying the impacts of habitat loss, fragmentation, and degradation on the species can guide habitat restoration efforts and inform strategies for protected area management.

Male Javan rhinoceros in its favorite element: water. In this image, it is possible to observe the characteristic ‚saddle', the nearly complete coverage of polygon-shaped epidermal growths, and the groove on the anterior surface of the horn
Samec nosorožce jávského ve svém oblíbeném živlu: vodě. Na tomto snímku je možné pozorovat především charakteristické „sedlo" na krku, polygonální vzor kůže a rýhu na přední hraně rohu

Photo/Foto Tobias Nowlan

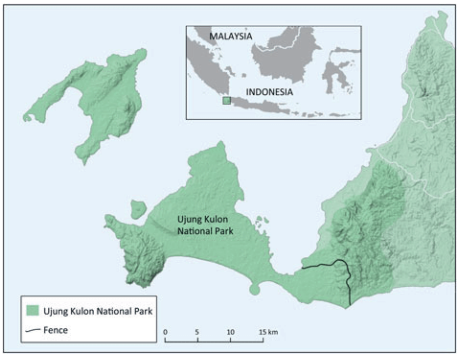
Conclusions

Thus, Haryono et al. (2016) propose starting an *in situ* Javan rhino program with four males and four females that are relatively unrelated, which the authors of this paper deem a sufficient and viable breeding cluster also for an *ex situ* program. The authors confirm the plan although further recommend prioritizing the establishment of two *ex situ* facilities, with two pairs in each one, **as *ex situ* breeding is the safest and most fruitful option to establish a second population of Javan rhinos, as experienced with the first Sumatran Rhino Project and Sanctuary**. For this purpose, animals fit for breeding should be selectively identified, after which the capture, acclimatization and management protocols that have been successfully implemented for the Sumatran rhinoceros *Dicerorhinus sumatrensis* can be adopted. Still, during capture, care must be taken to avoid excessive disturbance of other individuals and prevent seize females with calves. As the Javan rhinos live in relatively close proximity within the

UKNP territory, one rhino should be trapped per year. Avoiding disturbance, this staggered capture also allows for the refinement in any protocols before expanding the breeding program.

Specifically, any issues with the ecology, behavioural challenges, or integrating and breeding rhinos in an *ex situ* site, as well as the logistics of capturing and translocation, should be examined periodically to address any challenges in a timely manner. Once two sites are established, strategic exchanges of animals are also advised, as this would greatly enhance the genetic diversity.

In parallel with these initiatives, the protection measures at the UKNP need to be modernized and intensified to prevent poaching and disease spread. Given the growing sophistication of poaching syndicates, and the close proximity of local livestock to the park's wildlife, retaining the *status quo* can put the rhinos at risk of irrecoverable population loss (Manurung et al. 2023).



Ujung Kulon National Park
Národní park Ujung Kulon
Credit: Available via license: CC BY 4.0

Rhinoceros sondaicus is unfortunately 'conservation-reliant' species (Goble et al. 2012, Scott et al. 2010). A species is conservation reliant when the threats that it faces cannot be eliminated, but only managed. There are two forms of conservation reliance: population and threat-management reliance – its survival depends on conservation aimed at managing the threats it faces, given that there is a growing consensus that pressure cannot be totally eliminated, but only managed. Therefore, any initiative aimed at preventing the extinction of this highly valuable yet endangered species must start with careful conservation planning, which should include identification of sites in which conservation reliance is or is projected to be most well-defined.

These plans should also incorporate maintenance of viable populations, as even when the biological recovery goals have been attained, continued species-specific interventions will be required. These arguments apply to all 'conservation reliant' species not just *Rhinoceros sondaicus*. Nonetheless, for the Javan rhino to persist in the wild, each individual needs complete and dedicated human supervision throughout its lifespan. Moreover, the Javan rhino has already become 'refugee species' (Kerley et al. 2020). Refugee species are defined as those that can no longer access optimal habitat, but are confined to suboptimal habitats, with consequences of decreased fitness and density, and attendant conservation risks. As is the case with other species whose natural habitats have disappeared or have been adversely affected by human activities, the areas in which Javan rhino individuals reside are not only limited in size and resource diversity, but impose restrictions on their movement, diet, and reproduction. All these adverse effects have led to the marked decrement in the species fitness and density compared to historical records (Kerley et al. 2012). It is also worth noting that conservation efforts implemented in such suboptimal habitat tend to have limited benefit for the Javan rhino, as its capacity to improve fitness and density is severely restricted under such conditions (Kerley et al. 2020). In this context, the 'shifting baseline syndrome' (SBS; Pauly 1995) – SBS describes a gradual change in the accepted norms for the condition of the natural environment due to a lack of human experience, memory and/or knowledge of its past condition – also plays a role, as failing to adopt an objective measure when assessing the state of the system and the changes it underwent over a certain period may lead to an erroneous conclusion that conservation management activities are actually effective, even when refugee species are confined to marginal habitats (Kerley et al. 2012). According to Caughley (1994: 229), this risk is particularly severe for threatened species that have experienced a range contraction, as 'that the species ends up, not in the habitat most favourable to it, but in the habitat least favourable to the agent of decline'. Thus, it is safe to posit that widespread adoption of such conservation practices that are essentially based on cornering the refugee species in suboptimal habitats (such as the UKNP in the case of *Rhinoceros sondaicus*), while costly, is unlikely to yield desired outcomes. Therefore, *ex situ* action or combined conservation action integrating *in situ* and *ex situ* conservation management activities and facilities, like in case of Iberian Lynx and Kakapo recoveries, or the breeding centre for Sumatran rhinoceros, saola (if still around) and other rare ungulates in this region, is urgently needed.

Last appeal

The current situation of the two Indonesian rhino species pessimistically indicates that there are only about a dozen breeding females each of *R. sondaicus* and *D. sumatrensis* remaining in their natural habitats. This stark reality underscores the critical importance of implementing *ex situ* breeding to ensure the survival of both species. This imperative calls for the formulation of proactive policies and precise decision-making. Any hesitance to take action at this juncture can only be ascribed to concerns related to potential liabilities and a lack of due attention to the matter.

Acknowledgments

We would like to acknowledge the Rhino Resource Centre (RRC) for providing access to the most comprehensive collection of papers, without which our research on Javan rhinoceros would not have been possible. We strongly encourage supporting the stakeholders involved in this species conservation and raising awareness about the devastating impact of the senseless demand for rhinoceros horn products, leading to the catastrophic decline of rhinoceros populations.

Special thanks go to the anonymous reviewers and the authors of the images used in this manuscript. We express our gratitude to who responded to our requests for permission and also acknowledge the authors whom we were unable to contact, but have been given appropriate credits for their images.

REFERENCES/LITERATURA

ALLENDORF F. W. & LUIKART G., 2007. Conservation and Genetics of Populations. Blackwell Publishing LtD., Malden and Oxford and Victoria, xix + 642 pp.

AMMANN H., 1986. Contributions to the ecology and sociology of the Javan rhinoceros (*Rhinoceros sondaicus*). Inaugural dissertation, University of Basel, x + 1–229 pp.

ANTOINE P. O., 2012. Pleistocene and Holocene rhinocerotids (Mammalia, Perissodactyla) from the Indochinese Peninsula. Comptes Rendus Palevol 11(2–3): 159–168.

ASRIASTITA D., 2014. Karakteristik anatomi skelet kaki belakang Badak Jawa (*Rhinoceros sondaicus*). Thesis, Fakultas Kedokteran Hewan, Institut Pertanian Bogor, xii + 18 pp.

BARBOUR T. & ALLEN G. M., 1932. The lesser one-horned rhinoceros. Journal of Mammalogy 13(2): 144–149.

BARRIENTOS R., 2015. Adult sex-ratio distortion in the native European polecat is related to the expansion of the invasive American mink. Biological Conservation 186: 28–34.

BEDDARD F. E. & TREVES F., 1887. On the anatomy of the Sundaic rhinoceros. Transactions of the Zoological Society of London 12(5): 183–198.

BENDA P., ČERVENÝ J., EISEB S. J. & UHRIN M., 2020. Earless *Diceros bicornis* in the Etosha National Park, Namibia (Perissodactyla: Rhinocerotidae). Lynx n. s. (Praha) 51: 213–218.

BERKELEY E. V., 2011. Sex allocation, diet, and small population management of African rhinoceros. Ph.D. Thesis, Victoria University of Wellington, ix + 117 pp.

BRANDT J. R., COEVORDEN DE GROOT P. J. VAN, WITT K. E., ENGELBREKTSSON P. K., HELGEN K. M., MALHI R. S., RYDER O. A. & ROCA A. L., 2018. Genetic structure and diversity among historic and modern populations of the Sumatran Rhinoceros (*Dicerorhinus sumatrensis*). Journal of Heredity 109(5): 553–565.

BRITNELL J. A., LEWIS R. N., ELSNER-GEARING F., HARVEY N., STANBROOK E. & SHULTZ S., 2021. Species stereotypes as a result of unconscious research biases compromise conservation efficacy. Biological Conservation 261: 1–10.

BROOK S., COEVORDEN DE GROOT P. J. VAN, MAHOOD S. & LONG B., 2011. Extinction of the Javan rhinoceros (*Rhinoceros sondaicus*) from Vietnam. WWF Report VN 2011: 1–45.

BROOK S. M., COEVORDEN DE GROOT P. VAN, SCOTT C., BOAG P., LONG B., LEY R. E., REISCHER G. H., WILLIAMS A. C., MAHOOD S. P., TRAN MINH HIEN, POLET G., COX N. & BACH THANH HAI, 2012. Integrated and novel survey methods for rhinoceros populations confirm the extinction of *Rhinoceros sondaicus annamiticus* from Vietnam. Biological Conservation 155: 59–67.

CAVE A. J. R., 1969. Hairs and vibrissae in the Rhinocerotidae. Journal of Zoology 157(2): 247–257.

CAVE A. J. R. & AUMONIER F. J., 1963. The visceral histology of the Sumatran rhinoceros. Journal of the Royal Microscopical Society 82(1): 29–37.

CAUGHLEY G., 1994. Directions in conservation biology. Journal of Animal Ecology 63(2): 215–244.

CLOUT M. N., ELLIOT G. P. & ROBERTSON G. P., 2002. Effects of supplementary feeding on the offspring sex ratio of Kakapo: a dilemma for the conservation of a polygynous parrot. Biological Conservation 107(1):13–18.

COURCHAMP F., CLUTTON-BROCK T. & GRENFELL B., 1999. Inverse density dependence and the Allee effect. Trends in Ecology and Evolution 14(10): 405–410.

CRANBROOK EARL OF & PIPER P. J., 2007.The Javan rhinoceros *Rhinoceros sondaicus* in Borneo. Raffles Bulletin of Zoology 55(1): 217–220.

DARDA M., 2016. Karakteristik anatomi skelet tubuh badak jawa (*Rhinoceros sondaicus*). Thesis, Departemen Anatomi, Fisiologi, Dan Farmakologi, Fakultas Kedokteran Hewan, Institut Pertanian Bogor, xii + 12 pp.

DESMAREST A. G., 1822. Mammalogie ou Description des Espèces de Mammifères, Seconde Partie. Veuve Agasses, Paris, viii + 555 pp.

DINERSTEIN E., 2003. The Return of the Unicorns. The Natural History and Conservation of the Greater One-Horned Rhinoceros. Columbia University Press, New York, xx + 316 pp.

DINERSTEIN E., 2011. Family Rhinocerotidae, pp. 144–181. In: Wilson D. E. & Mittermeier R. A. (eds.): Handbook of the Mammals of the World. Vol. 2: Hoofed Mammals. Lynx Edicions, Barcelona, 886 pp.

ELLIS S. & TALUKDAR B., 2020. *Rhinoceros sondaicus*. The IUCN Red List of Threatened Species 2020: e.T19495A18493900. https://www.iucnredlist.org/species/19495/18493900. Accessed on 11 January 2023.

FERNANDO P. & MELNICK D. J., 2003. Genetic analysis of the Javan rhinoceros in relation to its management. Final report (Phase II). Center for Environmental Research and Conservation, Columbia University, New York, 15 pp.

FERNANDO P., POLET G., FOEAD N., NG L. S., PASTORINI J. & MELNICK D. J., 2006. Genetic diversity, phylogeny and conservation of the Javan rhinoceros (*Rhinoceros sondaicus*). Conservation Genetics 7: 439–448.

GARROD A. H., 1877. On some points in the visceral anatomy of the rhinoceros of the Sunderbunds (*Rhinoceros sondaicus*). Proceedings of the Zoological Society of London 1877(November 6): 707–711.

GIPPOLITI S., 2023. Conversation with Francesco Nardelli, 06 January.

GOBLE D. D., WIENS J. A., SCOTT J. M., MALE T. D. & HALL J. A., (2012). Conservation-Reliant Species. BioScience 62(10): 869–873.

GOKKON B., 2020. Two new Javan rhino calves are spotted in the species' last holdout. Mongabay Series: Asian Rhinos. https://news.mongabay.com/2020/09/two-new-javan-rhino-calves-are-spotted-in-the-species-last-holdout/. Accessed on 11 January 2023.

GOKKON B., 2023. Flawed count puts 'glorified' Javan rhinos on path to extinction, report says. Series: Asian Rhinos. https://news.mongabay.com/2023/04/flawed-count-puts-glorified-javan-rhinos-on-path-to-extinction-report-says/. Accessed on 11 April 2023.

GRAYSON K. L., MITCHELL N. J., MONKS J. M., KEALL S. N., WILSON J. N. & NELSON N. J., 2014. Sex ratio bias and extinction risk in an isolated population of Tuatara (*Sphenodon punctatus*). PLoS ONE 9(4): e94214. https://doi.org/10.1371/journal.pone.0094214.

GRIFFITHS M., 1993. The Javan rhino of Ujung Kulon: an investigation of its population and ecology through camera trapping. Directorate General of Forest Protection and Nature Conservation and the World Wide Fund for Nature Indonesia Program, Jakarta, 92 pp.

GROVES C. P., 1967. On the rhinoceroses of South-East Asia. Säugetierkundliche Mitteilungen 15(3): 221–237.

GROVES C. P., 1971. Species characters in rhinoceros horns. Zeitschrift für Säugetierkunde 36(4): 238–252.

GROVES C. P. & GUÉRIN C., 1980. Le *Rhinoceros sondaicus annamiticus* d'Indochine: distinction taxonomique et anatomique; relations phyletiques. Geobios 13(2): 199–208.
GROVES C. P., 1982. Asian rhinoceroses: down but not out. Malayan Naturalist 36(1): 11–22.
GROVES C. P., 1997. Die Nashörner - Stammesgeschichte und Verwandtschaft, pp. 14–32. In: Ganslooser U. (ed.): Die Nashörner: Begegnung mit urzeitliche Kolossen. Filander Verlag, Fuert, 258 pp.
GROVES C. P. & GRUBB P., 2011.Ungulate Taxonomy. John Hopkins University Press, Baltimore, ix + 416 pp.
GROVES C. P. & LESLIE D. M. Jr., 2011. *Rhinoceros sondaicus* (Perissodactyla: Rhinocerotidae). Mammalian Species 43(887): 190–208.
GRUBB P., 2005. Order Perissodactyla, pp. 629–636. In: Wilson D. R. & Reeder D. M. (eds.): Mammal Species of the World: A Taxonomic and Geographic, 3rd ed. Johns Hopkins University Press, Baltimore and Maryland, xxxv + 2142 pp.
HAGENBECK C., 1912. Beasts and Men: Being Carl Hagenbeck's Experiences for Half a Century among Wild Animals. Longmans, Green, and Co., London and New York, 328 pp.
HARYONO M., RAHMAT U. M., DARYAN M., RAHARJA A. S., MUHTAROM A., FIRDAUS A. Y., ROHAETI A., SUBCHIYATIN I., NUGRAHENI A., KHAIRANI K. O. & KARTINA, 2015. Monitoring of Javan Rhino population in Ujung Kulon National Park. Pachyderm 56: 82–86.
HARYONO M., MILLER P. S., LEES C., RAMONO W., PURNOMO A., LONG B., SECTIONOV, WALADI ISNAN, AJI B. D., TALUKDAR B. & ELLIS S., 2016. Population and habitat viability assessment for the Javan Rhino. Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, 70 pp.
HARPER F., 1945. Extinct and Vanishing Mammals of the Old World. New York, American Committee, International Wild Life Protection, New York, xv + 850 pp.
HERNESNIEMI E., BLOMSTEDT K. & FORTELIUS M., 2011. Multi-view stereo 3D reconstruction of lower molars of Recent and Pleistocene rhinoceroses for mesowear analysis. Palaeontologia Electronica 14(2): 1-15. palaeo-electronica.org/2011_2/246/index.html.
HILDEBRANDT T. B., HERMES R., GOERITZ F., APPELTANT R., COLLEONI S., MORI B. DE, DIECKE S., DRUKKER M., GALLI C., HAYASHI K., LAZZARI G., LOI P., PAYNE J., RENFREE M., SEET S., STEJSKAL J., SWEGEN A., WILLIAMS S. A., ZAINUDDIN Z. Z. & HOLTZE S., 2021. The ART of bringing extinction to a freeze - history and future of species conservation, exemplified by rhinos. Theriogenology 169: 76–88.
HITCHINS P. M., 1986. Earlessness in the black rhinoceros – a warning. Pachyderm 7: 8–10.
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. R. J. Brill, Leiden, xiii + 512 pp.
HORSFIELD T., 1824. Zoological Researches in Java, and Neighbouring Islands. Kingsbury, Parbury & Allen, London, 540 pp.
HOUCK M. L., RYDER O. A., VÁHALA J., KOCK R. A. & OOSTERHUIS J. E., 1994. Diploid chromosome number and chromosomal variation in the white rhinoceros (*Ceratotherium simum*). Journal of Heredity 85(1): 30–34.
HULLOT M., ANTOINE P. O., BALLATORE M. & MERCERON G., 2019. Dental microwear textures and dietary preferences of extant rhinoceroses (Perissodactyla, Mammalia). Mammal Research 64: 397–409.
IMPROTA R. & DE FRANCESCO T., 2022. Redetermination of the skeleton of the Asian rhinoceros in the Zoological Museum of the University Federico II, Naples (Italy). Bulletin of Regional Natural History 2(1): 1–9.
ISARANKURA NA AYUDHYA J., MERCERON G., WANNAPRASERT T., JAEGER J.-J., SHOOCONGDEJ R. & SURAPRASIT K., 2022. Dental mesowear and microwear for the dietary reconstruction of Quaternary Southeast Asian serows and gorals. Frontiers in Ecology and Evolution 10: https://doi.org/10.3389/fevo.2022.1000168.
JOUBERT E. & ELLOF F. C., 1971. Notes on the ecology and behaviour of the black rhinoceros *Diceros bicornis* Linn. 1758 in South West Africa. Madoqua Series 1(3): 5–53.
KACZENSKY P., BURNIK ŠTURM M., SABLIN M. V., VOIGT C. C., SMITH S., GANBAATAR O., BALINT B., WALZER C. & SPASSKAYA N. N., (2017). Stable isotopes reveal diet shift from pre-extinction to reintroduced Przewalski's horses. Scientific Reports 7(1): 5950. https://doi.org./10.1038/s41598-017-05329-6.

KERLEY G. I. H., KOWALCZYK R. & CROMSIGT J. P. G. M., 2012. Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat? Ecography 35: 519–529.
KERLEY G. I. H., TE BEEST M., CROMSIGT J., PAULY D. & SHULTZ S., 2020. The Protected Area Paradox and refugee species: The giant panda and baselines shifted towards conserving species in marginal habitats. Conservation Science and Practice. Vol. 2(6): e203. https://doi.org/10.1111/csp2.203.
KORODY M. L., FORD S. M., NGUYEN T. D., PIVAROFF C. G., VALLIENTE-ALANDI I., PETERSON S. E., RYDER O. A. & LORING J. F., 2021. Rewinding extinction in the northern white rhinoceros: Genetically diverse induced pluripotent stem cell bank for genetic rescue, Stem Cells and Development 30(4): 177–89.
LAURIE W. A., 1978. The ecology and behaviour of the greater one-horned rhinoceros (*Rhinoceros unicornis*). PhD. Dissertation, University of Cambridge, Cambridge, xxvi + 450 pp.
LAURIE W. A., 1982. Behavioural ecology of the Greater one-horned rhinoceros (*Rhinoceros unicornis*). Journal Zoology, 196(3): 307–341.
LAURIE W. A., LANG E. M. & GROVES C. P., 1983. *Rhinoceros unicornis*. Mammalian Species 211: 1–6.
LEADER-WILLIAMS N., 1993. Theory and pragmatism in the conservation of rhinos. pp. 69–81. In: Ryder O. A. (ed.): Rhinoceros Biology and Conservation. Zoological Society, San Diego, v + 368 pp.
LIU S., WESTBURY M. V., DUSSEX N., MITCHELL K. J., SINDING M. S., HEINTZMAN P. D., DUCHÊNE D. A., KAPP J. D., VON SETH J., HEINIGER H., SÁNCHEZ-BARREIRO F., MARGARYAN A., ANDRÉ-OLSEN R., DE CAHSAN B., MENG G., YANG C., CHEN L., VAN DER VALK T., MOODLEY Y., ROOKMAAKER K., BRUFORD M. W., RYDER O., STEINER C., BRUINS-VAN SONSBEEK L. G. R., VARTANYAN S., GUO C., COOPER A., KOSINTSEV P., KIRILLOVA I., LISTER A. M., Marques-Bonet T., Gopalakrishnan S., DUNN R. R., LORENZEN E. D., SHAPIRO B., ZHANG G., ANTOINE P. O., DALÉN L. & GILBERT M. T. P., 2021. Ancient and modern genomes unravel the evolutionary history of the rhinoceros family. Cell 184(19): 4874–4885.
LOCH C. W., 1937. *Rhinoceros sondaicus*: the Javan or lesser one-horned rhinoceros and its geographical distribution. Journal of the Malayan Branch of the Royal Asiatic Society 15(2): 130–149.
LOUYS J., CORLETT R. T., PRICE G. J., HAWKINS S. & PIPER P. J., 2014. Rewilding the tropics, and other conservation translocations strategies in the tropical Asia-Pacific region. Ecology and Evolution 4(22): 4380–4398.
LYDEKKER R., 1907. The Game Animals of India, Burma, and Tibet. Rowland Ward, London, xv + 409 pp.
MAGUIRE L. A., SEAL U. S. & BRUSSARD P. F., 1987. Managing critically endangered species: the Sumatran rhino as a case study: pp. 141–158. In: SOULE M. E. (ed.): Viable Populations for Conservation. Cambridge University Press, Cambridge, 189 pp.
MALLET C., CORNETTE R., BILLET G. & HOUSSAYE A., 2019. Interspecific variation in
the limb long bones among modern rhinoceroses-extent and drivers. PeerJ 7: e7647. 10.7717/peerj.7647.
MANURUNG T., HARDIANTO R. I. & PUTRA S. P., 2023. Javan Rhino in Jeopardy: Conservation Setbacks in Ujung Kulon National Park. Auriga Nusantara Jakarta, Indonesia, 32 pp.
MARGARYAN A., SINDING M.-H. S., LIU S., VIEIRA F. G., CHAN Y. L., NATHAN S. K., MOODLEY Y., BRUFORD M. W. & GILBERT M. T. P., 2020. Recent mitochondrial lineage extinction in the critically endangered Javan rhinoceros. Zoological Journal of the Linnean Society 190(1): 372–383.
MOODLEY Y. & ROBOVSKÝ J., in press. Phylogeny and systematics of extant rhinoceroses. In: Melletti M. & Talukdar B. (eds.): Rhinos of the World: Ecology, Conservation and Management. Cambridge University Press, in press.
MORLEY R. J., 2018. Assembly and division of the South and South-East Asian flora in relation to tectonics and climate change. Journal of Tropical Ecology 34(4): 209–234.
MUGGENTHALER E. K. VON, STOUGHTON J. W. & DANIEL J. C. Jr., 1993. Infrasound from the Rhinocerotidae, pp. 136–140. In: Ryder O. A. (ed.): Rhinoceros Biology and Conservation. Zoological Society, San Diego, v + 368 pp.
NARDELLI F., 1986. The conservation of the Javan rhinoceros (*Rhinoceros sondaicus* Desm.) - a proposal, pp. 59–64. In: Asian Rhino Specialist Group, 1987. Proceedings of the fourth IUCN/SSC Asian Rhino Specialist Group meeting, held in Jakarta 13–14 October 1986. Rimba Indonesia 21(1): 1–100.

NARDELLI F., 1988. Project to conserve the Javan rhinoceros (the lesser one-horned Asiatic rhinoceros - *Rhinoceros sondaicus* Desm.): project rationale and outline. Report to IUCN (unpublished), 55 pp.
NARDELLI F., 2013. The megafolivorous mammals of the rainforest: feeding ecology in nature and in controlled environment: a contribution to their conservation. International Zoo News 60(5): 323–339.
NARDELLI F., 2016.Current status and conservation prospects for the Javan rhinoceros *Rhinoceros sondaicus* (Desmarest 1822). International Zoo News 63(3): 180–202.
NARDELLI F., 2017. If we wish to save the Javan rhinoceros, we must work to know it (com-mentary). Mongabay Series: Asian Rhinos. https://news.mongabay.com/2017/06/if-we-wish-to-save-the-javan-rhinoceros-we-must-work-to-know-it-commentary/. Accessed on 14 January 2023.
OWEN-SMITH N., 1973. The behavioural ecology of the white rhinoceros. Dissertation, University of Wisconsin Madison, xxii + 786 pp.
OWEN-SMITH N., 1975. The social ethology of the white rhinoceros *Ceratotherium simum* (Burchell, 1817). Zeitschrift für Tierpsychologie 38(4): 337–384.
PAULY D., 1995. Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution 10(10): 430.
PEACOCK R. H., 1933. A Game Book for Burma and Adjoining Territories. H. F. and G. Witherby, London, 292 pp.
POLET g., TRAN VAN MUI, NGUYEN XUAN DANG, BUI HUU MANH & BALTZER M., 1999. The Javan rhinos, *Rhinoceros sondaicus annamiticus*, of Cat Tien National Park, Vietnam: current status and management implications. Pachyderm 27, 34–48.
PUTRA W. P. B., SYAMSUDIN M. & FIRDAUS A. Y., 2020. Population structure of Javan rhinoceros at Ujung Kulon National Park, West Java. Bulletin Plasma Nutfah 26(2): 103–108.
PUTRO HARYNATO R., 2023. Pendekatan baru konservasi Badak Jawa (*Rhinoceros sondaicus*) Desmarest, 1822. Policy Brief 2023: 1–5.
RAMONO W. S., SANTIAPILLAI C. & MACKINNON K., 1993. Conservation and management of Javan rhino (*Rhinoceros sondaicus*) in Indonesia, pp. 265–273. In: Ryder O. A. (ed.): Rhinoceros Biology and Conservation. Zoological Society, San Diego, v + 368 pp.
ROBOVSKÝ J. & ROOKMAAKER K. C., 2022. Rhinoceros specimens included in anatomical and morphological studies by Professor Alexander J. E. Cave (Perissodactyla: Rhinocerotidae). Lynx n. s. (Praha) 53(1): 333–350.
ROOKMAAKER L. C., 1977. The rhinoceros of Borneo: a 19th century puzzle. Journal of the Malayan Branch of the Royal Asiatic Society 50(1): 52–62.
ROOKMAAKER L. C., 1980. The distribution of the rhinoceros in Eastern India, Bangladesh, China and the Indo-Chinese region. Zoologische Anzeiger 205(3/4): 253–268.
ROOKMAAKER L. C., 1997. Records of the Sundarbans rhinoceros (*Rhinoceros sondaicus inermis*) in India and Bangladesh. Pachyderm 24: 37–45.
ROOKMAAKER L. C., 1998. The Rhinoceros in Captivity: A List of 2439 Rhinoceroses Kept from Roman Times to 1994. SPB Academic Publishing, The Hague, vi + 409 pp.
ROOKMAAKER L. C., 2002. Historical records of the Javan rhinoceros in North-East India. Newsletter of the Rhino Foundation of Nature in North-East India 4: 11–12.
ROOKMAAKER L. C., 2006. Distribution and extinction of the rhinoceros in China: review of recent Chinese publications. Pachyderm 40: 102–106.
ROOKMAAKER L. C., 2016.On the alleged presence of the two-horned Sumatran rhinoceros and the one-horned Javan rhinoceros in the Himalayan kingdom of Bhutan. Pachyderm 57: 116–117.
ROTH T. L., O'BRIEN J., MCRAE M., BELLEM A., ROMO S., KROLL J. & BROWN J. L., 2001. Ultrasound and endocrine evaluation of the ovarian cycle and early pregnancy in the Sumatran rhinoceros (*Dicerorhinus sumtrensis*). Reproduction 121(1): 139–49.
SANTIAPILLAI C., 1990. Status of the Javan rhino in divide - Ujong Kulon National Park. Tiger Paper 17(2): 1–8.
SANTIAPILLAI C. & SUPRAHMAN H., 1986. The proposed translocation of the Javan rhinoceros. Biological Conservation 38(1): 11–19.
SARAGUSTY J., DIECKE S., DRUKKER M., DURRANT B., FRIEDRICH BEN-NUN I., GALLI C., GÖRITZ F., HAYASHI K., HERMES R. & HOLTZE S., 2016. Rewinding the process of mammalian extinction. Zoo Biology 35(4): 280–292.

SCOTT J. M., GOBLE D. D., HAINES A. M., WIENS J. A. & NEEL M. C., 2010. Conservation reliant species and the future of conservation. Conservation Letters 3(2): 91–97.
SEAL U. S. & FOOSE T., 1989. Javan rhinoceros: Population Viability Analysis. IUCN/SSC Captive Breeding Specialist Group, Apple Valley, 100 pp.
SCOTT S. E., CAIN B., DE KORT S. R., JOHNSON B., KHAYALE C., VERSTEEGE L. & BETTRIDGE C. M., 2023. Group composition impacts reproductive output and population viability in captive white rhinoceros. Animal Conservation 26(3): 290–302.
SCHELLHORN R., 2018. A potential link between lateral semicircular canal orientation, head posture, and dietary habits in extant rhinos (Perissodactyla, Rhinocerotidae). Journal of Morphology 279(1): 50–61.
SODY H. J. V., 1941. De Javaansche neushoorn, *Rhinoceros sondaicus*, historish en biologisch. Buitenzorg, Archipel Drukkerij en, pp. i-vii, 1-156, figs. 1-25.
SODY H. J. V., 1959. Das Javanische Nashorn, *Rhinoceros sondaicus*, historish und biologisch. Zeitschrift für Säugetierkunde 24(3–4): 109–240.
STEPHENS P. A. & SUTHERLAND W. J., 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology and Evolution 14(10): 401–405.
STRIEN N. J. VAN, 1986. The Sumatran rhinoceros *Dicerorhinus sumatrensis* (Fisher, 1814) in the Gunung Leuser National Park, Sumatra, Indonesia: its distribution, ecology and conservation. Mammalian Depicta 12: i–vii + 1–200.
SURAPRASIT K, JAEGER J.-J., SHOOCONGDEJ R., CHAIMANEE Y., WATTANAPITUKSAKUL A. & BOCHERENS H., 2020.Long-term isotope evidence on the diet and habitat breadth of Pleistocene to Holocene Caprines in Thailand: Implications for the Extirpation and Conservation of Himalayan gorals. Frontiers in Ecology and Evolution 8: 67. https://doi.org/10.3389/fevo.2020.00067.
TAYLOR L. A., KAISER T. M., SCHWITZER C., MÜLLER D. W. H., CODRON D., CLAUSS M. & SCHULZ E., 2013. Detecting inter-cusp and inter-tooth wear patterns in rhinocerotids. PLoS ONE 8(12): e80921. https://doi.org/10.1371/journal.pone.0080921.
TRIFONOV V. A, MUSILOVÁ P. & KULEMSINA A. I., 2012.Chromosome evolution in Perissodactyla**.** Cytogenetic and Genome Research 137(2–4): 208–217.
WEDEKIND C., 2012. Managing population sex ratios in conservation practice: how and why?, pp. 81–96. In: Povilitis T. (ed.): Topics in Conservation Biology. InTech, available from: http://dx.doi.org/10.5772/2141.
WILSON S. G., 2021. Factors shaping the conservation of the critically endangered Javan Rhinoceros – *Rhinoceros sondaicus*. Ph.D. thesis, School of Biological Sciences, University of Queensland, Brisbane, viii + 268 pp.
ZIN-MAUNG-MAUNG-THEIN, THAUNG-HTIKE, TSUBAMATO T., TAKAI M., EGI N. & MAUNG-MAUNG, 2006. Early Pleistocene Javan rhinoceros from the Irawaddy Formation, Myanmar. Asian Paleoprimatology 4: 197–204.