ORIGINAL ARTICLE



Suspected Sunda clouded leopard (*Neofelis diardi*) predation attempts on two reintroduced Bornean orangutans (*Pongo pygmaeus wurmbii*) in Bukit Batikap Protection Forest, Central Kalimantan, Indonesia

Jacqueline L. Sunderland-Groves^{1,2} · Maryos V. Tandang¹ · Fiet Hayu Patispathika¹ · Anna Marzec³ · Andrea Knox¹ · Anton Nurcahyo¹ · Simon J. Husson¹ · Jamartin Sihite¹

Received: 14 December 2019 / Accepted: 25 June 2020 © Japan Monkey Centre and Springer Japan KK, part of Springer Nature 2020

Abstract

In February 2017 and August 2018, respectively, two Bornean orangutans (*Pongo pygmaeus wurmbii*) reintroduced into the Bukit Batikap Protection Forest in Central Kalimantan were found in weakened physical condition and with deep puncture wounds. The first individual was a sub-adult male, and the second an adult female whose 6- to 8-week-old infant was missing. Both individuals were rescued and transported back to the field base camp for treatment. Experienced veterinarians treating the injuries reported that the type of wounds appeared consistent with those expected from an attack by a large felid. The Sunda clouded leopard (*Neofelis diardi*) is the largest felid known to inhabit Bukit Batikap Protection Forest, and we suspect that these cases were unsuccessful predatory attacks by this species. Given the severity of his condition when found, the male orangutan would probably have died without medical intervention; however, both orangutans fully recovered following intensive treatment and were successfully returned to the forest. Predation attempts on orangutans are infrequently reported, thus our observations add to the body of knowledge about possible predation by clouded leopards on reintroduced, rehabilitant orangutans.

Keywords Bornean orangutan · Sunda clouded leopard · Predation · Reintroduction

Introduction

Most reports of felid predation and attempted predation on great apes, though rare, concern African great apes and include both fatal and non-fatal attacks on chimpanzees (*Pan troglodytes*), gorillas (*Gorilla* spp.) and bonobos (*Pan paniscus*) (summarized in Klailova et al. 2012). There are fewer published accounts of felid predation on orangutans (*Pongo* spp.), which continue to survive in rapidly dwindling numbers on the islands of Borneo and Sumatra (Ancrenaz

et al. 2016; Singleton et al. 2017; Utami-Atmoko et al. 2017). On Sumatra, Rijksen (1978) reported incidents of tiger predation on wild and rehabilitant orangutans, and both successful and unsuccessful clouded leopard attacks on rehabilitant orangutans. In Indonesian Borneo, where tigers are absent, two wild female orangutans with dependent young were possibly attacked by clouded leopards in Tuanan, a long-term orangutan research site located in Central Kalimantan (Marzec et al. 2016; van Noordwijk et al. 2018). In Sabah, Malaysian Borneo, a suspected clouded leopard attack in Danum Valley preceded the deterioration and death of a wild juvenile female orangutan (Kanamori et al. 2012). Despite only a handful of reports, clouded leopards are a recognized orangutan predator (Phillipps and Phillipps 2016) and are known to prey on other primate species including gibbons (Morino 2011) and proboscis monkeys (Nasalis larvatus) (Matsuda et al. 2008). Further, mobbing of a clouded leopard by langurs, gibbons (Wilcox et al. 2016) and orangutans (Oram, unpublished data in van Noordwijk et al. 2018) suggest that clouded leopards

Published online: 04 July 2020



[☐] Jacqueline L. Sunderland-Groves jacqui.sunderland-groves@ubc.ca

Borneo Orangutan Survival Foundation, Jalan Kumbang No. 31, Bogor, West Java, Indonesia

Faculty of Forestry, Department of Forest Resources Management, University of British Columbia, 2424 Main Mall, Vancouver, BC, Canada

³ University of Zurich, Rämistrasse 71, 8006 Zürich, Switzerland

are seen as a threat by orangutans, at least immatures (van Noordwijk et al. 2018).

Only a few non-human predators pose a threat to orangutans on Borneo: the Sunda clouded leopard (Neofelis diardi), snake species including pythons (Python reticulatus), and crocodiles (Crocodylus spp.). Sun bears (Helarctos malayanus) may scavenge on dead carcasses, but are primarily frugivores that supplement their diet with invertebrates, honey and small mammals (Fredriksson et al. 2006; Wong et al. 2002, 2004) and are not known to attack orangutans (Kanamori et al. 2012; Knott et al 2019). All of these species occur in the Bukit Batikap Protection Forest in Central Kalimantan, Indonesia, a focal site of the Borneo Orangutan Survival (BOS) Foundation, where 175 Bornean orangutans (Pongo pygmaeus wurmbii) were reintroduced with the purpose of establishing a new, viable population to bolster conservation prospects of this Critically Endangered species.

Multiple factors influence orangutan reintroduction success, including foraging ability, disease, parasitic infection, skill-related injuries and assaults by predators, conspecifics and humans (Russon 2009). Wild-born orangutans face these risks too, but they are generally greater in reintroduced rehabilitated orangutans which were separated from their mothers at a young age and thus lost opportunities to learn skills including predator avoidance. Teaching orangutans how to avoid predators in a rehabilitation setting is often not feasible because predators are usually absent. Although the BOS Foundation attempts to instill predator avoidance behaviour by using rubber snakes to create fear of potentially dangerous reptiles, due to the difficulties involved, teaching orangutans about other dangerous species such as large felids is not attempted. Rehabilitation efforts, therefore, focus on encouraging the orangutans to feed, travel, and nest arboreally and limit the time they spend on the forest floor. It should be noted, however, that the clouded leopard is an expert tree climber (Chiang and Allen 2017).

Limited to the islands of Borneo and Sumatra (Hearn et al 2015), the Sunda clouded leopard (*Neofelis diardi*) is a medium-sized cat measuring up to 2 m in length with tail length being roughly equal to body length, and an average weight of 11–23 kg (Chiang and Allen 2017). Because of their elusive nature their ecology is not well known; however, their varied diet includes terrestrial birds, ungulates, primates, rodents, domestic animals and occasionally fish and snakes (Hearn et al. 2016; Chiang and Allen 2017). They are morphologically (Kitchener et al. 2006; Christiansen 2008) and genetically (Buckley-Beason et al. 2006; Wilting et al. 2007) distinct from mainland clouded leopards (*Neofelis nebulosa*), with craniomandibular morphology that resembles that of primitive saber-toothed cats. Their bladelike upper canines are elongated in

proportion to the skull, and combined with an enlarged gape (Christiansen 2006, 2008), allow them to inflict a powerful bite (Therrien 2005) to the back of the head, neck or upper limbs (Rabinowitz et al. 1987; Kitchener 1991; Ewer 1998; Grassman et al. 2005). Clouded leopards hunt prey that are of similar size to or smaller than themselves, but they may also hunt much bigger species (Rabinowitz et al 1987; Grassman et al. 2005) such as sambar deer (Mohamed et al. 2009). Recent surveys indicate that they spend a larger proportion of time on the ground than previously thought (Hearn et al. 2015), and may be more terrestrial on Borneo given the absence of tigers (Rabinowitz et al. 1987). This absence of tigers is also thought to influence clouded leopard activity patterns, and whilst they are active during the day, they are predominantly nocturnal (Adul et al. 2015; Cheyne and MacDonald 2011). The clouded leopard population is estimated at roughly 3,800 mature individuals spread across Borneo (Hearn et al. 2015), and Bukit Batikap is one of a handful of locations considered important for their conservation in Central Kalimantan (Hearn et al. 2016).

Here we document our discovery of two reintroduced orangutans with external injuries, 18 months apart, in locations separated by just over 1 km (Fig. 1). We describe their injuries and explain why we suspect they were caused by clouded leopards.

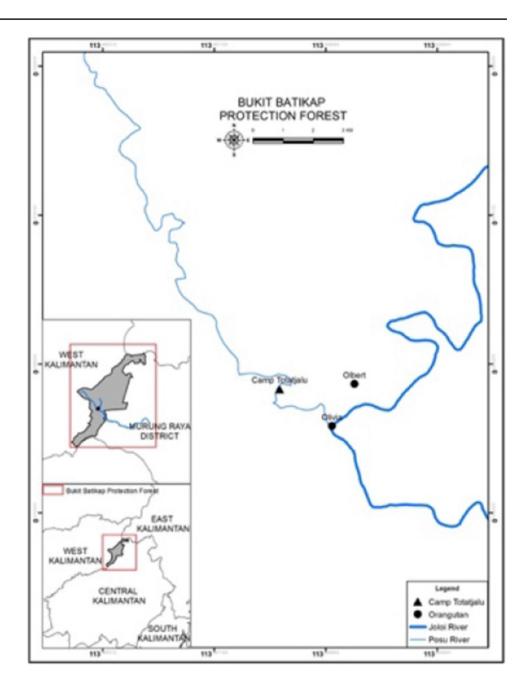
Methods

Study site

Located in the Murung Raya district of Central Kalimantan, Indonesia, Bukit Batikap Protection Forest is situated within the Muller-Schwaner mountain range that forms the central spine of Borneo from which all its major rivers originate. The habitat comprises undisturbed tropical rainforest surrounding the headwaters of the Joloi and Busang rivers, two major tributaries of the Barito river. The topography ranges from 100 m to 1,580 m with vegetation in the lower altitude areas dominated by species of the Dipterocarpaceae family. As the elevation increases from 200 to 750 m, hill forest occurs with fewer dipterocarp species, and depauperate kerangas heath forest is found at higher elevations. The area is protected as Hutan Lindung (Protection Forest) to conserve watersheds. Logging is prohibited, hence the forest remains largely intact, although some small-scale, illegal logging occurs. Local communities farm around their immediate villages, and people enter the forest to collect forest and non-forest products, such as gaharu (agarwood; Aquilaria malaccensis), gold, and swiftlet nests, and also to fish or hunt. In 2012, the BOS Foundation commenced orangutan reintroductions within a core area of Batikap covering 35,267 ha, which was estimated to be of sufficient



Fig. 1 Geographic location of Bukit Batikap Protection Forest, and positions of the two orangutan retrievals



size to support up to 312 individuals. From our research station, Camp Totat Jalu (00.0410 N 113.4990 E) (Fig. 1), reintroduced orangutans are monitored either through radiotracking or direct observations based on knowledge of their ranges.

Orangutan reintroduction

Orangutan reintroductions took place in Batikap between 2012 and 2017, comprising 98 wild-born, ex-captive rehabilitants, 36 individuals who were born on prerelease islands, and 41 who were rescued at an older age and had retained some of their natural skills and hence

were categorized as semi-wild. Notably, the rehabilitated orangutans had spent most of their lives learning forest survival skills from human surrogates, whereas the semi-wild orangutans had benefited from substantial learning in the wild from their mothers pre-captivity. Prior to reintroduction, all the orangutans were assessed on their wild skills and screened for disease, and those above 6 years of age were implanted with a novel radiotracking device to aid post-release monitoring (Robins et al. 2013). Post-release monitoring is recommended by the International Union for Conservation of Nature (Beck et al. 2007) to assess post-release health, behaviour and adaptation.



Orangutan profiles

The two orangutans we discuss were reintroduced into the study area in April 2016, together with two other males and eight females. Sub-adult male Olbert was approximately 12 years old upon release and weighed 44 kg; adult female Olivia was estimated at 15 years old and weighed 54 kg. Olbert was brought to the BOS Foundation's rehabilitation centre in Central Kalimantan, Nyaru Menteng in 2007 as a 3–3.5 year old, and demonstrated good forest skills. He progressed through rehabilitation, and given his history of early learning in the wild, was classified as semi-wild. Olivia arrived at Nyaru Menteng in early 2003 as a 1- to 1.5-year-old infant. She progressed through the entire process of rehabilitation, and hence was classified as a rehabilitant.

Results

Olbert

Olbert was observed or radio-tracked 73 times from the day of his reintroduction to the day he was found critically injured. During this time, he appeared to experience some difficulties adapting and also periods of illness. For 3 days in June 2016, he was inactive and on 1 day remained in his nest for the entire day. In September Olbert again looked unwell, and in early December appeared weak and thin. He was monitored daily, during which time he repeatedly nested early and on some days remained in his nest. Out of growing concern for his health, he was given supplementary food and a deworming treatment. Olbert was subsequently seen on 7 days and radio-tracked on 1 day, with the last sighting on 9 January 2017. On 4 February 2017, Olbert was located by the post-release monitoring team along an existing trail, feeding on the ground. He was severely underweight and had sustained two large wounds, one to the left side of his head (Fig. 2a, b) and another to his left upper arm (Fig. 3a-c). He was anesthetized using a dart gun, placed on a hammock stretcher and transported to camp where a thorough examination was conducted (Fig. 4). The injuries were not fresh and damage to soft tissue and muscle through fly maggot infestations made it difficult to measure the original size of the wounds; however, the puncture holes were prominent and slender (Fig. 3c). The wound to his arm appeared as a distinct tear to the skin, caused either by a fang or claw, and according to photographs taken at the time, the puncture wounds in his upper arm were approximately 3 cm, 3.5 cm and 5.5 cm apart (Fig. 3c). Numerous scratches and wounds were found on his back and other parts of his body, including a smaller wound to the front of his shoulder, which appeared to connect through the arm to the large puncture wound in his upper arm (Fig. 3a, b). His wounds were flushed and antibiotics, analgesic and anti-inflammatory medication administered.

The following day, Olbert's immediate condition seemed to have improved; however, an additional wound was located on the left scrotum, which was also infested with maggots. Due to an inadequate supply of required drugs and supplies at camp, a further anaesthesia was scheduled once these arrived. Olbert's condition deteriorated during the night and he was once again anaesthetized, placed on intravenous fluids and administered a combination of drugs to treat infection. Although the wounds were cleaned thoroughly, maggots persisted deep inside the wounds to his arm and back, which could only be completely removed with specialist medical tools.

Over the following 2.5 months, Olbert was anaesthetized a total of nine times to clean the wounds and administer medication. These efforts were continually hampered by flies laying eggs in his clean wounds despite the use of deterrent spray. By 20 March the wounds on Olbert's head were healed to the point at which the skin could be sutured; however, two puncture wounds on his arm continued to require attention.

Fig. 2 a, b Injuries sustained to the left side of Olbert's head (*arrows* show puncture wounds and scratches)







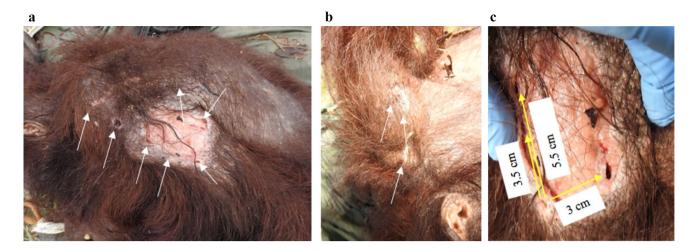


Fig. 3 Injuries (arrows show scratches and puncture wounds) sustained to Olbert's left upper arm (a), side of arm (b), front of shoulder (c) (with measurements between puncture wounds)



Fig. 4 Olbert's condition once he had been sedated and transported to camp

On 6 April, more than 2 months after Olbert was found injured, his wounds had healed, and on 23 April 2018 he was re-released close to the point where he was originally found (Fig. 1).

Prior to getting injured Olbert was often observed on the ground either feeding, resting or travelling. He sometimes descended to the ground to investigate human observers, possibly in search of company. Before the injuries Olbert spent 28% of his daily activity budget on the ground (n=265 h observation), compared to just 5% following his recovery and re-release (n=66 h).

Olivia

In September 2016, five months after her reintroduction, Olivia appeared to have lost weight and looked skinny; however, she was feeding well and no intervention was deemed necessary. Early in 2018, Olivia presented physical signs of pregnancy and on 19 July she was observed with her first newborn in Batikap. Olivia and her baby were observed again in late July and early August, and although previously being well known for harassing human observers, Olivia now appeared more cautious, only giving chase if humans persisted in following her. The baby's grip on Olivia appeared weak; however, Olivia was seen on 13 August in good health, with her baby clinging to her. On 21 August the team again observed Olivia but were unable to confirm the presence of her infant, and 2 days later she was observed in the same location without her infant. She had lost weight (weight at recapture was estimated at 35 kg) with joint and hip bones visibly protruding, and she had two large maggotinfested wounds near her anus (Fig. 5). She made no attempts to chase the monitoring team and was coaxed using food into a transport cage, then transported to the transit cage close to the camp. Whilst awaiting veterinary support, she was given oral antibiotics and provided with a variety of food, liquids and nesting materials. Olivia appeared to maintain a good appetite although she was lethargic, lying almost continually in her nest, picking at her wounds. Five days later Olivia's appetite decreased and her wounds appeared to have increased in size. Once the veterinarian arrived, Olivia was anaesthetized, placed on an intravenous drip and her wounds were cleaned and measured. The first wound was small, roughly $2 \text{ cm} \times 0.05 \text{ cm}$, and the second wound larger at 4 cm × 2 cm. There were puncture wounds within the larger wound, each up to 4 cm deep and spaced 0.5 cm apart. The following day Olivia's health had greatly improved and she continued to heal quickly. She was re-released into the forest on 9 September 2018.

Olivia was frequently observed on the ground. She often watched the monitoring team intently and she sometimes



Fig. 5 Olivia's wounds to her anus (a) and puncture wounds within the larger wound (b) (30 August 2018)





aggressively chased people. Prior to her injuries Olivia spent 35% of her activity budget on the ground (n=206 h), and after her re-release this increased to 63% (n=49 h). Her interest in people also increased, from 7 to 13% of her activity budget.

Discussion

In the cases we report on here, the type of scratches and wounds, and depths and distances of puncture holes sustained by the orangutans are largely consistent with the dentition of a large carnivore, although the distances between puncture wounds do not completely match expected distances. The inter-canine width of a clouded leopard is around 3 cm (Grassman et al. 2005). The distance between the wounds we encountered varied, possibly because they were inflicted by the upper and lower canines, or from different bites. The scratches, teeth marks and slash wounds indicated a large felid, which in Batikap could only be the clouded leopard. All injuries were on the orangutans' backs or rear ends, suggesting attacks from behind, a known killing strategy of the clouded leopard (Rabinowitz et al. 1987). Another wound on Olbert's left upper arm bore a striking resemblance to one sustained by a young female orangutan believed to have been attacked by a clouded leopard in Sabah (Kanamori et al. 2012). Whilst clouded leopards do hunt in trees (Matsuda et al. 2008) they are believed to be mostly terrestrial. Rehabilitated, reintroduced orangutans tend to spend significantly more time on the ground (Grundmann 2006) than wild Bornean orangutans (Loken et al. 2013; Ancrenaz et al. 2014; Ashbury 2015). In Batikap, reintroduced orangutans were infrequently found at heights between 0 and 5 m (Nayasilana et al. 2017); however, Olbert and Olivia spent more time on the ground than other orangutans in Batikap, and we speculate that they were attacked on the ground. Although we acknowledge that Olbert and Olivia may have descended upon detecting human observers, they both appeared at ease on the ground: Olivia with her newborn, Olbert possibly too physically weak to climb.

Animals other than clouded leopards can also deliver deep bite wounds, including orangutans during male-male fighting, for example (Utami Atmoko 2000; Utami Atmoko et al. 2009). Conflicts between orangutans generally result in facial wounds or the loss of digits, and in rare cases, death (Galdikas 1985; Knott 1998; Marzec et al. 2016). The experienced BOS Foundation veterinarians are familiar with orangutan-inflicted wounds, and concluded that those sustained by Olbert and Olivia did not fall into that category. Nor were either of these individuals flanged adult males, the usual recipients of wounds sustained in conflict.

Infanticide cannot be ruled out in Olivia's case, though only one suspected infanticidal attack in wild orangutans has been reported, in which the mother lost her baby and part of her left foot from a suspected male orangutan bite (Knott et al. 2019).

Sun bears and hunting dogs are less likely candidates, as the types of injuries on the orangutans did not appear to be consistent with those inflicted by these species. In particular, bears generally attack indiscriminately using their forepaws and teeth, and the long, thick claws of a sun bear would have delivered very prominent scratch wounds. Furthermore, there are no recorded sun bear attacks on orangutans (see Knott et al. 2019), and they are generally passive, nonconfrontational animals. The bite size, bite force and killing strategy of domestic hunting dogs also rules them out as injuring the orangutans. When dogs attack and kill orangutans, multiple dogs are involved, biting different parts of the body simultaneously in a prolonged attack. Olbert and Olivia's injuries are inconsistent with this scenario, and had dogs been involved the orangutans would probably have been killed.

It is interesting to compare the post-attack survival of these two orangutans with outcomes in other reported cases. In one case reported by Kanamori et al. (2012), despite being



lighter and smaller than Olbert or Olivia, the young female victim managed to escape, but grew increasingly weak and succumbed to septicaemia 7 days later. Both Olbert and Olivia were weakened when they were found injured, and although they ate small amounts of food they were largely inactive for 3–5 days while being treated in camp; presumably they would have died without adequate care. In North Sumatra, Rijksen (1978) reported that one adolescent rehabilitant female died from a deep cut to her abdomen inflicted by a clouded leopard, and another was only saved thanks to surgery. At that site adolescents were generally wounded rather than killed outright, whereas juveniles were killed during the attacks, leading Rijksen (1978) to suggest that in the hunting technique of the clouded leopard 'the prey is not pursued after the initial strike'. He further suggested adolescent and older orangutans may be too big for clouded leopard predation, and because young orangutans stay close to their mothers for protection, clouded leopards were probably no more than occasional predators on the species. However, clouded leopards occasionally successfully prey on animals larger than themselves [e.g., a sambar deer weighing an estimated 30–35 kg (Mohamed et al. 2009); a bearded pig weighing 20-25 kg (Wilting, unpublished data cited in Mohamed et al. 2009)].

As a new mother who spent time on the ground, Olivia may have been an easy target for a clouded leopard. We speculate that the predator may have settled for her infant as the meal, resulting in the comparative lack of wounds on Olivia. One adult female orangutan suspected to have been attacked by a clouded leopard in Tuanan, Central Kalimantan was often found on the ground and was in poor condition before her injuries, which resulted in her death and the orphaning of her uninjured 3.5-year-old infant (van Noordwijk, personal communication; Marzec et al. 2016; Noordwijk et al. 2018). An autopsy revealed eight puncture wounds (holes) on the right side of the nape of the neck, two large and around 3 cm deep, and four puncture wounds to the left, one of which damaged the skull. A second female victim of a suspected clouded leopard attack survived her injuries but was discovered without her infant (van Noordwijk et al. 2018). However, we cannot confidently discount alternative explanations for the disappearance of Olivia's infant; for example, as a first-time mother she may have provided inadequate care, the infant might have been fatally sick, or suffered an accident.

We speculate that Olbert's injuries were also sustained whilst he was on the ground, given his known terrestrial behaviour and bouts of illness. Furthermore, his head and upper arm wounds indicated an attack from behind, unlikely to have been executed arboreally. It is noteworthy that following his return to health and re-release, Olbert was rarely recorded on the ground but mostly travelled and fed arboreally. Since the events described here, both Olbert and

Olivia have surpassed their 2-year milestone in the forest, and are presumably more experienced and wiser.

Conclusion

Rehabilitant, reintroduced orangutans face challenges adapting to life in the wild because of their history of human care. They must learn multiple skills, including how to avoid dangerous humans and non-human species, and this learning has to continue post-release. Human surrogates can teach the rehabilitants up to a certain point, but ultimately their longterm reintroduction success is down to each individual's ability to adapt and learn necessary survival skills. The Bukit Batikap Protection Forest was chosen as a reintroduction site for orangutans because it contains a vast area of undisturbed, diverse lowland rainforest with relatively low human activity, and high elevation ridges that act as a dispersal barrier. Macdonald et al. (2018) reported strong, positive associations between clouded leopard occurrence and these same habitat conditions. Potentially, Batikap could support higher densities of clouded leopards than elsewhere in Borneo, although no quantitative surveys have been carried out to date. Nevertheless, clouded leopards occur throughout the orangutan's natural range, and if they are indeed the cause of the injuries described here, then they must be considered a natural threat to young or unhealthy orangutans everywhere, albeit a relatively minor one. Potential clouded leopard predation is something wild orangutans have to manage, and reintroduced rehabilitated orangutans have to adapt to. Our basic criterion for successful orangutan reintroduction is for an individual to live free without human intervention for a period of 12 months post-release. Of the 175 orangutans reintroduced into Batikap, at least two thirds have reached this 1-year milestone, with 20 infants raised by reintroduced females (unpublished data). This indicates that most reintroduced orangutans in Batikap are successfully dealing with the challenges of adaptation, including predator avoidance.

Acknowledgements The BOS Foundation's Central Kalimantan Orangutan Reintroduction Program is supported by partner organisations including BOS Australia, BOS Deutschland, BOS Schweiz, BOS UK and Save the Orangutan. We would like to express our sincere thanks to the following for supporting our work in Bukit Batikap during this study: Zoos Victoria and the Commonwealth of Australia through the Department of Environment and Energy; the US Fish and Wildlife Service Great Ape Conservation Fund; the Orangutan Project; the Margot Marsh Biodiversity Foundation; and Orangutan Outreach. We thank the Indonesian Government, the Ministry of Environment and Forestry, the Directorate General of Natural Resources and Ecosystem Conservation Ministry of Environment and Forestry, Central Kalimantan's Conservation of Natural Resources Agency (BKSDA), the Province of Central Kalimantan and the Regency of Murung Raya for their enthusiastic support, and our sincere appreciation to the people of Kecamatan Seribu Riam. We are indebted to the BOS Foundation field team for the many hours spent gathering



post-release data in Batikap, and to Alizée Martin and Ahmat Suyoko. Finally, we are grateful to Susan Cheyne for providing comments on earlier versions of this manuscript, to Maria van Noordwijk for sharing unpublished observations and to two anonymous reviewers of this manuscript. The photographic images we present were taken by Anna Marzec, Pak Johanis and Andrea Knox.

References

- Adul A, Ripoll-Capilla B, Limin SH, Cheyne SM (2015) Felids of Sebangau: camera trapping to estimate activity patterns and population abundance in Central Kalimantan, Indonesia. Biodiversitas 16:151–155. https://doi.org/10.13057/biodiv/d1602
- Ancrenaz M, Sollmann R, Meijaard E, Hearn AJ, Ross J, Samejima H, Loken B, Cheyne SM, Stark DJ, Gardner PC, Goossens B, Mohamed A, Bohm T, Matsuda I, Nakabayasi M, Lee SK, Bernard H, Brodie J, Wich S, Fredriksson G, Hanya G, Harrison ME, Kanamori T, Kretzschmar P, Macdonald DW, Riger P, Spehar S, Ambu LN, Wilting A (2014) Coming down from the trees: is terrestrial activity in Bornean orangutans natural or disturbance driven? Sci Rep 4:4024. https://doi.org/10.1038/srep04024
- Ancrenaz M, Gumal M, Marshall AJ, Meijaard E, Wich SA, Husson S (2016) *Pongo pygmaeus*. The IUCN Red List of threatened species 2016. http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS. T17975A17966347.en
- Ashbury AM, Posa MRC, Dunkel L, Spillmann B, Utami Atmoko SS, van Shaik CP, van Noordwijk MA (2015) Why do orangutans leave the trees? Terrestrial behavior among wild Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, Central Kalimantan. Am J Primatol 77:1216–1229. https://doi.org/10.1002/ajp.22460
- Beck B, Walkup K, Rodrigues M, Unwin S, Travis D, Stoinski T (2007) Best practice guidelines for the re-introduction of great apes. SSC Primate Specialist Group of the World Conservation Union, Gland, p 48
- Buckley-Beason VA, Johnson WE, Nash WG, Stanyon R, Menninger JC, Driscoll CA, Howard J, Bush M, Page JE, Roelke ME, Stone G, Martelli P, Wen C, Ling L, Duraisingam RK, Lam VP, O'Brien SJ (2006) Molecular evidence for species-level distinctions in clouded leopards. Curr Biol 16:2371–2376. https://doi.org/10.1016/j.cub.2006.08.066
- Cheyne SM, Macdonald DW (2011) Wild felid diversity and activity patterns in Sabangau peat-swamp forest Indonesian Borneo. Oryx 45(1):119–124. https://doi.org/10.1017/S003060531000133X
- Chiang PJ, Allen ML (2017) A review of our current knowledge of clouded leopards (*Neofelis nebulosa*). Int J Avian Wildl Biol 2:148–154. https://doi.org/10.15406/ijawb.2017.02.00032
- Christiansen P (2006) Sabertooth characters in the clouded leopard (*Neofelis nebulosa* Griffiths 1821). J Morphol 267:1186–1198. https://doi.org/10.1002/jmor.10468
- Christiansen P (2008) Species distinction and evolutionary differences in the clouded leopard (*Neofelis nebulosa*) and Diard's clouded leopard (*Neofelis diardi*). J Mammal 89:1435–1446. https://doi.org/10.1644/08-MAMM-A-013.1
- Ewer RF (1998) The carnivores. Cornell University Press, Cornell Fredriksson GM, Wich SA, Trisno (2006) Frugivory in sun bears (*Helarctos malayanus*) is linked to El Niño-related fluctuations in fruiting phenology, East Kalimantan, Indonesia. Bio J Linn Soc 89:489–508. https://doi.org/10.1111/j.1095-8312.2006.00688
- Galdikas BMF (1985) Adult male sociality and reproductive tactics among orangutans at Tanjung Puting Reserve. Folia Primatol 45:9–24. https://doi.org/10.1159/000156188

- Grassman LI Jr, Tewes ME, Silvy NJ, Kreetiyutanont K (2005) Ecology of three sympatric felids in a mixed evergreen forest in North-Central Thailand. J Mammal 86:29–38. https://doi. org/10.1644/1545-1542(2005)086<0029:EOTSFI>2.0.CO;2
- Grundmann E (2006) Back to the wild: will reintroduction and rehabilitation help the long-term conservation of orangutans in Indonesia? Soc Sci Info 45:265–284. https://doi.org/10.1177/0539018406063643
- Hearn A, Ross J, Brodie J, Cheyne S, Haidir IA, Loken B, Mathai J, Wilting A, McCarthy J (2015) *Neofelis diardi* (errata version published in 2016). The IUCN Red List of threatened species 2015. http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS. T136603A50664601.en. Accessed 12 Jun 2019
- Hearn AJ, Ross J, Macdonald DW, Bolongon G, Cheyne SM, Mohamed A, Samejima H, Brodie JF, Giordano A, Alfred R, Boonratana R, Bernard H, Loken B, Augeri DM, Heydon M, Hon J, Mathai J, Marshall AJ, Pilgrim JD, Hall J, Breitenmoser-Würsten C, Kramer-Schadt S, Wilting A (2016) Predicted distribution of the Sunda clouded leopard *Neofelis diardi* (Mammalia: Carnivora: Felidae) on Borneo. Raffles B Zool Suppl 33:149–156
- Kanamori T, Kuze N, Bernard H, Malim TP, Kohshima S (2012) Fatality of a wild Bornean orangutan (*Pongo pygmaeus morio*): behaviour and death of a wounded juvenile in Danum Valley, North Borneo. Primates 53:221–226. https://doi.org/10.1007/ s10329-012-0297-3
- Kitchener A (1991) The natural history of the wild cats. Comstock, Cornell
- Kitchener AC, Beaumont MA, Richardson D (2006) Geographical variation in the clouded leopard, *Neofelis nebulosa*, reveals two species. Curr Biol 16:2377–2383. https://doi.org/10.1016/j.cub.2006.10.066
- Klailova M, Casanova C, Henschel P, Lee P, Rovero F, Todd A (2012) Non-human predator interactions with wild great apes in Africa and the use of camera traps to study their dynamics. Folia Primatol 83:312–328. https://doi.org/10.1159/000342143
- Knott CD (1998) Orangutan in the wild. Natl Geogr Mag 194:30–57
 Knott CD, Scott AM, O'Connell CA, Scott KS, Laman TG, Riyandi STW (2019) Possible male infanticide in wild orangutans and a re-evaluation of infanticide risk. Sci Rep 9:7806. https://doi.org/10.1038/s41598-019-42856-w2
- Loken B, Spehar S, Rayadin Y (2013) Terrestriality in the Bornean orangutan (*Pongo pygmaeus morio*) and implications for their ecology and conservation. Am J Primatol 75:1129–1138. https:// doi.org/10.1002/ajp.22174
- Macdonald DW, Bothwell HM, Hearn AJ, Cheyne SM, Haidir I, Hunter LTB, Kaszta Z, Linkie M, Macdonald EA, Ross J, Cushman SA (2018) Multi-scale habitat selection modeling identifies threats and conservation opportunities for the Sunda clouded leopard (*Neofelis diardi*). Biol Conserv 227:92–103. https://doi.org/10.1016/j.biocon.2018.08.027
- Marzec AM, Kunz JA, Falkner A, Utami Atmoko SS, Alavi SE, Moldawer AM, Vogel ER, Schupplil C, van Schaik CP, van Noordwijk MA (2016) The dark side of the red ape: malemediated lethal female competition in Bornean orangutans. Behav Ecol Sociobiol 70:459–466. https://doi.org/10.1007/s00265-015-2053-3
- Matsuda I, Tuuga A, Higashi S (2008) Clouded leopard (*Neofelis diardi*) predation of proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. Primates 49:227–231. https://doi.org/10.1007/s10329-008-0085-2
- Mohamed AZ, Samejima HI, Wilting AN (2009) Records of five Bornean cat species from Deramakot Forest Reserve in Sabah, Malaysia. Cat News 51:12–15
- Morino L (2011) Clouded leopard predation on a wild juvenile siamang. Folia Primatol 81:362–368. https://doi.org/10.1159/000324303



- Nayasilana IN, Hadisusanto S, Wijayanto H, Utami Atmoko SS, Prasetyo D, Sihite J, van Schaik CP (2017) Behavioral ecology of reintroduced orangutans in the Bukit Batikap, Central Kalimantan, Indonesia. Biodiversitas 18:875–886. https://doi.org/10.13057/ biodiv/d180303
- Phillipps Q, Phillipps K (2016) Phillipps' field guide to the mammals of Borneo and their ecology: Sabah, Sarawak, Brunei, and Kalimantan. Princeton Field Guides, Princeton
- Rabinowitz AR, Andau P, Chai PPK (1987) The clouded leopard in Malaysian Borneo. Oryx 21:107–111. https://doi.org/10.1017/S0030605300026648
- Rijksen HD (1978) A field study on Sumatran orangutans (Pongo pygmaeus abelii, Lesson 1827), In: Veenman H, Zonen BV (eds) Ecology, behaviour and conservation. Wageningen, the Netherlands
- Robins JG, Ancrenaz M, Parker J, Goossens B, Ambu L, Walzer C (2013) The release of northeast Bornean orangutans to Tabin Wildlife Reserve, Sabah, Malaysia. In: Soorae PS (ed) Global re-introduction perspectives: 2013. Further case studies from around the globe. IUCN/SSC Reintroduction Specialist Group, Gland, Switzerland and Environment Agency-Abu Dhabi, Abu Dhabi, UAE, pp 215–221
- Russon AE (2009) Orangutan rehabilitation and reintroduction: successes, failures, and role in conservation. In: Wich SA, Atmoko SSU, Setia TM, van Schaik CP (eds) Orangutans geographic variation in behavioral ecology and conservation. Oxford University Press, New York, pp 327–350
- Singleton I, Wich SA, Nowak M, Usher G, Utami-Atmoko SS (2017)
 Pongo abelii. The IUCN Red List threatened species. https://doi.
 org/10.2305/IUCN.UK.2017-3.RLTS.T121097935A115575085
- Therrien F (2005) Feeding behaviour and bite force of sabretoothed predators. Zool J Linn Soc 145:393–426. https://doi.org/10.111 1/j.1096-3642.2005.00194.x
- Utami Atmoko S (2000) Bimaturism in orang-utan males: reproductive and ecological strategies. PhD thesis, University of Utrecht
- Utami Atmoko SS, Singleton I, van Noordwijk MA, van Shaik CP, Mitra Setia T (2009) Male-male relationships in orangutans in

- orangutans. In: Wich SA, Atmoko SSU, Setia TM, van Schaik CP (eds) Orangutans geographic variation in behavioral ecology and conservation. Oxford University Press, New York, pp 225–233
- Utami-Atmoko S, Traylor-Holzer K, Rifqi MA, Siregar PG, Achmad B, Priadjati A, Husson S, Wich S, Hadisiswoyo P, Saputra F, Campbell-Smith G, Kuncoro P, Russon A, Voigt M, Santika T, Nowak M, Singleton I, Sapari I, Meididit A, Chandradewi DS, Ripoll Capilla B, Ermayanti, Lees CM (eds) (2017) Orangutan population and habitat viability assessment: final report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN
- van Noordwijk MA, Utami Atmoko SS, Knott CD, Kuze N, Morrogh-Bernard HC, Oram F, Schuppli C, van Schaik CP, Willems EP (2018) The slow ape: high infant survival and long interbirth intervals in wild orangutans. J Hum Evol 125:38–49. https://doi.org/10.1016/j.jhevol.2018.09.004
- Wilcox CH, Supiansyah A-A, Zainuddin J, Rahman CSM (2016) Predator mobbing and interspecies cooperation: an interaction between gibbons, langurs and a clouded leopard. Asian Primates J 6:20–26
- Wilting A, Buckley-Beason VA, Feldhaar H, Gadau J, O'Brien SJ, Linsenmair KE (2007) Clouded leopard phylogeny revisited: support for species recognition and population division between Borneo and Sumatra. Front Zool 4:15. https://doi. org/10.1186/1742-9994-4-15
- Wong ST, Servheen C, Ambu L (2002) Food habits of Malayan sun bears in lowland tropical forests in Borneo. Ursus 13:127–136
- Wong ST, Servheen CW, Ambu L (2004) Home range, movement and activity patterns, and bedding sites of Malayan sun bears *Helarctos malayanus* in the rainforest of Borneo. Biol Conserv 119:169–181. https://doi.org/10.1016/j.biocon.2003.10.029

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

